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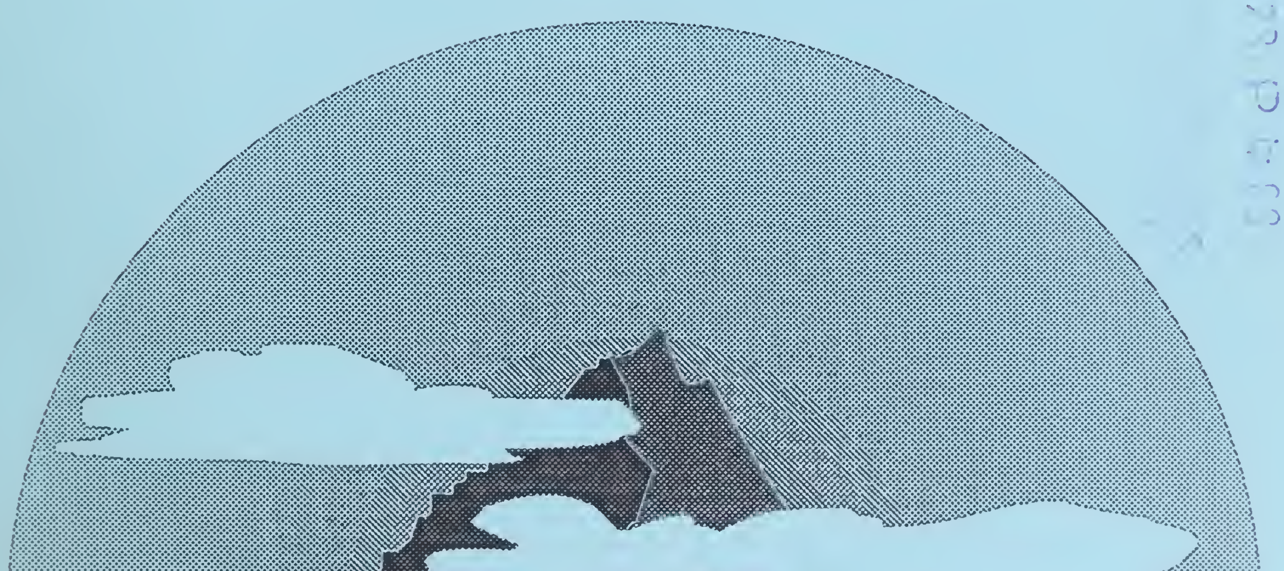
Report RM-GTR-264**

Biodiversity and Management of the Madrean Archipelago:

The Sky Islands of Southwestern United States and Northwestern Mexico

September 19-23, 1994
Tucson, Arizona



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Abstract

This conference brought together scientists and managers from government, universities, and private organizations to examine the biological diversity and management challenges of the unique "sky island" ecosystems of the mountains of the southwestern United States and northwestern Mexico. Session topics included: floristic resources, plant ecology, vertebrates, invertebrates, hydrology and riparian systems, aquatic resources, fire, conservation and management, human uses through time, and visions for the future.

Note: As part of the planning for this symposium, we decided to process and deliver these proceedings to the potential user as quickly as possible. Thus, the manuscripts did not receive conventional Forest Service editorial processing, and consequently, you may find some typographical errors. We feel quick publication of the proceedings is an essential part of the symposium concept and far outweighs these relatively minor distractions. The views expressed in each paper are those of the author and not necessarily those of the sponsoring organizations or the USDA Forest Service. Trade names are used for the information and convenience of the reader, and do not imply endorsement or preferential treatment by the sponsoring organizations or the USDA Forest Service.

USDA Forest Service
General Technical Report RM-GTR-264

July 1995

Biodiversity and Management of the Madrean Archipelago:

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CONTENTS

PLENARY SESSION

FLORISTIC RESOURCES

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[1] *Los numeros in parentesis indican la numerción de los resumenes en Español, comenzando en la pagina 643. Algunas de las traducciones se hiceiron a partir de las projectos originales, y podrian no reguir con precision las versiones originales en Inglés.*

PLANT ECOLOGY

VERTEBRATES

INVERTEBRATES

HYDROLOGY AND RIPARIAN SYSTEMS

AQUATIC RESOURCES

FIRE

CONSERVATION AND MANAGEMENT

HUMAN USES THROUGH TIME

VISIONS FOR THE FUTURE

POSTER PRESENTATIONS

RESUMENES EN ESPAÑOL

Welcoming Comments

Denver Burns[1]

On behalf of the Rocky Mountain Forest and Range Experiment Station, I bid you a warm welcome to this first conference on the Madrean Archipelago. The Rocky Mountain Station has a long and proud history of research in the Southwest beginning in the first decade of the 1900's. The Fort Valley Experimental Forest near Flagstaff and the Santa Rita Experimental Range here near Tucson were early examples of Forest Service Research activities in Arizona.

Over the years, name changes and organizational changes have occurred, but the research interest of the Forest Service has continued for over 85 years in broad areas of understanding the functioning of watersheds, range, and forests. Today we have researchers from many laboratories across the country active in Arizona.

Throughout the decades, Forest Service Research has worked with partners at major universities and colleges to combine and apply our resources and intellectual capability to the problems at hand. During our long tenure in Arizona, Forest Service scientists have been located on the campuses of the University of Arizona, Arizona State University, and Northern Arizona University. Today, in Flagstaff, we and Northern Arizona University share a building called The Southwest Forest Science Complex. We also have a few scientists at Arizona State and the University of Arizona.

A year and a half ago, I asked Len DeBano if he would be interested in moving to Tucson to apply his knowledge of resource issues in Arizona to three major issues. First, the Coronado National Forest had requested assistance in working with the many non-governmental researchers interested in the Sky Islands. Second, we wanted to reaffirm our partnership with the University of Arizona, and third, we needed to re-examine some of the early studies and data for application in ecosystem management.

Len took the challenge and has accomplished far more than even the high expectations of all who know him. Len has been a force to bring this conference to today's opening. He has also taken on the additional assignment of spearheading the Borderlands Ecosystem Management demonstration research project, a partnership of the Forest Service and many other organizations.

While Len would say many people contributed to this conference, and they did, Len was leader for the Rocky Mountain Station, and I want to acknowledge his work and add my thanks. Pete Ffolliott, University of Arizona, also played a major role.

Just as the Sky Islands are not constrained by the U.S./Mexican Border, neither is the long history of cooperation with the government and institutions in Mexico. Across-the-border cooperation is another way we share knowledge and expertise. Alfredo Ortega-Rubio, from the Centro de Investigaciones Biologicas del Noroeste, in La Paz, Baja California Sur, coordinated south-of-the-border contributions to this conference.

As I looked through the program, I was struck by the number of organizations represented on the program and by the comprehensiveness of the topics. This week will be a milepost in the search for knowledge and understanding about a special part of our world.

So, to all here, I again extend a warm welcome to you on behalf of the Rocky Mountain Station, and I wish you success and satisfaction with this meeting.

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[1] *Director, Rocky Mountain Forest and Range Experiment Station.*

The Sky Island Conference: Looking Back, Looking Ahead

Leonard F. DeBano[1] **and Peter F. Ffolliott**[2]

A general discussion at the conclusion of the conference considered the state-of-knowledge and possible future directions of research and management in the Madrean Archipelago. The participants entered into a dialogue on the success of the conference in meeting: 1) the goals of the conference, and 2) people's expectations. A summary of this dialogue and the comments prepared by the moderators of the concurrent sessions of the conference are presented here.

INTRODUCTION

The Madrean Archipelago represents an area of exceptional biodiversity and great biogeographical interest located in an incomparable geological setting. The region is thus of considerable interest to researchers, managers, and other stakeholders in the southwestern United States, northern Mexico, and throughout the world. Thousands of publications have resulted from the research efforts and management experiences in the region. Many studies are currently being conducted on floristic and aquatic resources, vertebrate and invertebrate biology, environmental ecology and conservation management, and historical perspectives of people's use of the natural resources on both sides of the border. The results of many of these studies are contained in these proceedings of the conference.

BACKGROUND OF CONFERENCE

This conference was planned to bring together researchers, managers, environmentalists, and other stakeholders interested in sharing information and ideas on the natural resources of the Madrean Archipelago. The conference was organized to satisfy one of the goals put forth in an earlier conference on the status of natural science research in the Chiricahua Mountains (Barton and Sloane 1992). Over 100 invited, contributed, and poster papers were presented at this Sky Island conference on topics ranging from hydrology and riparian systems to the biology of vertebrates and invertebrates to forest ecology and the effects of fire. The presenters of these papers came from both sides of the border between the United States and Mexico to share their knowledge.

A general discussion was held at the conclusion of the conference to consider the state-of-knowledge and possible future directions of research and management in the Madrean Archipelago.[3] The participants entered into a dialogue on the success of the conference in terms of the initial purpose of the conference and if it met people's expectations. A summary of this dialogue and the comments prepared by the moderators of the concurrent sessions of the conference is summarized in this paper. The authors have arranged the contents of the dialogue among the participants and the comments of the moderators to provide a degree of consistency in their presentation.

The discussion points and moderators' comments presented in this paper are not meant to be all-inclusive with respect to the total state-of-knowledge and directions that research and management should take in the Madrean Archipelago. Rather, they reflect only the discussion at the conclusion of the conference and the notes of the session moderators. No attempt was made to "prioritize" the discussion points or comments.

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[2] *Peter F. Ffolliott is Professor, School of Renewable Natural Resources, University of Arizona, Tucson, AZ.*

[3] *The discussion at the concluding session of conference was moderated by: Dr. Patrick Reid, School of Renewable Natural Resources, University of Arizona, Tucson, AZ.; Dr. Tony Burgess, The Desert Laboratory, University of Arizona, Tucson, AZ.; and Dr. Luis Bojorquez, Centro de Ecologia, UNAM, Mexico, D.F.*

STATE-OF-KNOWLEDGE AND GAPS TO BE FILLED

Many of the papers presented in the conference dealt with maintaining biodiversity, reviewing current state-of-knowledge information, and discussing the aspects of achieving management goals. In a large part, therefore, these proceedings of the conference represent a state-of-knowledge about the biodiversity and management of the ecosystems found in the Madrean Archipelago. However, the participants also pointed to important gaps in our knowledge that need to be filled. There was a general feeling that biodiversity is rapidly eroding and that actions must be taken quickly to reverse this trend.

It was felt that the effects of land management interventions in the ecosystems of the Madrean Archipelago are only partially understood in terms of biodiversity response. Questions to be answered include - "How does the biodiversity of the grassland ecosystems respond to grazing by livestock?" "What effects do fuelwood harvesting and fire have on biodiversity in the forest and woodland ecosystems?" "How does the increasing recreational use of the lands on both sides of the border alter biodiversity?" There is a need for regional coordination in attempting to answer these questions.

There is also a need to identify the biological connections between mountain ranges in the Madrean Archipelago, and to maintain the genetic flow between ranges. Corridors between the mountain ranges need to be managed to prevent artificial insularization. However, knowledge of ecological processes and their relationships to ecosystem dynamics is prerequisite to the planning of effective management. Coordinated and interdisciplinary research efforts are required to understand these relationships.

More specific gaps in knowledge were also mentioned by the participants, or contained in the moderators' comments. Knowledge of vertebrate and invertebrate community structures is incomplete. Attempts to alleviate this situation are noteworthy in many instances, but basic research should be intensified because of the high diversity of populations in the Madrean Archipelago. Species listings are incomplete in the United States and there is relatively little information from Mexico. It is difficult to effectively manage for the maintenance of biodiversity without this information.

There is a general lack of knowledge of the floristic resources in the Mexican portion of the Madrean Archipelago region. Furthermore, the dynamics of species compositions are poorly known on both sides of the border. Information on extinctions and colonization is also incomplete. Maintaining biodiversity requires a "balancing act" between the rates of local extinction and colonization. The impacts of introduced exotic species, livestock grazing, catastrophic fires, soil erosion, and extirpations of montane species on native floristics are largely unknown.

Information on the biology of fish species and the management practices necessary to maintain biodiversity of many fish populations is available for many situations. However, the state-of-knowledge on other aquatic resources is largely insufficient. For example, the following questions should be addressed - "What is the rate of dispersion of frogs across specified landscapes?" "How are the aquatic habitats of macro invertebrates affected by changing water levels?" "What are the effects of fire and its management on aquatic ecosystems and biota?" More baseline surveys of aquatic ecosystems are also required. It likely will become necessary to reduce the human-induced factors influencing the fragmentation of habitats.

Fire research in general needs attention. Information on the structure of vegetative communities and the composition of vertebrate and invertebrate populations in response to fire frequency is insufficient. The long-term consequences of large wildfires (as occurred throughout the region in the summer of 1994) on natural and cultural resources are largely unknown. The roles of prescribed burning in achieving fuel reductions and altering habitats need further study. The effects of fire on the natural resources of the Madrean Archipelago is the central theme of a conference to be held at the Universidad de Sonora in Hermosillo, Sonora, in the Spring of 1996. Initial planning for this conference has been initiated.

Research in watershed hydrology and the functioning of riparian systems has focused largely on the issues of water supply and on erosion processes and control. However, there is also a need to consider the hydrologic requirements of many native plant species. The relationships of watershed condition to the health of riparian and wetland systems is an important issue on both sides of the border. The response of vegetative communities to a deterioration of riparian health is also unknown.

It was noted by the conference participants that the indigenous people in the Madrean Archipelago, and particularly in Mexico, have knowledge of natural resources and their use that should be included in the knowledge base for this region. Much of this knowledge is exchanged orally among people in many instances and, therefore, should be recorded to enhance the interpretations of research findings.

The knowledge gaps to be filled in Mexico are difficult to assess in many respects. Mexican researchers desire to publish their findings in "prestigious" journals, as do scientists everywhere, and publication in English is generally favored over articles in Spanish. Basic researchers do not always communicate with applied researchers, and there is little emphasis on extension activity or "technology transfer" of Mexican research results. As a consequence, natural resource managers in Mexico frequently do not have ready access to the information necessary to "manage better," resulting in limited applications of new technologies. Therefore, while there often appear to be gaps in knowledge, it may be that the information to fill these gaps is simply not available to the managerial clientele in Mexico. The implementation of US technology, however, must be tested in Mexico within an environment reflecting their own economic and social goals.

The participants generally agreed that this conference provided a valuable forum for the exchange of ideas among the diverse interest groups in attendance. However, the participants also stressed the point that it is critical for people to leave the conference with a commitment to continuing the dialogue initiated among researchers, managers, and other stakeholders on both sides of the border. In achieving this end, the continuing development of "databases" for the use of researchers and managers in the United States and Mexico is a high priority. The development of efficient avenues for exchanging information across the border is also necessary. A challenge to the stakeholders in the Madrean Archipelago is to become actively involved in the early "planning stages" of proposed research programs and management interventions.

It was suggested that institutions such as the Rocky Mountain Forest and Range Experiment Station, the School of Renewable Natural Resources at the University of Arizona, the Research Station of the American Museum of Natural History, and their counterparts in northern Mexico (such as the Centro Ecologia de Sonora and the Centro de Investigaciones Biologicas) could serve as facilitators for future conferences on topics of interest to the stakeholders in the Madrean Archipelago. A consortium of these institutions could also function as a depository and "central clearing house" for the transfer of information generated by these conferences and that resulting from research and management in the region.

MAJOR ISSUES CONFRONTING RESEARCHERS AND MANAGERS

The major issues confronting researchers and managers of the Madrean Archipelago are many, as pointed out by the conference participants. Some of these issues are unique to either the United States or Mexico, while many issues are common to the borderlands in general and, therefore, should be addressed jointly by researchers and managers in both countries.

The participants felt that a scientific basis for ecosystem management in the Madrean Archipelago has not yet been adequately established. There was a consensus that a fundamental difference exists between past and present management of ecosystems. In the past, ecosystems were largely managed to extract commodities, contrasted to ecosystem management today which emphasizes system integrity, and with the understanding that management practices must fit into the ecosystem without destroying its integrity. As a consequence, systems management of the ecosystem, rather than functional management of natural resources, should be encouraged.

It was concluded that biodiversity goals are key to land and natural resource stewardship on both sides of the border, and should be integrated into management strategies whenever possible. An approach to attaining this goal likely involves an "administrative structure" that goes beyond agencies' responsibilities. Institutional barriers need to be eliminated and international cooperation must be encouraged. The problems of scattered and generally uncoordinated leadership must be resolved.

Among the major issues of concern are those related to the maintenance of ecosystem viability. People on both sides of the border will still require use of natural resources for various purposes, but these uses should occur within the framework of this viability. Importantly, people must be recognized as being an integral part of the ecosystems, rather than being outside of the systems looking in, and their needs must be addressed in maintaining ecosystem viability.

In considering the multiple use of natural resources, the conference participants felt that multiple use should equate to multiple values. It will be necessary, therefore, to express the goals of multiple use in terms of both market and nonmarket values. Options for multiple use management in the future must consider nonmarket values in addition to commodity values to be all-inclusive.

From the Mexican perspective, there is a lack of financial support for ecological research. Baseline data sets are needed for most of the Madrean Archipelago region in Mexico. There appears to be a general lack of coordination among internal institutions and stakeholders, and this is further complicated with interventions of international donors. The people of Mexico need to review the roles of outside interest-groups on internal decision making.

It is generally recognized that the cultural history of Mexico is different from that in the United States with respect to value systems and, to some extent, the perceptions that people place on the values of natural resources. It is not surprising, therefore, that a program of research and management must work in Mexico within the framework of a different value system than a program in the United States. Issues are not only biological; cultural values also need to be considered in formulating research and management efforts. Environmental education at all levels should be stressed.

To many of the participants, there currently is too much emphasis on transferring technology from the United States to Mexico without working out the technologies for applications in Mexico, resulting in technology being "transferred" without an appreciation of the biophysical and socioeconomic environment in Mexico. It is important that this situation be rectified whenever possible.

It is also necessary that the flow of knowledge from Mexico to the United States be enhanced. In many situations, it is likely that the collective experiences of the scientific communities in Mexico can contribute to filling perceived knowledge gaps in the United States. However, the researchers and managers in the United States must become aware of the Mexican experiences for this to happen.

GOALS FOR RESEARCH AND MANAGEMENT

It is imperative that the goals for research and management in the Madrean Archipelago be tied to goals that are supported generally by the institutions and stakeholders involved. While it is impossible to consider all of the possible goals for specific research and management in this paper, the participants in the conference identified many central goals that, in their collective opinion, warrant serious consideration. For example, it is important to think in terms of goals that "favor" maintaining or, if possible, enhancing biodiversity. It was suggested that these goals entail preserving a "wilderness aspect" in the mix of research and management priorities. These goals can be realized only through scientific knowledge. It will be necessary, therefore, to pursue the attainment of scientific knowledge on how the biological and non-biological dimensions of ecosystems function. A balance between planned, problem-oriented, coordinated research and the necessary freedom, spontaneity, and creativity in scientists' choice of research problems is prerequisite to obtaining this knowledge. The intensity of these human pressures (e.g. urbanization of natural ecosystems) will continue to jeopardize these goals.

Researchers and managers should expand upon the mechanisms for the transfer of resource information to all stakeholders in the region. In this regard, it is becoming increasingly important to maintain a dialogue with all stakeholders in the Madrean Archipelago in relation to the status of research and management efforts, the status of inventory and monitoring, and the prevailing policies on natural resource uses. Impediments to attaining these goals, including a lack of funding and the lack of interagency and intersectoral cooperation, must be minimized.

There is a need to work with responsible agencies and interested stakeholders in establishing funding priorities in relation to ecosystem management. There is also a need to identify the more important "actors" involved in ecosystem management who understand the framework of decision making and priorities with respect to funding. If not handled in a systematic manner, however, the establishment of funding opportunities can end up in uncoordinated and largely piecemeal efforts.

It was generally agreed that sustainability and viability are the heart of ecosystem management. One key ingredient to responsive ecosystem management is maintaining biodiversity, including genetic diversity, of native plants. Policies on the use of plants for revegetation and rehabilitation purposes are also needed to ensure ecosystem integrity. The strengthening of genetic partnerships among federal and state agencies, universities, and private organizations is encouraged.

There is a need for research and management that recognizes the biological integrity of the borderlands but is still able to accommodate the differences between Mexico and the United States. Part of this effort could be the establishment of a regional information center, which would serve as a central depository for relevant information from both countries. This information center might translate the literature into both languages and use a common terminology to facilitate the use of this literature.

Finally, the commonly encountered fragmentation of agendas among institutions and between institutions and stakeholders should be eliminated whenever possible in establishing goals for research and management. Building a consensus on the central goals and priorities of research and management will be necessary to meet the challenges confronted by researchers and managers in the Madrean Archipelago.

A CONCLUDING COMMENT

A frequent debate that we have all heard is whether a big conference such as this is useful and effective in comparison to a smaller symposium that addresses specific topics. We believe that this conference, while "big" to some people, can play an important role in planning for the future of the Madrean Archipelago that could not be adequately filled by smaller symposia on more specific, often limited subjects. The conference participants highlighted many of the recent, continuing, and planned efforts of the research and management communities in the region. In achieving this purpose, however, it will be necessary to increase the level of communication among people of diverse interests and concerns.

We also believe that a potential has been established for the researchers, managers, and other stakeholders in the Madrean Archipelago to cooperate in a setting of mutual interests, principles, and knowledge. For this to happen requires a recognition of the ecological characteristics of the natural resource base, the level of ecological knowledge held by all stakeholders, the social and economic objectives involved, the heterogeneity of the stakeholders and organizational structures in the region, and the cultures of the people involved. These topics were considered in the papers presented in the conference and by the participants in the closing session; hopefully, they will be the focus of research and management in the future.

LITERATURE CITED

Barton, A. M.; Sloane, S. A., eds. 1992. Chiricahua Mountains research symposium: Proceedings. Southwest Parks and Monuments Association, Tucson, Arizona, 126p.

The Madrean Sky Island Archipelago: A Planetary Overview

Peter Warshall[1]

Abstract.—Previous work on biogeographic isolation has concerned itself with oceanic island chains, islands associated with continents, fringing archipelagos, and bodies of water such as the African lake system which serve as "aquatic islands". This paper reviews the "continental islands" and compares them to the Madrean sky island archipelago. The geological, hydrological, and climatic context for the Afroalpine, Guyana, Paramo, low and high desert of the Great Basin, etc. archipelagos are compared for source areas, number of islands, isolating mechanisms, interactive ecosystems, and evolutionary history. The history of scientific exploration and fieldwork for the Madrean Archipelago and its unique status among the planet's archipelagos are summarized.

In 1957, Joe Marshall published "Birds of the Pine-Oak Woodland in Southern Arizona and Adjacent Mexico." Never surpassed, this elegant monograph described the stacking of biotic communities on each island mountain from the Mogollon Rim to the Sierra Madre. He defined the Madrean archipelago as those island mountains with a pine-oak woodland. In 1967, Weldon Heald (1993), from his home in the Chiricahuas, coined the addictive phrase—"sky islands" for these insular mountains of the North American borderlands. Weldon Heald's catch phrase immortalized Joe Marshall's meticulous observations. Today's conference is the first solely dedicated to understanding Madrean sky island biology, beauty, and needs for management and conservation.

There are about 40 sky islands (fig. 1) between the Mogollon Rim and the Sierra Madre Occidental (Warshall, in press). Mt. Graham on the Pinaleno mountains is the tallest peak (10,712 feet). Relief between valleys and peaks ranges from 1250 to 6750 feet (McLaughlin, 1992), but is typically between 3000 and 5000 feet. The Madrean region has exceptional species richness, super-species complexes, unusual neoendemics and archeoendemics, an exceptional mixture of species from the Nearctic and Neotropic regions, important influences from the eastern (North American Prairies Province of Takhtajan, 1986) and western biogeographic provinces, a wealth of genetically unique cultivars in the Sierra Madre Occidental, and a myriad of mysteries concerning the distribution of disjuncts, species "holes," and species "outliers" on individual mountains (e.g., Ramamoorthy, 1993). The northernmost sky islands are the only place in North America where you can climb from the desert to northern Canada in a matter of hours (Warshall, 1986). The sky islands pose numerous puzzles about vertical migration strategies used by plants and animals both annually and over glacial time periods.

These interests in ecology and evolution mix with the other citizen interests in skiing, grazing, hunting, fishing, escaping the heat, summer homes, telescopes and radio towers, bird watching, rock-climbing, military practice maneuvers, fuelwood cutting, camping, mining, sacred Native American values and ceremonies, archaeological sites, as well as preservation of sky island habitat for threatened and endangered species. Underpinning all these interests is the exceptional beauty of the sky islands—their layering of peaks in a dusty sunset, lines of vibrant riparian along arid yellow slopes, the contrast of snow and desert, the baffling complexity of erratic ridge lines, the power of fires, and the subtle tones of blue-gray limestone, speckled granite, and pastel volcanics.

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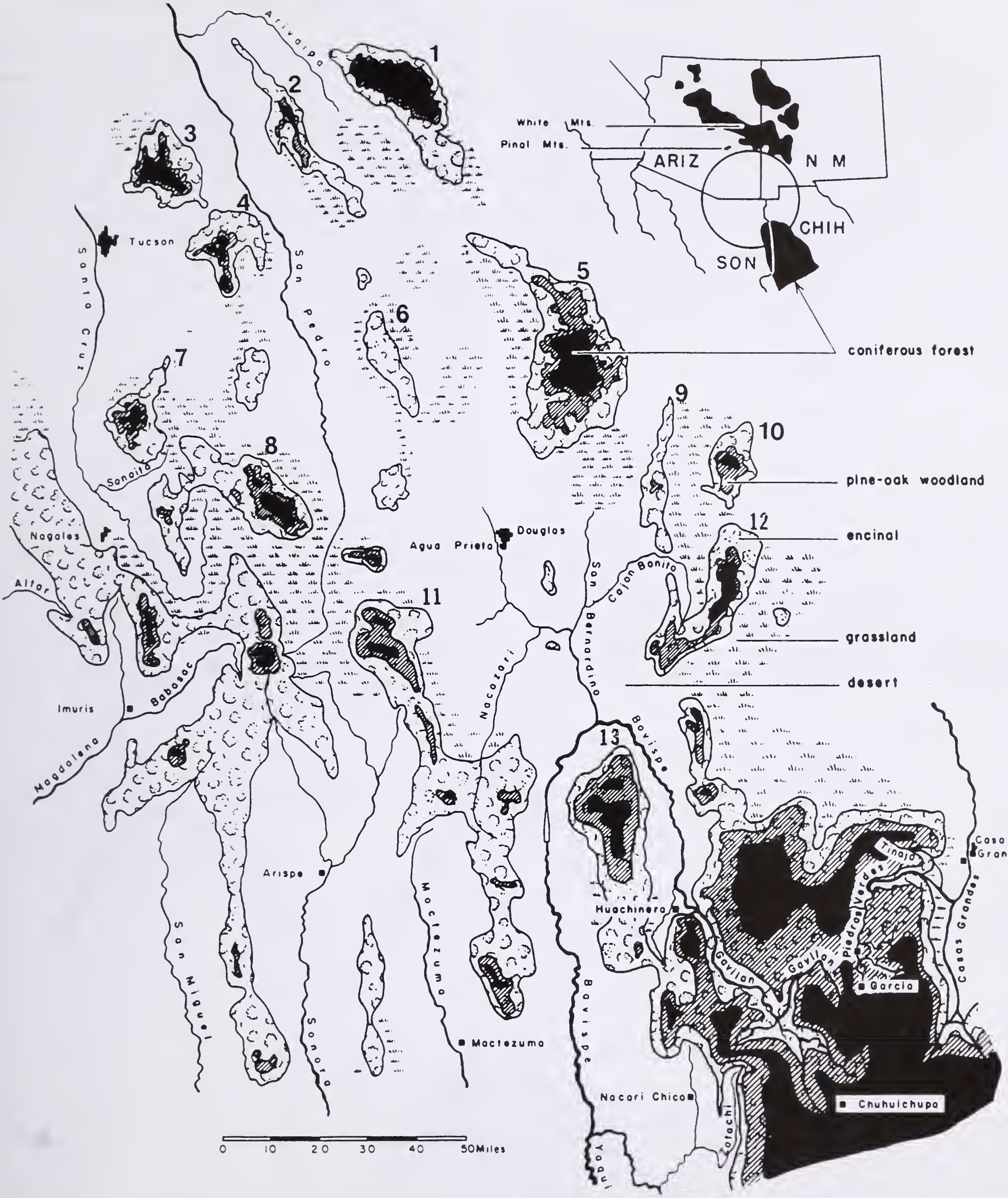

Figure 1.—The Madrean Sky Island archipelago (based on Marshall, 1957).

WHAT ARE SKY ISLANDS?

Sky islands are a type of continental or inland terrain made up of a sequence of valleys and mountains. All sky islands have a stack of biotic communities that allow vertical (as well as aspect) migration annually or during one of the planet's long-term climatic events. The valleys act as barriers or bridges to the colonization by new species that attempt to cross the intervening valley. The valleys become barriers when they contain an ecology alien to the migrating species. By analogy with the saltwater seas between oceanic islands, the higher elevation biotic communities of sky island mountains are isolated by each valley's "sea" of alien vegetation. The mountains, like the Galapagos or other oceanic islands, act as isolated cradles of evolution.

In the Madrean archipelago, the valleys and mountains are roughly parallel. The stacked biotic communities (fig. 2) include: montane coniferous forests; oak-pine (coniferous) woodlands; tropical deciduous forest; oak savanna (deciduous vs. evergreen oaks predominate); short-grass prairie; subtropical thornscrub; and subtropical desert (Brown, 1982). The "heart" of the Madrean archipelago (its defining characteristic) is the oak-pine woodlands (Marshall, 1957). The barrier "seas" include the short-grass prairie, the subtropical thornscrub, and subtropical desert.

SKY ISLANDS OF THE PLANET

There are about twenty sky island complexes on the planet (table 1 and fig. 3). All the continents with, perhaps, the exception of Australia, harbor sky island complexes. The information on the sky island complexes of Eurasia, China, and southeast Asia remains incomplete because of the difficulty of obtaining English translations (Suslov, 1961; Aiken, 1992). Most of the literature has focused on the mountains themselves, not the importance of the valleys between them. There has been remarkably lithe work comparing the planet's continental island ecosystems (Carlquist, 1963), their palaeogeographic history, floristic and faunal source areas, and valley barriers.

By creating a parallel typology with recent classifications of oceanic islands such as isolated island "chains" (Hawaii), "continent associates" (Madagascar, Philippines), and "fringing archipelagos" (the southern Japanese or Sea of Cortez island groups), we can approximate a classification for the continental islands. Table 1 classifies continental island clusters on the basis of their geographic axis, latitude, whether they are coastal or inland, the number per complex, and the configuration of each grouping. Configurations include: stepping stone archipelagos (mountains and valleys spaced between two cordilleras), isolated massif(s) with outlier sky islands, linear

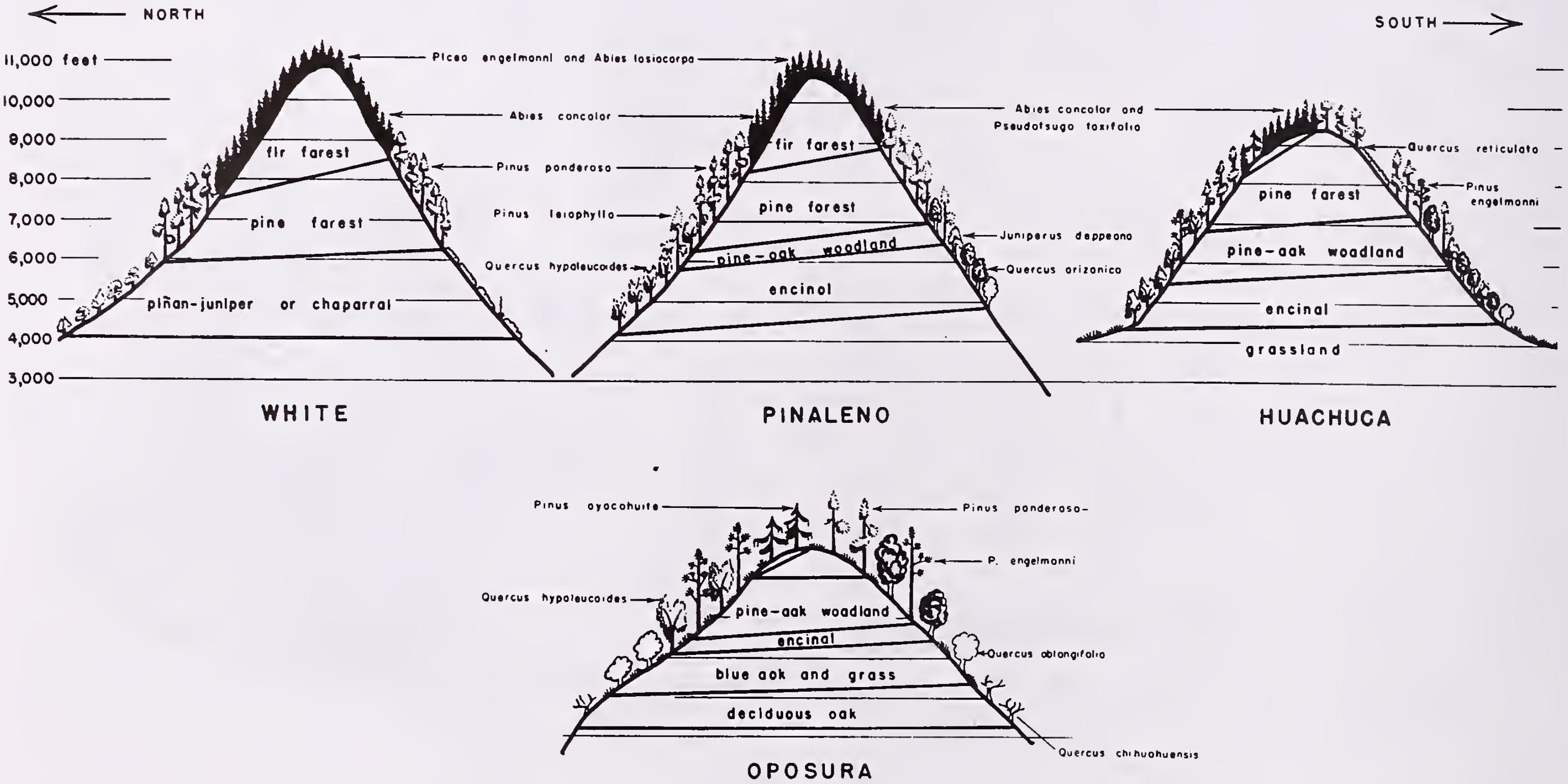

Figure 2.—Example "stacking" of biotic communities of the Madrean archipelago (Marshall, 1957). Note the position of the oak-pine woodlands.

chains of outlier mountains/valleys at one end of a cordillera, and completely isolated groups of mountains. A surprisingly large number of complexes (e.g., the Adamoua, Baja Peninsula, and East African arc) contain both oceanic islands and sky islands with both saltwater and vegetative "seas." Like all typologies, there are ambiguously categorized groupings.

Planetary Examples

The four descriptive variables used to classify sky islands act in concert. Compare the Madrean stepping stone configuration with the isolated archipelago of the Western Ghats of India (not illustrated), the isolated cluster of the Pantepuis of Brazil, Guyana, and Venezuela (fig. 5) and the East African arc and the Ethiopian massif complexes (fig. 6) . The Western Ghats (Manickam, 1992) comprise a north-south cluster of tropical mountains spanning about six degrees of latitude.

Table 1.—Sky Island Types

Type	Examples
Stepping stone archipelago between two mountain chains	Madrean archipelago Great Basin archipelago Altai/Tien Shan Basin Meso-American massifs
Isolated massif with outliers	Ethiopian highlands East African arc Saharan massifs Atlas Mountains Jabal Lubnan Adoumoua Mountains Drakenbergs Central European massifs Caucaso-Iranian massifs
Cordillera with outliers	Chaine Annimatique (Vietnam) Malay peninsula Baja California peninsula Coastal Cordillera (SA) Southern Andes
Isolated sky island chains	Western Ghats Pantepuis
High altitude sky islands	Punas and paramos (SA) Himalayas

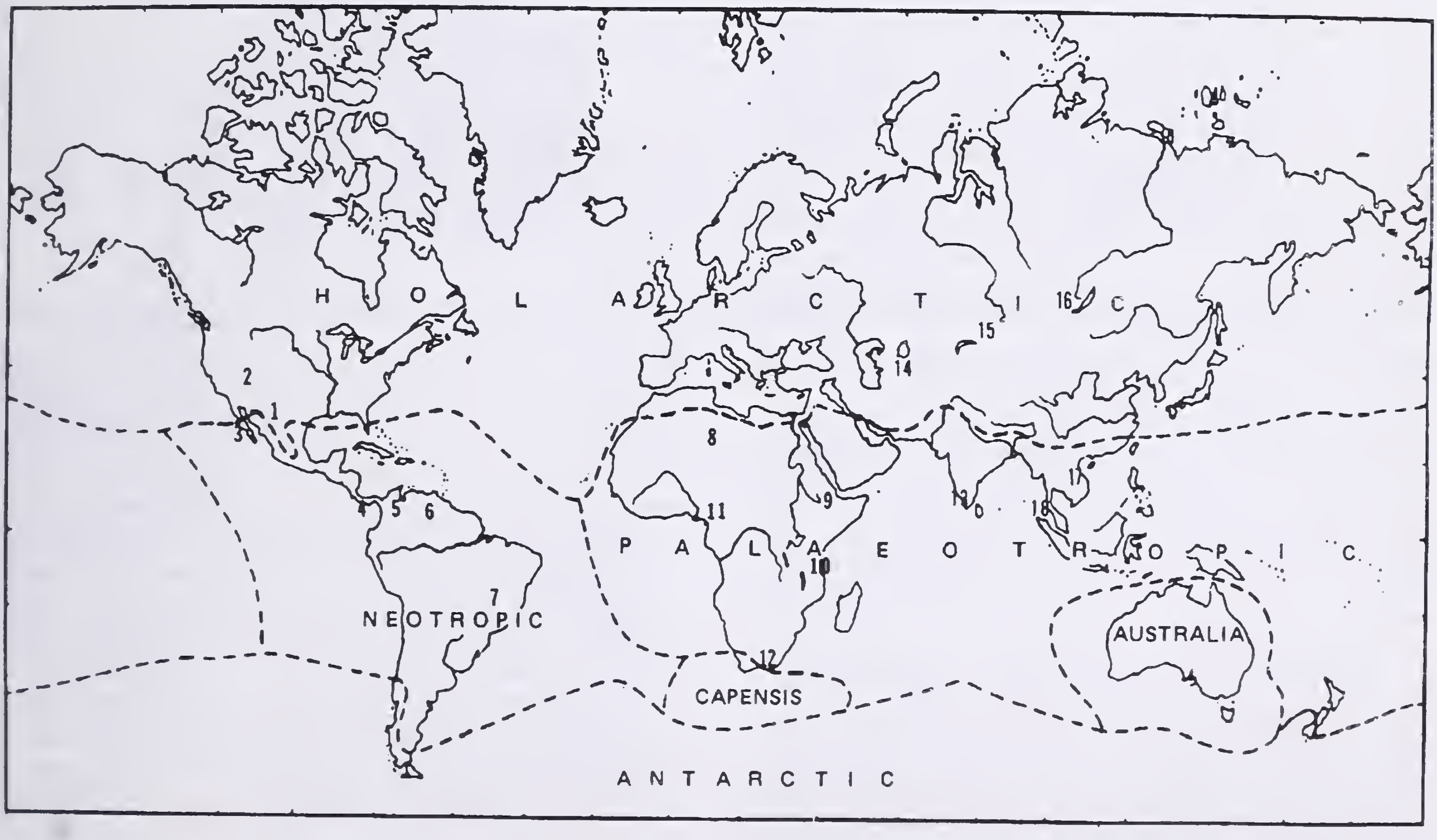

Figure 3.—Locations of sky island complexes mentioned in text on a map of the Floristic Realms of the planet. Only the Madrean archipelago straddles two; Floristic Realms. (1) Madrean; (2) Great Basin; (3) Baja California (4) Meso American; (5) Coastal Cordillera; (6) Pantepuis; (7) Brazilian shield; (8) Saharan massifs; (9) Ethiopian Highlands; (10) East African arc; (11) Cameroon Bight; (12) Southern African complex; (13) Western Ghats; (14) Caucaso Iranian massifs; (15) Altai/Tien Shan; (16) Trans-Baikal; (17) ChaineAnnimatique; (18) Malay peninsula. High valley "islands" can be found in the northern Andes and Himalayas.

They are isolated from the nearest cordillera, the Himalayas, by over 1,200 miles. The Western Ghats are further isolated to the south and west by the Laccadive Sea. On the north and east, the valley barriers are, at the present, highly humanized landscapes with pockets of Deccan thornforests. The Western Ghats contain about five distinct mountain with one major valley (the Palghat gap) subdividing the archipelago. Sometimes, Sri Lanka has been included as an oceanic island within the sky island archipelago. In part, the high endemism of the montane Malabar rainforests which cover the Western Ghats can be traced to its former Gondwanaland connection.

The Pantepuis (Minestero, 1985; Fittkau, 1969; Steyermark, 1982; deGranville, 1982; Haffer, 1987) form a scattered, isolated tropical series of 15 large and 20 smaller sky islands. The Pantepuis cluster shows no distinct axial direction and relief is relatively small (about 2000 feet). In this part of South America, a "tepui" means a "sky island." The major "barriers" isolating the individual tepuis are rivers, many with "blackwater" (acid) waters. The southern boundary, the gigantic Amazon Basin, separates it from the sky island complex of the Brazilian shield, over 1500 miles away. Both the Pantepuis and the shield once were parts of the same plateau and contain numerous parallel taxa. On the west, the Orinoco River and, to the east, the Essequibo River act as major barriers. Only to the northeast do a few tepuis approach the outlier mountains of the coastal cordillera, including the offshore islands along the Caribbean coast. The inter-mountain valley "seas" include savanna, caatinga, and chaparral as well as the "blackwater" rivers.

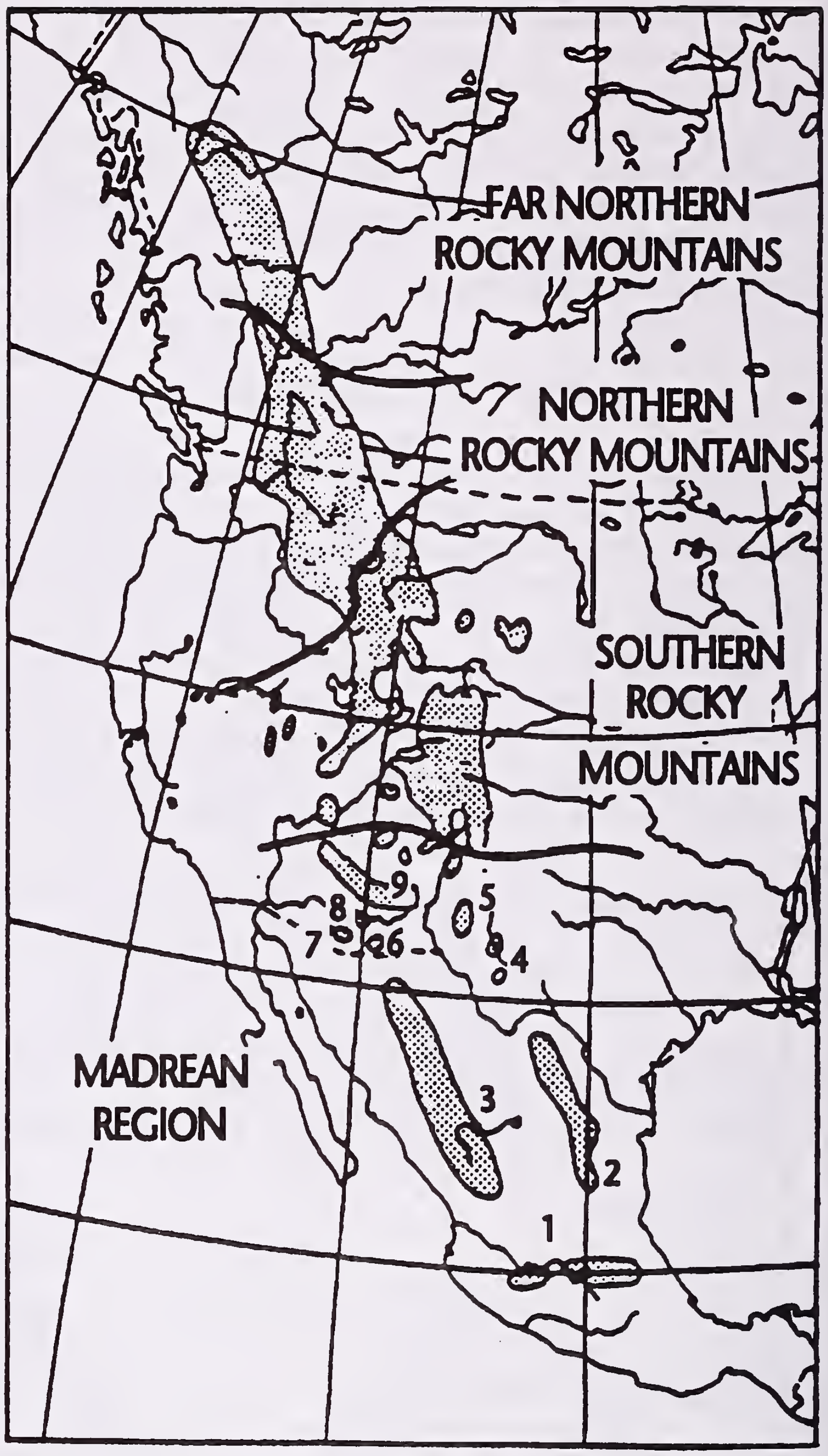

Figure 4.—Location of the archipelago as a stepping stone between the Rocky Mountain cordillera to the north and the Sierra Madre to the south (modified from Peet, 1988). Approximate boundaries of the four major floristic provinces indicated by solid lines. Major Sierra Madre mountains include: (1) Trans-Mexican volcanic belt; (2) Sierra Madre Oriental, and (3) the Sierra Madre Occidental which is the nearest Mexican source area for the Madrean archipelago.

The Madrean sky islands shown include (6) Chiricahua mountains, (7) Santa Catalina Mountains, and the (8) Pinalenos Mountains. The Mogollon Mesa (9) is the nearest Rocky Mountain source area for the Madrean archipelago.

The Sierra Madre Oriental sky island complex includes (4) the Davis Mountains and (5) Sierra Blanca.

Both the Ethiopian complex and the Zanj or East African arc complex (Kingdon, 1990) gained their relief from the great East African rift valley (see below). The Ethiopian complex centers on the high elevation basaltic plateau that rifted into two massifs (the Simien and Bali mountains). The Ethiopian complex is isolated by the White Nile to the west; the Kenyan, Somalian and Saudi deserts as well as the Red and Arabian Seas. It has a strong north-south axis covering seventeen degrees of latitude with fifteen to twenty peaks greater than 9,000 feet in elevation. The relief is typically 5000 feet. The valley barriers include harsh desert, acacia/commiphora bushland, and dry savanna. The isolated biotic communities include the higher elevation juniper / podocarpus, montane bamboo, ericaceous tree / shrub and afro-alpine belts. In its largest dimensions, the Ethiopian sky island complex includes the Asir/Hadramawt sky island complex of Yemen and Saudi Arabia.

The East African arc massifs, sky islands and three oceanic islands (Pemba, Mafia, and Zanzibar) create a rough geographic circle involv-

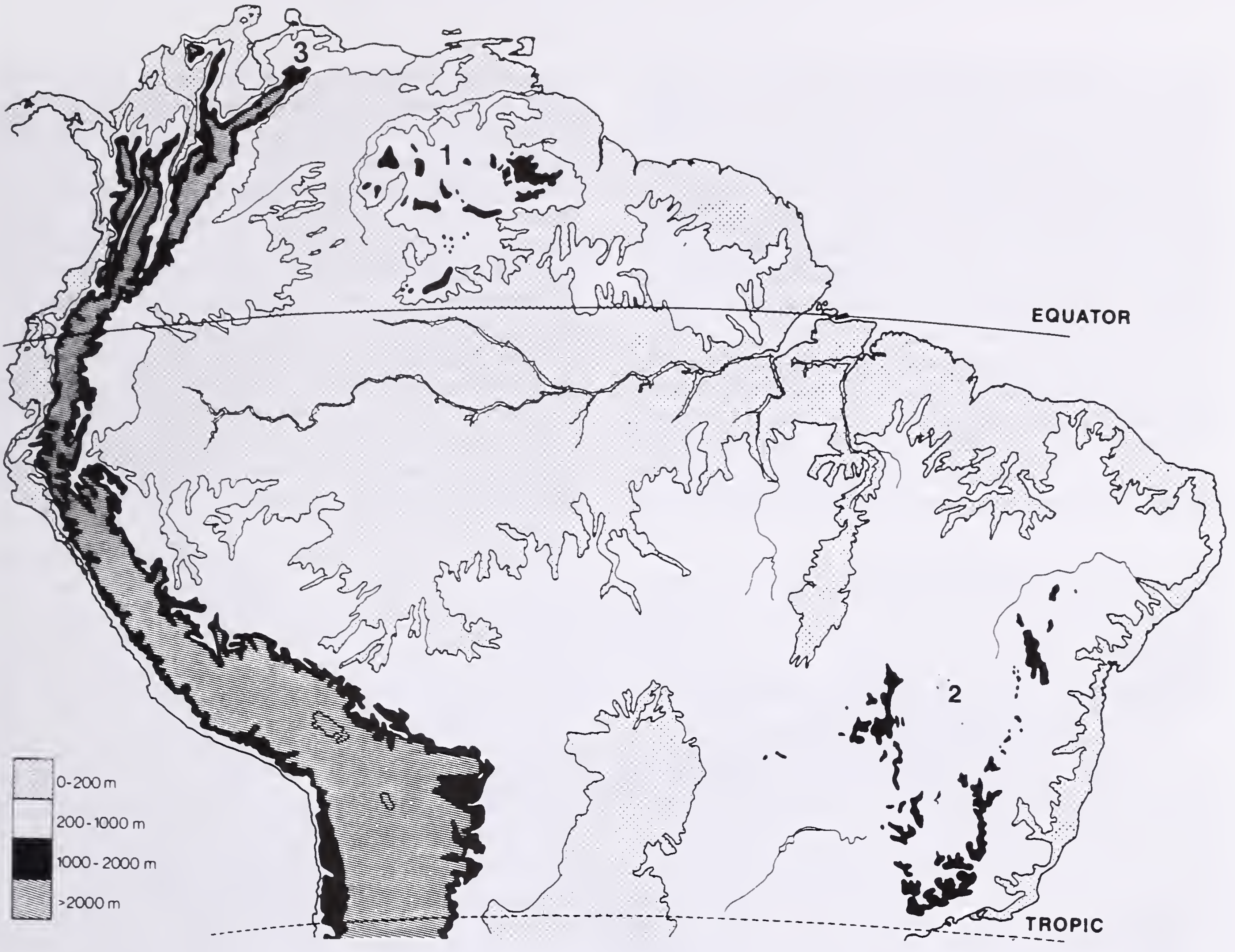

Figure 5.—Three South American sky island complexes are shown: (1) The pantepuis; (2) the Brazilian shield; and (3) the Coastal Cordillera.

ing seven African nations and twelve degrees of equatorial latitude (fig. 6). The circle comprises older massifs such as the Ruwenzori (Monts Mitumbe), Kipengere, and Udzungwa ranges; the Nyika and Rukiga plateaus, and the Mau escarpment combined with many more recent isolated mountains including the Usambara, Uluguru, Mt. Kilimanjaro, Mt. Meru, and Mt. Elgon. Relief exceeds 9,000 feet for the seven highest isolated volcanos. Rift valley lakes (e.g., Lake Victoria and Lake Tanganyika) and, of course, the Congo River Basin and Indian Ocean act as important barriers to gene flow. The valley barrier is predominantly savanna. The montane communities parallel those of the Ethiopian massif.

Finally, the north Andes and Himalayas contain a contrasting variant - high altitude island *valleys*.. These cordilleras have "sky island" valleys or plateaus embedded within the mountain ranges. The valleys contain exceptional pockets of endemism. For instance, the South American paramos (the alpine belt) have acted as "population traps" during repeated glacial events (Prance, 1987; Kant, 1989; Haffer, 1987). These high elevation, sky island valleys form a special group of continental islands similar to isolated lakes (e.g., Baikal, Malawi) and caves.

The Madrean Archipelago: Comparisons

The Madrean archipelago is a "stepping stone archipelago" between two mountain chains (the Rocky Mountains and its plateaus and the Sierra Madre plateau and its mountains) arranged in a roughly north-south axis (figs. 1 and 4). Archipelagos between two cordilleras may have greater opportunities to increase biological diversity because the configuration provides two source areas instead of one. In general, north-south axes (e.g., the Madrean archipelago, Baja Peninsula, Western Ghats, Malay Peninsula) also provide for a greater amount of climatic variation than east-west axes (e.g., the Himalayas, Eurasian ranges, Coastal Cordillera of South America) and, perhaps, greater potential for evolutionary differentiation. Compare the Madrean archipelago to the Great Basin. The Great Basin is a sky island cluster two cordilleras but its axis, between two major source areas, is predominantly east to west.

The Madrean archipelago is a mid-latitude sky island complex, along with the Saharan massifs, the South African complex, the Atlas Mountains (Morocco), the Great Basin, the Baja California peninsula, and perhaps a range in China. (Other possible mid-latitude sky islands complexes" the Caucaso-Iranian, Central European Highlands, Jabal Lubnan—appear to be so altered by human influences that it is difficult to determine what biological information remains.) These mid-latitude complexes experience greater annual and decadal climatic flux. The Madrean is unique, even among mid-latitude sky island complexes, because temperate and subtropical climatic regions interfinger with tropical climates found in the Caribbean.

The tropical sky island complexes include the Meso-American massifs; Ethiopian and Adamoua and East African highlands in Africa; the Coastal Cordillera, the Pantepuis and Brazilian Shield clusters of South America; and the Western Ghats, the Malay Peninsula and Chaine Annimatique of

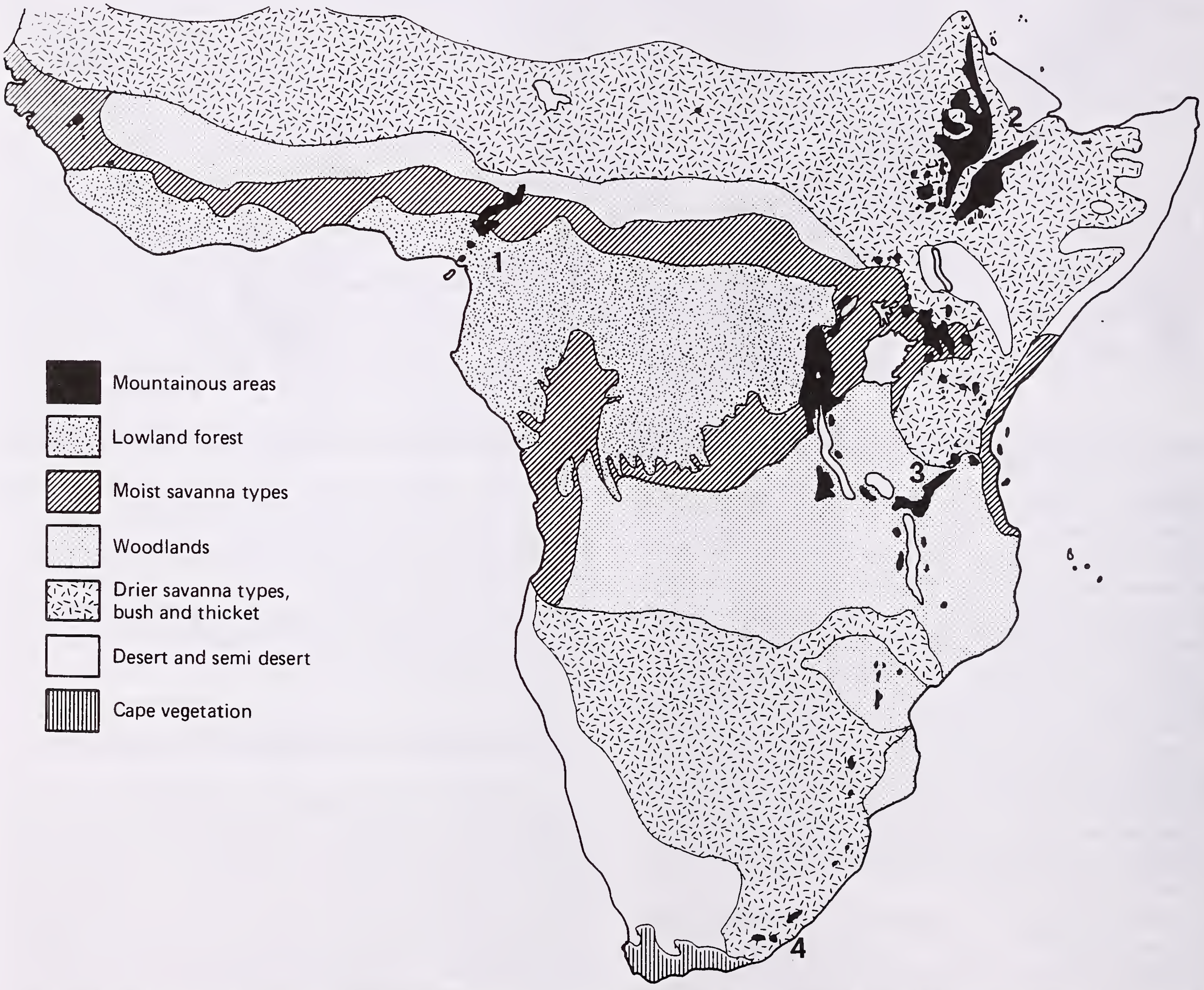

Figure 6.—Four African sky island complexes are shown: (1) The Adoumoua chain in Cameroons; (2) the Ethiopian Highland complex; (3) the East African arc complex or Zanj; and (4) the South African complex.

South Asia. In recent geological time, the fluctuation of pluvials or inter-pluvials has had a major influence on whether the valley vegetation was a bridge or a barrier. The Ethiopian region is the only tropical sky island complex that harbored significant glaciation.

Distinctly northern complexes, higher than 40 degrees latitude, include the Altai/Tien Shan and Dzungarian basin ranges; the heavily altered Pyrennes and Scottish Highlands and a fewer other CIS ranges. These areas lost their biota during the glacial periods and have only recently (about 10 to 15,000 years ago) been recolonized.

Along with the Pantepuis, the Brazilian shield, the Great Basin, and most of the Eurasian ranges, the Madrean archipelago is distinctly inland. The Madrean has a special feature—the lowest pass or mountain gap in the Rocky Mountain cordillera between northern Canada and the Isthmus of Tehuantepec. The low elevation pass encouraged east-west movement of animals and plants from valley to valley. Otherwise, the Chihuahuan and Mohave deserts (the desert "seas") and the Gila River geographically isolate the Madrean archipelago. As previously mentioned, the inland configurations are the true sky island complexes. Many of the others are bordered on one side by an ocean or large lakes. Some are surrounded on two sides by ocean. Peninsula sky island complexes have very limited opportunities for colonization because two or three sides are ocean compared to distinctly inland clusters.

The Madrean Archipelago contains a large number of sky islands per complex (N = 40). Only the Great Basin (N = 25 to 50 depending on definition), the East African arc (N = two massifs, about 30 sky islands, and three oceanic islands), and Pantepuis (N = 15 large and about 20 smaller sky islands) have comparable numbers of isolated mountains. Depending on how boundaries are drawn, the Ethiopian complex has two major massifs and about 12 smaller sky islands without the addition of the Horn of Africa mountains and those of Saudi Arabia and Yemen. All other groupings are less than 15 isolated mountains with the majority containing only about five.

In summary, North America's Great Basin and Madrean archipelagos appear unique on the planet for the number of mountains and the stepping stone arrangement between roughly parallel valleys and mountains. Only the Madrean archipelago has the distinct north-south connection to two major cordilleras and crosses from temperate to subtropical latitudes. This topography, relief, and location explain a large part of the biological richness and diversity of the Madrean archipelago.

Table 2.—Geology and the Sky Islands

Type	Examples
Relictual or Subsequent	Most Tepuis (Venezuela)Western Ghats (India)Brazilian shield
Tectonic or Original	East African arc volcanoes
A. Accumulation mountains (flood basalts, volcanics)	Mt. Camoroun
B. Deformation mountains	Himalayas
B1. Fold mountains	Andes (altiplano)
B2. Dislocation mountains (horst/graben)	Great Basin Madrean Archipelago African Rift Valley mountains Altai Trans-Baikal
B3. Laccolith mountains	

HOW WERE THE SKY ISLAND COMPLEXES CONSTRUCTED?

The geologic history of each sky island complex provides the stage for its evolutionary and ecological history. The four most important characters are: the nature of the bedrock, the general shape of the mountains and valleys as controlled by erosive and tectonic forces, the timing of mountain building, and the creation and destruction of barriers and bridges to migration of living organisms. Table 2 classifies the sky island complexes by the geologic process which formed the highlands and the topographic relief between valley and mountain (Mani and Giddings, 1980).

The Western Ghats, most of the tepuis, and the Brazilian shield complex are relictual or subsequent mountains, i.e. mountains that started as a plateau and were increasingly dissected by river erosive forces. For instance, the Pantepui's geologic history both constrained and encouraged the rich endemism of its montane flora. The majority of tepuis are hard sandstone with acid lithification (soil-forming properties). Most tepuis are flat-topped mountains (providing more habitat for colonization) with steep cliffs and talus slopes (creating diverse habitats). The evolving flora had to be acidtolerant and, despite the high rainfall, xeric in growth form. The few tepuis of granitic composition were not exceptionally differentiated from the sandstone tepuis. Granite also produces acid-soils. Plant colonization between sandstone and granitic tepuis encountered no immediate "soil barrier."

Tectonic or "original" mountains include mountains (1) built-up by volcanic ash and flood basalts; (2) deformation mountains resulting from continental folding or rifting; and (3) laccolith mountains. I could find no insular laccolithic mountains that were also sky islands.

At least six sky island complexes are combinations of mountain bedrock from volcanic ash and/or flood basalts with subsequent deformation. For instance, the flood basalt mountain cluster of the Ethiopian Highlands was fragmented and gained relief by the sinking of the East African rift valley. Volcanism stopped three to four million years ago, allowing recolonization without further geological disturbance. The Ethiopian highlands are relatively flat-topped (vs. peaked) because of their plateau origin and age. The flatness provided an extensive area for afroalpine populations to evolve.

Similarly, the Madrean sky islands are deformation mountains from continental rifting that began about 13 million years ago. The mountains did not rise as much as the valleys sank. This 'basin and range" or "horst/graben" development exposed older rocks derived from a highly diverse geologic past: multiple marine invasions, caldera explosions and lava flows, and metamorphic core complexes. "Basin and range" tectonics controlled the parallel valley and mountain sequence so unique to North America and largely shaped the large number of "cradles" of evolutionary differentiation.

As opposed to the Ethiopian complex, each individual Madrean sky island is a remarkable mixture of rock types. Exposed rock types include intrusive igneous rocks (granite), extrusive volcanics (rhyolite, dacite, basalts), metamorphics (gneiss, schists, quartzite), and sedimentary rocks (limestones, shale, conglomerates). For example, the Chiricahua mountains are, in large part, an individual volcano overprinted by Great Basin-type dislocation. The Chiricahuas are the planet's largest recorded volcano whose ash flows contributed to parts of five different sky islands in the Madrean archipelago. In contrast, the Pinalenos, the Santa Catalinas, the Rincons, and the Dragoons are metamorphic core complexes. Each core complex is extensively gneis or granite. Other sky islands are predominantly limestone or various limestones (e.g., Huachucas) and almost all the sky islands have remnant slopes with limestone outcrops.

The Sierra Madre source area for the archipelago is the largest rhyolite mass on the planet with 4,000 foot deep sequences in the Barranca del Cobre. The major Rocky Mountain source area for the archipelago is the Mogollon Rim and Colorado Plateau, one of the largest intact sedimentary sequences on the planet. These relatively flat source areas have been instrumental in feeding colonizing species to the archipelago.

The evolutionary and ecological consequences of this mix of rock types and horst/graben rifting are: (1) a confusing array of piedmont, terrace and valley soils that support a huge diversity of grasses, shrubs, and trees (R. McAuliffe and T. Burgess, this volume); (2) talus slopes which, for instance, support a remarkable diversity of snails (McCord, this volume); (3) limestone slopes and outcrops that greatly increase the diversity of plants on particular sky islands (McLaughlin, 1993 and this volume); and (4) altitudinal limits that extend beyond "typical" climatic zones because of the water holding capacities and heat characteristics of particular rock substrates (Shreve, 1922).

In addition, there are other climatic/geologic derived habitats that increase the floral diversity (e.g., the morainal-related cienagas of the Pinalenos from the last glaciation (Warshall, 1986), the seeps of the Galiuros, the relictual clay valleys of the San Rafael and similar unstudied valleys in

Mexico, the aerosol-derived caliche soils of some lower slopes and valleys, and the remnant sand dunes in the Animas, San Simon and other valleys.)

HOW DID IT HAPPEN? BARRIERS, BRIDGES, AND SOURCES

The palaeogeographic history of sky islands has become an exciting and controversial topic. Does stability or instability or what combination of the two generate high levels of biodiversity? Some biologists like to emphasize proximate causes such as the most recent glacial events, the mountain's areal size, ruggedness, exposure, aspect, altitude, distance to nearest sky island, and distance to assumed major source area. Others emphasize the long-term historical framework of planetary palaeogeography. It is beyond the scope of this paper to review sky island speciation theories (see Bush, 1994 for the Amazon region; Journal of African Ecology, 1981 for East Africa).

The Madrean sky islands are uniquely situated in this controversy because all kinds of evidence—pack rat middens, pollen cores, lake sediments, tree rings, fossils, geomorphic surface dating, sea temperatures, radiocarbon and other isotope dating—can be brought forward to argue for various driving forces toward increased speciation. In the southwest, the history of winter vs. summer rainfall and the decoupled influences of temperature vs. rainfall can help explain when the valley vegetation was a barrier that restricted gene flow or when the valleys were bridges that encouraged gene flow.

From a partial review of the literature of the planet's sky islands available in English, I would like to summarize a few lessons. First, sky island species richness can have complex sources and migration routes. For instance, *Bursera is* an African genus that migrated through Laurasia and across North America to the present southwest in the upper Cretaceous/Eocene (Sousa, 1993). Other plants colonized the archipelago after the Panama landbridge connection (Wendt, 1993). A simple model based on changing precipitation and/or temperature for the last glacial period can only explain a small part of the Madrean archipelago's diversity and richness.

Second, the richness of certain Madrean taxa (e.g., flightless beetles, talus snails) may be better explained by the down-falling of the valleys with subsequent vicariant allopatry than by climatic/vegetation flux. Third, other types of barriers and bridges besides valley vegetation occur (Table 3). These include the Pleistocene lakes such as Cochise Lake in the Wilcox playa, the ancient Gila River which was connected to the Yaqui River, and the presence of extensive alluvial fans and roaring rivers in the Pleistocene. These river/lake barriers and bridges are essential in describing the diversity of fish in the Madrean archipelago (Hendrickson, 1980). Fourth, there is a complex interaction between vertical and aspect migration on each individual mountain, the genetic/phenotypic plasticity of the taxa, speciation rates, and climatic/vegetation change. Certain sky islands have provided "safe sites" for organisms because of their latitude and topography. Some sky islands have more frequent colonization attempts because of riparian corridors or valley configuration. Still other sky islands have maintained and added diversity because the invading flora and/or flora had great phenotypic or genotypic plasticity (e.g., *Erigeron)*. These complex interactions await researchers.

Table 3.—Sky Island Bridges and Barriers.

Bridges	Barriers
River and river systems	Riparian systems in arid lands
Lakes	Stepping stones (hills, mts.)
Coastlines	Wind, water, and animal dispersal
High altitude cordilleras	Valleys/gaps with favorable soils climat or ecology
Valleys with alien climate, soils or ecology	Alluvial fans (?) in arid lands Phenotypic/genotypic plasticity

Nevertheless, the Madrean archipelago indicates that regions of maximal disturbance (vs. maximal stability) can encourage species richness, if not endemism, in particular taxonomic groups. The continental position of the archipelago and its relation to three major storm fronts can only have created highly erratic rainfall and temperature regimes. In the past two million years, 15 to 20 glacial fluxes (each about 90,000 years) with short "reprieves" lasting 10 to 15,000 years have influenced the biodiversity of the archipelago. The Madrean archipelago has been spared the "wipe out" experienced by sky island complexes of more northern latitudes (e.g., Eurasian) where the glaciers covered the land's surface. Only the Pinaleno mountains appears to have experienced a small montane glacier.

LIFE ON THE MADREAN SKY ISLANDS

Sky island complexes tend to have greater species richness, greater endemism, more clinal variation, more biogeographical specialties, and unique cultivars compared to other inland terrains. A comparison of planetwide sky island diversity is beyond the scope of this paper. Instead, I will briefly describe the "big picture" of biodiversity in the Madrean archipelago. McLaughlin (this volume) provides more detail on the flora.

The Sierra Madre of Mexico, the Madrean archipelago and other outlier sky islands have been identified as one of the three "megadiversity" centers of the planet. It is the only group of sky islands straddling two major floristic (the Neotropic/Holarctic) and two faunal realms (Neotropic/Nearctic) on the planet (Walter, 1979). The Ethiopian complex borders two faunal province boundaries but lies within one floristic realm. The Drakenbergs and other South African sky islands are associated with the unique Capensis floristic realm which partially explains the regions outstanding number of floral endemics (Takhtajan, 1986).

Reflecting this floristic/faunal straddle and the relatively recent landbridge between North and South America, the Madrean archipelago and its two immediate sources areas contain the biogeographic limits of 14 plant families (northern limit); 11 bird families (seven at their southern limit; four at their northern limit), 30 bird, over 35 reptile, and about 15 mammal species. The bioregion supports the second highest plant endemism between the Pacific coast and the Great plains (McLaughlin, this volume). Sixty percent or more of the plants of the dry forest, oak/pine woodlands, and deserts are probably endemic (Rzedowski, 1993). Similarly, the ant fauna (S. Cover, this volume), the lichens, the snails, the reptiles, the birds, and the mammals show exceptional species richness and/or endemism. The bioregion is considered the most diverse sector of the United States for ants, mammals and reptiles.

The archipelago harbors many poorly studied groups (e.g., Buchman, this volume; Carl Olson, personal communication) and many taxonomically confusing groups (e.g., McCord, this volume). But, as opposed to other regions, detailed systematic investigations have led to more species or subspecies ("splitting"), not fewer ("lumping"). For instance, *Erigeron pringlei,* a local fleabane, on detailed investigation, was split into four species, including a new endemic to the Pinalenos *(E. heliographus).* A new frog was recently discovered in Ramsey Canyon *(Rana subaguavocalis).* The Mt. Graham red squirrel *(Tamasciuris hudsonicus grahamensis),* previously considered one of twenty-six subspecies, now appears increasingly unique.

The Madrean archipelago is the planet's center for the long coevolutionary history of several species groups. The coevolution of squirrels, woodpeckers, jays and one parrot, the woodland's mycorrhizal, epigeous and hypogeous mushrooms and truffles (States, 1992) centers in the Madrean pine/oak woodlands. The coevolution of agaves with bats and hummingbirds centers in the semi-desert grasslands and thornscrub.

There are innumerable mysteries: Why do some localities have only pines or only oaks, while others have pine/oak woodland? Why are there no chipmunks on the Huachucas? Why does the Mexican chickadee *(Parts sclateri)* stop at the Chiricahuas and not cross the 35 miles to the Pinalenos where the Mt. Chickadee (P. *gambeli)* starts? How have the talus snails coevolved with the varied rock substrates and lichens of the individual sky islands? Why does it appear that many southern mammals have expanded into the northern sky islands and beyond in the last half-century? How important is vertical migration up-and-down slope and from the flanks into the valley toward maintaining population stability?

SUMMARY

From a planetary point of view, the Madrean sky island archipelago has these unique features:

- It is an archipelago between two cordilleras (the Sierra Madre Occidental and the Rocky Mountains);
- The archipelago contains an extraordinary number of sky islands per complex;
- The complex has a north-south axis spanning about eight degrees of latitude but contains a distinct east-west valley bridge through the Deming Gap of the Rocky Mountains;
- The islands have a mixed geological composition apparently unrivaled in other areas of the planet;
- The islands have a moderate to high relief (5,000 feet) compared to other valley/mountain complexes with the obvious exceptions of the Himalayas and Andes;
- The Madrean archipelago is the only sky island complex to straddle two major floristic and two major faunal realms as well as the convergence of three major climatic zones (tropical, subtropical, and temperate);

Its mid-latitude position placed it at the edge of glacial influences without experiencing any of the mass extinctions that occurred in the sky island complexes of the more northern latitudes;

The Madrean archipelago endemism and species richness probably reflects a palaeogeographic history in which maximal disturbance with a large turnover of species (e.g., the Pleistocene megafauna) produces great biodiversity, It is not a region of maximal stability.

I have not mentioned one major influence on the planet's sky islands - humans. The influence of Iron Age deforestation and the spread of domestic livestock have permanently changed many sky island valleys and mountains. The Horn of Africa, for instance, has had livestock since 5,000 BC. The Mediterranean mountains have experienced livestock and significant treecutting since about 1,000 BC. The loss of diversity cannot be retrieved or fully known in sky island groups such as the Pyrennes, the Atlas Mountains of Morocco, or the Cabal Lubnan of Lebanon. The Madrean archipelago and its admirers are lucky. Major Iron Age and domestic livestock influences on the Madrean archipelago started less than 200 years ago.

However, the pace and intensity of human influence has been accelerating. 150 species of concern—species listed as vulnerable—dwell within the sky island archipelago, excluding bats (Warshall, in press; Sky Island Alliance, 1992). The jaguar, grizzly, ocelot and graywolf have been extirpated from the United States portion of the archipelago and are probably extirpated from the Mexican portion. Genetic swamping or replacement from translocated species (e.g., hybridization of rainbow and Apache trout, *Salmo gairdneri X Oncorhynchus apache;);* invasion by over sixty non-native plants which have naturalized and degraded valley and desert vegetation (E. Pierson and J. McAuliffe, this volume); long-term declines of some game species, especially band-tailed pigeons *(Columba fasciata);* and urban pressure that has fragmented, if not eliminated, the corridors between various sky islands are clear and present harms.

Policy and attitudes concerning livestock raising and fire management are in a state of flux with attempts to understand "more natural" or "better" or "more balanced" management practices. Piecemeal destruction of both the remaining forest and aquatic habitats is a major concern in both the Coronado Forest and in Mexico. Increasingly, Mexico and the United States realize that some problems and some solutions are international. Binational inventories of the sky island flora and fauna will require close cooperation among scientists and meetings like the present conference. Mexico remains the best source for some animals that are now near extinction in the United States (e.g., black-tailed prairie dog, *Cynomys ludovicianus,* or thick-billed parrot, *Rhynchopsitta pachyrhyncha)* and cross-border cooperation may be necessary to reintroduce the Mexican wolf, *Canis lupus baileyi,* manage various races of pronghorn as well as migratory birds, bats, and butterflies. In short, to conserve both nations' unique natural heritage, a deep commitment to preserving minimal viable habitats for resident and migratory species is paramount. Part of this effort is understanding the unique position of the sky island archipelago in the Earth's family of continental island ecosystems.

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Prominence of the Sierra Madre Occidental in the Biological Diversity of Mexico

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Abstract.—The conifer-oak forests that cover the five mountainous morphotectonic provinces of Mexico occupy about 21% of Mexico terrestrial surface and are the most diverse with the greatest richness and degree of endemism of vascular plants. The Sierra Madre Occidental is prominent in Mexico's biological diversity because it is the northern most extension of the major Mexican mountain chains and the largest morphotectonic province. As such, it serves biogeographically as a barrier, a north-south corridor, a refuge and a center of adaptive radiation. The benefits derived from the Madrean forests for humans can be measured in terms of local and national values. Management for non-timber forest products may provide greater economic benefit to residents.

INTRODUCTION

Of the eleven morphotectonic provinces that are defined by distinctive physiographic and geologic-tectonic features, five are mountainous and covered with conifer-oak forests (Ferrusquía 1993). Even though these forests account for 21% of Mexico's territory, they are richest in vascular plants species (ca. 7,000 species or 24% of the vascular flora) and have the greatest number of endemics (ca. 4,000 species or 32% of the endemic flora) (Rzedowski 1993).

The Sierra Madre Occidental Morphotectonic Province is the largest of the Mexican provinces and covers about 289,000 km^2 or 14.68% of Mexican land surface (Ferrusquía 1993). Covering parts of the states of Sonora, Chihuahua, Durango, Sinaloa, Zacatecas, Nayarit and Jalisco, the Sierra Madre Occidental ranges in altitude from 200 m to over 3,000 m with 65% of the area between 2000-3000 m. The altitude rather than the 10° latitude spread has a more significant effect on climate which in general is temperate humid (Cfb, Cwa) and tropical (Aw). The dominant land forms are sierras and plateaus. The Pacific drainages include the Yaqui, Mayo, Del Fuerte, Culiacán, San Lerenzo, Mezquital, and Atengo rivers while the eastern drainages include the Casas Grandes, Santa María, Conchos, and Nazas rivers. The few geological studies recognize upper and lower volcanic complexes in the largest volcanic field of Mexico and one of the largest in the world with 200 to 400 calderas, some up to 40 km in diameter. The lower volcanic complex is adnesitic and was formed between 100 to 45 Ma while the upper volcanic complex is extensive silicic ignimbrite, about 1000 m thick, and developed about 54 to 34 Ma. Local Tertiary and Quaternary sedimentary clastic bodies are deposited in depressions.

VEGETATION

The vegetation of the Sierra Madre Occidental is dominated by the conifer-oak forests and bounded on the east by the Chihuahua desert and grasslands and on the west by the Sonoran desert and the dry tropical forests (Rzedowski 1978). The forests in higher altitudes consist of various species of *Pinus* while moist pockets harbor other conifers of the genera *Abies*, *Picea* and *Pseudotsuga*. In addition to several taxa of *Quercus*, other hardwoods of the mixed forests include *Alnus*, *Arbutus* and *Populus* trees. The marginal forests on the east slope have piñon pines and dryland oaks (e.g., *Quercus emoryi* Torr., *Q. grisea* Liebm.) while the western transition zone in the canyons have barrancan oaks (e.g., *Q. albocincta* Trel., *Q. tuberculata* Liebm.). The deep barrancas cut into the western flank of the Sierra Madre Occidental and provide

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the opportunity for the growth of many tropical elements in riparian habitats as well as on the dry, steep slopes. Although the classifications of communities are not comparable, published vegetation descriptions that cover the northern Sierra Madre Occidental are available for the borderland of southwestern USA and adjacent Mexico (Brown 1982, Muldavin and DeVelice 1987), the state of Sonora (COTECOCA 1974), northeastern Sonora (White 1948), southern Sonora and adjacent Chihuahua (Gentry 1942), northern Chihuahua (LeSueur 1945) and Durango (González 1983).

The flora of the Sierra Madre Occidental is one of the poorest known in Mexico (Dávila and Germán 1991). The first botanical specimens known from the sierras of Durango were obtained by Martín de Sessé y Lacasta, Juan de Castillo, José Mariano Mociño, Atanasio Echeverría and Vicente de la Cerda of the royal Scientific Expedition of New Spain. Between October 21, 1791, and January, 1792, they travelled between Alamos, Sonora, and the city of Durango (McVaugh 1972). The existence of specimens of *Fouquieria macdougalii* Nash [*Echeveria paniculata* Sessé & Mociño] of the dry tropical forest of the western slopes of the Sierra Madre and *Gentianella detonsa* (Rothr.) G. Don subsp. *superba* (Greene) J.M. Gillett [*Gentiana ciliata* Mociño & Sessé] of the pine-oak forests of northwestern Mexico and adjacent Arizona (Gillett 1957) verify these Spanish and Mexican explorers' initial botanical work in the Sierra Madre Occidental. The next major contribution to the floristic knowledge of the area was made in 1846-1847 by the German medical doctor F.A. Wislizenus (1848), who collected plants at the base of the Sierra Madre west of Chihuahua while a prisoner of war; many new species were described by George Engelmann of Missouri Botanical Garden. Between November 23, 1849, and February 22, 1850, the British botanist Berthold Seemann (1852-1857) documented plants between Mazatlan, Sinaloa, and the city of Durango. Later in 1885, Edward Palmer made extensive plant collections in the barrancas and sierras of southwestern Chihuahua which were distributed by the Harvard University and the Smithsonian Institution (Gray 1886, Watson 1886). They were followed by others at the end of the 19th century such as C.G. Pringle, Carl Lumholtz, C.V. Hartman, F.E. Lloyd, E.A. Goldman, E.W. Nelson, C.H.T. Townsend and C.M. Barber. The 20th century saw more extensive collections by various botanists as the rugged mountains and barrancas became more accessible (Knobloch 1979).

Although no systematic floristic surveys have been completed for the region, selected local studies in Chihuahua and Durango suggest that the vascular flora consists of between 2,200 and 3,000 species although estimates are as high as 3,500-4,000 (Felger and Dahl no date). The three characteristic trees of the flora are pines, oaks and madroños. The north temperate genus *Pinus* has 100 species worldwide of which 45.5% are native to Mexico (Styles 1993). The Sierra Madre Occidental with about 18 species along with Transvolcanic Mountains and the southern Sierras are the richest areas in Mexico. With 450 species primarily in temperate and subtropical in the northern latitudes, *Quercus* is represented in the western hemisphere by 200-225 species (Nixon 1993). Mexico is home to 135 to 150 species of which 86 are endemic. Although not as rich as central and southern Mexico with 60-75 species, northwestern Mexico has approximately 41 species. The United States with 87 species of oaks shares 31 with Mexico along the northern border. The attractive trees of the genus *Arbutus* have 20 species in world of which 9 are native to Mexico (González and González 1992). Six of these grow in the Sierra Madre Occidental. The madroños are the least studied of these major trees. None the less they have complex relationships associated organisms. For instance, a fungal anamorph of *Sirosporium antenniforme* (Berk. & Curtis) Bukak & Serebrianikow grows in the foliar hairs of *A. tessellata* (Sorensen 1987) while the communal and quasisocial butterfly with primitive morphology and advanced behavior, *Eucheira socialis* Westwood, lives exclusively on the madroños (Kevan and Bye 1991). Hence Mexico is home to 30% to 45% of all the species of these three characteristic Madrean tree genera. Within Mexico, the Sierra Madre Occidental houses 66%, 30% and 33% of the nation's madroños, oaks and pines, respectively, that cover the five mountainous morphotectonic provinces.

The Sierra Madre Occidental is a major center for diversity of succulents and perennial herbs as well. The 136 species of *Agave* on the American continent are native to Mexico (Gentry 1982). The three areas richest in species are the Sierra Madre Occidental, the south-central Sierra Madre Oriental and the southern Tehuacan Valley of Puebla (Reichenbacher 1985). The area richest in wild beans (*Phaseolus* a genus of about 40 species) is the western slope of the Sierra Madre Occidental where 19 species grow (Delgado 1985, Nabhan 1990).

FLORA AND PHYTOGEOGRAPHIC PATTERNS

The phytogeographic patterns of the flora of the Sierra Madre Occidental are not well known. The lack of adequate local floras in northwestern Mexico does not permit a floristic analysis comparable to that for adjacent USA. The Apachian Element could be centered in the mountains of southeastern Arizona, southwestern New Mexico and northeastern Sonora or it could be a northern extension of the Sierra Madre Occidental (McLaughlin 1986). This mountain chain serves as a corridor, a barrier, as well as a refuge for endemics. The northwest-southeast orientation of western Sierra Madre has served as a corridor for southern migration of temperate plants as well as the northern migration of tropical flora.

The mountains of Chihuahua and Durango host the southern most American extension of northern temperate genera with such species as *Aquilegia skinneri* Hook. (Munz 1946), *Helianthella quinquenervis* (Hook.) A. Gray, *Ligusticum porteri* C. & R. and *Parnassia townsendii* B.L. Robinson (Bye and Soltis 1979). Certain species common in eastern USA with extensions through Mexico and into Guatemala have their western most range in Sierra Madre Occidental; such examples include *Ostrya virginiana* (Mill.) K. Koch and *Prunus serotina* Ehrh. A similar eastern USA - Mexico pattern is seen at the generic level with *Tilia* in which four species are in the USA and one Mexican taxon, *T. mexicana* Schlecht., the oldest living American species, which reaches its northwest limit in the northern Sierra Madre Occidental (Jones 1968). Wide ranging Rocky Mountain species such as *Pseudotsuga menziesii* (Mirb.) Franco and *Populus tremuloides* Michx. occur as isolated populations with a few individuals in the sierra and extend into central Mexico.

The western slopes of the Sierra Madre Occidental provide habitats for the northern extension of many tropical elements. The dry tropical forests have such northern limit endemic species of their respective genera as *Cocoloba goldmanii* Standley, *Jarilla chocola* Standley and *Dioscorea remotiflora* Kunth, as well as northern limits of extensively distributed plants to the south such as *Tabebuia chrysantha* (Jacq.) Nicholson and *Ceiba acuminata* (S. Wats.) Rose. The riparian habitats of the western canyons host plants with similar patterns such as *Clethra mexicana* DC., *Ficus petiolaris* HBK., and *Oreopanax peltatum* Linden.

The Sierra Madre Occidental is the center of species richness for many Mexican genera such as *Agastache, Dahlia, Oxalis, Psacalium, Tithonia.* Often these mountains not only host the widest ranging species (e.g., *Dahlia coccinea* Cav.) but also endemic species (e.g., *Dahlia sherffii* Sorensen) (Sorenson 1969). The Sierra Madre's western drainages and adjacent coastal plain define biogeographic limits for species of Mexican genera such as *Datura lanosa* Barlcay ex Bye (Bye et al. 1991) and *Fouquieria macdougalii* Nash (Henrickson 1972).

Not only are endemic species products of differentiation within the generic range but also products of more dynamic biogeographic processes. *Ceanothus ochraceus* Suesseng., the species with the most primitive characteristics of the genus and that grows in the semi-xeric mountains of Chihuahua and Durango, probably represents the ancestor that gave rise to the 55 species that radiated throughout North America to occupy more xeric and more mesic habitats (Stebbins 1972). Other endemics are relicts that have retreated due to altered environmental conditions. The presence of pollen of *Picea* in southern Veracruz during the middle Pliocene (ca. 2.4 Ma) suggests that the continental climate of Mexico has warmed up (Graham 1993). Today three species of spruce grow in northern Mexico; *P. chihuahuana* Martínez and *P. mexicana* Martínez are found in the northern Sierra Madre Occidental (Taylor et al. 1994). The 26 populations of *P. chihuahuana* are small with an estimated total number of individuals of 17,000 (Sánchez and Narvaez unpubl.). The increased human pressures on the existing stands, the lack of regenerative aggressiveness and pollen flow corridors (Gordon 1968), and the 95% seed mortality caused by larvae of predating moths (*Cydia phyllisi* Miller) (Secretaría de Agricultura y Recursos Hidraúlicos 1993) suggest that this species may not survive in the near future.

Species with disjunct distribution or vicariant species indicate evolutionary divergence in response to fragmentation and barriers in the past. *Pinus discolor* Bailey & Hawksworth of the mountains of Chihuahua and Durango and adjacent Arizona and New Mexico also grows at the southern end of the Sierra Madre Oriental in the states of San Luis Potosi, Queretaro (Zavala and Campos 1993). In the pine-oak forests of northern Sierra Madre Occidental, *Ratibida latipalearis* Richards is a vicariant of *R. coahuilensis* B. Turner of the oak woodlands of northern Sierra Madre Oriental

(Richards 1968, Turner 1988). In the dry tropical vegetation, closely related species of *Parthenium* similar to the ancestral form are vicariants; on the western slopes of the Sierra Madre Occidental of Chihuahua and Sonora *P. stramonium* Greene grows while in the states of Puebla and Oaxaca in southeastern Mexico *P. tomentosum* DC. is found (Rollins 1950). Although disjunct and vicarious distributions are natural, the role of humans in long distance dispersal should be considered as well such as the case of *Agave applanata* Koch ex Jacobi which is native to the highlands of central Veracruz and adjacent Puebla and found growing seemingly "wild" in the mountains of Chihuahua and Durango (Gentry 1982).

CULTURAL ASPECTS

Indigenous residents of the Sierra Madre Occidental include speakers of such languages as Pima, Tarahumara, Guarijio, Mayo, Yaqui, Tepehuan, Cora, and Huichol which represent minor concentrations when compared to central and southern Mexico (Olivera et al. 1987). Although the absolute number of native speakers in Mexico is on the increase, there is a decrease in the number of individuals native speakers in the regions of the Sierra Madre (Valdés and Menéndez 1987). The decline in the use of native languages is often correlated with the decrease of knowledge and use of native plants.

The employment of native plants to satisfy daily needs of the inhabitants of the Sierra Madre Occidental was complemented by the cultivation of introduced cultivars. The documentation of the changes in the plant exploitation over time is difficult due to the few studies carried out in archaeological and historical contexts. Few botanical materials have been identified from excavations in the sierras of Chihuahua (Ascher and Clune 1960, Clune 1960, Miller 1987, Montúfar 1992) and Durango (Brooks et al. 1962). The entrance of the Sierra Madre Occidental by the Catholic Church permitted the Spanish government to systematically register various facts about the missions through "Relaciones Geográficas" and "Relaciones Topográficas de los Pueblos". Although no detailed study has been carried out on the plants contained in the reports for the 18th century, Pennington (1963, 1969, 1980) correlated the plants mentioned in these unpublished documents with those used by contemporary native peoples in Chihuahua and adjacent Sonora. There are few documented studies of useful plants in the northern Sierra Madre Occidental during the 19th century. One example is the field exploration of Edward Palmer in the Sierra Tarahumara in 1885 which was partially published by Gray (1886) and Watson (1886). Of the 128 registers of economic plants, 113 can be identified. When these plants are compared to those employed currently, only 71 species (63%) continue to be used (Bye et al. in press). The remaining plants are not known today for a given utility. Consequently, 37% of the ethnobotanical knowledge of the 19th century Tarahumara has been lost in one hundred years.

Present day use of plants by native peoples and mestizos in the northern Sierra Madre Occidental is documented by few studies. Of the major anthropocentric use category of plants, the most frequent are those for remedial and alimentary purposes. It is estimated that 400 native plant species are used as medicine while 300 are consumed as food. Ethnobotanical data exist for the Mountain Pima of Chihuahua (Laferrière 1991, Laferrière et al. 1991), the Tarahumara of Chihuahua (Bye 1979, 1981, 1985, Bye et al. 1975, Cardenal 1993, Mares 1982, Pennington 1963), the Tepehuan of Chihuahua (Pennington 1968), the Warihio of Chihuahua-Sonora (Gentry 1963), the Tepehuan of Durango (González 1991), and the Pima Bajo of Sonora (Pennington 1980).

The density of contemporary inhabitants of the Sierra Madre Occidental is low. Current statistics show that in the Sierra Tarahumara there are 3.6 inhabitants per km^2 and that the economic measures indicate that the forest, cattle and mining is unilaterally extractive in the direction of the major cities. Industries are to the east and to a smaller degree to Sonora and Sinaloa (Enríquez 1988). The institutional economic pressures carried by mestizo residents and outside industries who perceive the social space and natural resources differently than the Tarahumara have created conflict between these cultures (Bassols et al. 1986, Lartigue 1983, Vatant 1990).

FOREST RESOURCE EXPLOITATION

Official Mexican government statistics take into account those forest products that are exported from the region. For example in the state of Chihuahua for the year 1990 (anon. 1992), the timber products of the Sierra Madre Occidental (1,578,701 m^3 or 350,176,260,000 old pesos) greatly out weighed the non-timber products (candelilla, palmilla, orégano) mostly from the foothills and desert (890,597 kg or 1,983,368,000 old pesos). This pattern for the pine-oak forests is the same in Durango but is strikingly different in the central and southern Mexico states where non-timber products such as resins and medicinal roots balance the timber products (Vargas and Terrazas 1990).

Even though there are no economic evaluations of the value of local plant resources in local economy of the Sierra Madre Occidental, local and regional trade of certain non-timber forest products has been recognized as important. The Tarahumara Indians of the barrancas and sierras exchange such items as food plants and products (*Agave* spp., *Coursetia glandulosa* A. Gray), dye plants (*Haematoxylon brasiletto* Karst., *Indigofera suffruticosa* Mill., *Erythrina flabelliformis* Kearney), chiltipín (*Capsicum annuum* var. *glabriusculum* (Dunal) Heiser & Pickersgill), fibers (*Yucca* spp., *Dasyliron* spp., *Nolina* spp.) and medicinal plants (*Buddleia* spp., *Litsea glaucescens* HBK., *Hintonia latiflora* (Sessé & Mociño ex DC.) Bullock, *Jatropha platanifolia* Standley) (Bennett and Zingg 1935).

Of the 300 plants used medicinal by the Tarahumara, about 50 enter the local markets. In a study of 47 plants that originate from the western mountains of Chihuahua, 30 of these are used in a similar fashion by both the Tarahumara and the mainstream Mexicans (Bye 1986). The continued employment by both cultural groups assumes that the vegetal remedies are effective in the same human physiological system and could indicate the potential for economic development. The current condition of such plants as "matarique", "chuchupate", and "té de milagro" suggest that careful integration of a sustainable forest management plan with the socioeconomic development of the residents of the Sierra Madre Occidental is needed urgently. Between 1978 and 1987, the prices at the suppliers, wholesale and retail levels rose dramatically. In the case of "matarique" (which is used to treat diabetes and arthritis), the price per kilo of dry roots increased US$4.50 to US$7.50, US$6.50 to US$11.00 and US$9.00 to US$16.25, respectively. During the period this dominant element of the "matarique" medicinal plant complex (defined as a group of taxonomically distinct plants that share common names, uses and morphochemical traits; Linares and Bye 1987) was *Psacalium decompositum* (Gray) H. Robins. & Brett. of the pine-oak forests of northern Sierra Madre Occidental and was commercialized throughout Mexico and adjacent USA. The rising prices were attributed to scarcity of the most effective form. Even though not considered as efficacious, the substitute, *P. peltatum* (HBK.) Cass. of the Transvolcanic Mountains of central Mexico, began to replace the dominant form in the market.

As with the case of "matarique", the prices of "chuchupate" at the suppliers, wholesale and retail levels rose similarly. The market price per kilo of dry roots of "chuchupate" (which is used to treat gastrointestinal ailments and pains), increased US$1.50 to US$8.00, US$2.50 to US$12.50 and US$3.50 to US$18.00, respectively. "Chuchupate" (*Ligusticum porteri*) grows in the shaded pine-oak forests of northern Sierra Madre Occidental but has rapidly declined due to overcollecting to satisfy national and international demands and to destruction of the forest habitat. Tarahumara collectors in 1987 received US$0.33 per kg of dried root or 22% of the suppliers price or 1.8% of the crude retail value. In addition to the crude drug, it is one of two major ingredients of a commercial product called "Copangel" which is sold in the health food stores and pharmacies to treat dyspepsia, gastritis and stomach ulcers. Clinical trails in a Mexico City hospital confirmed the effectiveness of the herbal remedy (Mundo et al. unpubl.).

The undisturbed "chuchupate" forest habitat has on the average 60 adult plants equivalent to 7.5 kg of dried roots per 100m^2. Using the general figures of natural plants densities in the forest, the price paid to indigenous collectors and the retail value of the finished product (US$5 per 100 capsules), the value of the "chuchupate" pine-oak forest habitat can be estimated. A 100m^2 plot of this habitat in terms of "chuchupate" is worth US$2.47 in direct gain by a Tarahumara collector or, in terms of the retail product "Copangel", US$749.93. If only 10% of the population is harvested and the regeneration cycle is 10 years long, one hectare of "chuchupate" has an annual worth of US$24.70 to the collector. That hectare of forest would be valued at $74,993 based upon the retail product.

Using timber profits to which the Tarahumara have a right to collect, Enríquez (1988) calculated that each year a Tarahumara family receives US$4.30 per hectare for harvested timber and pulp. That hectare of forest would have a value of $5,000 based upon the timber and pulp sales.

Although "chuchupate" seldom occupies uniformly a hectare, does not have an insatiable market and is not the sole non-timber forest product in that plot, these general figures suggest that integrative non-timber resource management of critical habitats within the forest mosaic would return more financial benefit to the local residents than exploitive cutting. Also, increasing the profit margin for the collectors could make forest habitat management more attractive to the inhabitants of the Sierra Madre Occidental.

"Té de milagro" or "chucaca" (*Packera candidissima* (Greene) Weber & Löve) is a massive ground cover that invades clear cut areas in the pine-oak forests of Chihuahua. The leaves are drunk as a tea for alleviating kidney pain and are prepared as a wash or salve to treat skin ailments. "Hierbamil" is a commercial product sold as a syrup or a cream in Mexican pharmacies. At first glance, this plant has commercial potential as part of a clear cut forest management plan. Unfortunately, the plant has one of the highest concentrations of hepatotoxic pyrrolizidine alkaloids (Bah et al. 1994). Development of non-timber forest products, in addition to considering cost/benefit analyses, must consider the toxicology of the products to the consumers.

FOREST DAMAGE AND FOREST MANAGEMENT

As mentioned above, overcollecting of certain plants and the destruction of habitat has altered the biological diversity of the Sierra Madre Occidental. Clear cutting and overgrazing are major factors in the alteration of certain forest communities. Inappropriate land use such as the plowing of the high wet "llanos" (which naturally do not have tall trees) for afforestation plantings has lead to the extinction of the endemic *Taushia allioides* Bye & Const. (Bye and Cosntance 1979). Fire is considered to be an important element altering the forests of Chihuahua and Sonora (García 1983, Dieterich 1983). Preliminary observations on certain plants suggest that the flora is adaptive to periodic, light fires and/or long dry spells. Thick scales, concentrated needles and dense bark protect the young seedlings of *Pinus engelmannii* Carr. Perenial herbs with tuberous tap roots (e.g., *Cologania* spp.) or thick rhizomes with radiating roots below (e.g., *Psacalium* spp., *Roldana* spp.) survive surface fires. Shrubs (e.g. *Ceanothus* spp.) and grasses (e.g., *Muhlenbergia* spp.) sprout vigorously after fires. Upon firing, *Arctostaphylos pungens* HBK., which forms a dense chaparral and prevents the establishment of seedlings under the crown through light competition and deposit of allelopathic substances in the soil, dies back without sprouting, thus opening the habitat for colonization by a more diverse flora. Controlled burning is now being considered as a management tool in the pine-oak forests of Chihuahua (Sánchez and Dieterich 1983).

CONCLUSIONS

The Sierra Madre Occidental is prominent in the biological diversity of Mexico, one of the megadiversity countries of the world. It is the largest morphotectonic province in Mexico with a great range of altitude. Its northwest-southeast orientation has allowed it to function as a barrier to east-west migration as well as a corridor for movement of northern elements south and vice versa. The conifer-oak forest that covers the mountains is the most diverse in Mexico in terms of species richness of vascular plants as well as degree of endemism.

Various ethnic groups live diffusely in the sierras and the associated western barrancas. The non-timber forest products play a role in the local and national economies even though they are not registered in the official surveys. Some plants have the potential to develop into viable economic enterprises. The changes in land use affect, often negatively, the abundance and survival of some plants in the region.

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The USDA Forest Service Perspective On Ecosystem Management

David G. Unger[1]

I have been asked to discuss with you how the Forest Service will be moving forward in the next few years with respect to ecosystem management. I've also been asked to discuss some of the challenges that hindered in furthering concepts of Ecosystem Management. My comments will be general. I encourage you to hear Art Briggs and others this afternoon discuss in more detail how EM planning is underway in this region.

There are really two things that I want to stress today. The *first* is the commitment of the Forest Service to ecosystem management; recognizing it is not a goal unto itself, but a means to an end—and that end is sustainable ecosystems and sustainable uses of those ecosystems.

Secondly, I want to stress the critical importance of effective partnerships. Collaboration, consultation and communication are essential to the practice of ecologically sound forestry and range management, both on the local and landscape level scale. By building on our long-term relationships and searching out new ones, we will continue to improve the stewardship of America's forests and range resources.

ECOSYSTEM MANAGEMENT—AN APPROACH

What do we mean by ecosystem management. Ecosystem management is a way of thinking about the landscapes we work with.

Let me repeat that ecosystem management is not an end, but a means to an end. It is a way of thinking about the landscapes we work with.

Although there are several interpretations of what "ecosystem management" means, every definition has the same key concepts. The one I will use today defines ecosystem management as an approach to the management of natural resources that strives to maintain or restore the sustainability of ecosystems and to provide present and future generations a continuous flow of multiple benefits in a manner harmonious with ecosystem sustainability.

THE FOREST SERVICE—MOVING AHEAD

How are we moving ahead in putting this philosophy into practice in the Forest Service? First, we are viewing our work in a more holistic way, looking at the interaction between management activities, emphasizing integrated action, and looking at different scales in planning and carrying out work. With an ecosystem management approach, we step back from the forest stand or range allotment and focus on the landscape. We look at the larger environment in order to integrate the human, biological, and physical dimensions of natural resource management.

Strategically, we are focusing on three desired outcomes:

1 Enhanced protection of ecosystems.
2. Restoration of deteriorated ecosystems.
3. Providing benefits within the capabilities of ecosystems.

More specifically, we are moving ahead in the following areas:

Changes in Policies and Laws

This is leading to consideration of changes in the way we develop and revise forest plans. Proposed changes in our planning regulations are nearing completion. Also, there are several areas where we may need to ask Congress to revise our statutory framework. Our Office of General Counsel is reviewing existing laws to see if there are ways for the Forest Service to implement ecosystem management more efficiently.

Another Need is to Establish an Operating Framework

The Forest Service, in cooperation with other agencies, has adopted an ecological unit frame-

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work to provide a scientific basis for ecosystem management. The framework is a classification and mapping system for stratifying areas into ecological units that have common biological and environmental factors such as climate, physiography, water, soils, air, and natural communities.

Building on this system, we are particularly please about an agreement that we have signed with the Soil Conservation Service and the Bureau of Land Management that will result in the development of a common ecological map of the United States. We will be working with the Environmental Protection Agency, National Biological Survey, Fish and Wildlife Service, U.S. Geological Survey, and other State and federal agencies and groups to develop a Memorandum of Understanding through which this work can be accomplished. I want to stress the point that no one set of lines on a map identifying ecological units can serve all purposes. But it gives us a starting point for assessments and planning.

Assessments and Applications

The next step - gathering information and putting it to work. Several assessments are underway at large scales. The assessments that provided the information used in developing the President's Forest Plan for the Pacific Northwest are the best known. Others have been conducted on forest health in Eastern Oregon and Washington and are under way in the Upper Columbia River Basin and the Sierra Nevada range in California.

These assessments are designed to gather state-of-the-art information. The information then can be used to amend forest plans and develop project proposals. We have to recognize that national resource systems in our environment are incredibly complex and it is unlikely we will ever completely understand how ecosystems work. We have however, learned a great deal. We will build on our collective knowledge to measure the health of our forests and rangelands and the plant and animal communities of ecosystems. In place after place across the U.S., our land managers are working with land people to develop and implement strategies that conserve biological diversity and maintain aesthetic values, while producing needed commodities.

In the Southwest, there are many partners in this application area. One of these groups was singled out last year for the National Ecosystem Management Award from the Chief of the Forest Service for the Yavapi project on the Prescott National Forest. This project not only resulted in meeting the desired conditions set forth by private landowners, the Forest Service, and other federal and state agencies, but had spin-off benefits beyond the original goal. Specifically, there was a goal to have grass within the area high enough in the spring to provide hiding cover for antelope fawns. Through adjustments in management this goal was accomplished. The spin-off cam when the highly controversial activity of aerial gunning of coyotes was no longer needed for protection of fawns from predators. I point this out to illustrate that we don't know, as yet, all the benefits that can be derived from ecosystem management. We are attempting to find out though, which leads me to my next topic.

Monitoring and Evaluation

The purpose of monitoring is to find out what the efforts of our actions are. More important is to adapt our management to incorporate new information. Monitoring can not continue to be treated as an appendage and it can not be done based on future funding. Monitoring must be part and parcel of everything we do, and we will need the informed interest and participation of our stockholding in accomplishing it.

As we proceed on this course, we see that we need to measure more than the activities and outputs of the past - we need to measure outcomes - the conditions that demonstrate healthy, sustainable ecosystems. This change is a strongly significant one.

It will be no surprise to anybody in this room that the underpinning of good resource management has always been and will continue to be science. In implementing ecosystem management, we will enhance the use of science in the decision-making process. This will mean strengthened independence of our research arm, as well as development of guidelines for upfront and continuous collaboration of scientists and decisionmakers, and upgrading of the technical skills of our workforce. Good examples are the process we used to develop PACFISH, our strategy for protection of sensitive salmon stocks in the Northwest, and the collaboration between researchers and managers now taking place in revising the Tongass Forest Plan in Alaska.

Collaboration and Partnerships

Ecosystem management means commitment to working with more partners than we've had in the past, because ecosystems cross boundaries. By working with our partners, we are best positioned to foster sustainable communities and ecosystems. Together, we can encourage the use of non-regulatory approaches, respect for private property rights and information sharing with interested and willing partners.

I cannot overemphasize the role that the philosophy of EM is playing in bringing different players together at the table. At the federal level, the Forest Service is participating on an Interagency Ecosystem Management Coordination Team with the BLM, Fish and Wildlife Service, National Park Service, Department of Defense, and the Soil Conservation Service to share information, to coordinate projects of interest across agency lines, and to develop a forum for the development of new concepts. The Forest Service is working with the BLM and the Soil Conservation Service on several joint action plans. We have staff working with the President's Commission on Sustainable.

Development, the National Biological Survey, the State Department, EPA, the National Association of State Foresters, the National Association of Conservation Districts, and the World Bank. We are key participants in a White House initiative to conduct 10 case studies in EM, and are working with over 20 other countries, including Mexico, to develop criteria for sustainable forest management with the U.S. Agency for International Development, the Peace Corps, the United Nations, and other international agencies.

In the Southwest you are working together in forums such as this one, through the series of symposia with universities funded by Forest Service management and research branches, the Southwest Forest Consortium, The Rio Grande Basin Ecosystem Council, and the Malpai Borderlands Project. This project, with its leadership from the private sector, is an excellent example of the kind of collaboration that will be needed for successful ecosystem management.

But we must do more. We must truly institutionalize collaboration and create opportunities for reasonable people to come together to discuss issues, learn from one another, and work toward a consensus on how resources should be managed.

As a final stop in listing things we are doing to promote ecosystem management, I want to mention organizational change. It's occurring at the local and regional levels as we find ways to cross over traditional functional boundaries. At the national level, Congress is helping by authorizing us to reduce our line items and to create a new category for ecosystem planning, inventory and monitoring.

We are also looking at ways to organize our work at every level of the Forest Service to facilitate the integration, skills development and training that will help us advance ecosystem management. We've already combined our Land Management Planning, Environmental Coordination, and Ecosystem Management staffs at the Washington Office level.

WHAT ARE SOME CHALLENGES AHEAD?

All federal agencies, including the Forest Service, are facing declining budgets and workforces. During the past two years, we've downsized by nearly 4,000 positions. We need to find a way to address staffing needs by retraining existing employees and by emphasizing ecosystem management skills when we hire new employees.

Another challenge is the issue of private property rights. Because ecosystems cross boundaries, ecosystem management has arisen as a concern to some private landowners. The Forest Service has never sought and does not seek any authority for regulation or oversight on non-National Forest System lands. Our approach with private landowners will continue to be one of cooperation and assistance on a voluntary basis. We will continue to respect the rights and interests associated with private lands and indvidual goals, and will encourage the voluntary use of our ecosystem management techniques by any landowner or manager who finds them useful.

Ecosystem management is an evolving concept. New ideas take time to mature. As Diane Madden of the Coronado National Forest and I were discussing this morning, we don't know all the answers. Hopefully, we won't take too many wrong turns, but I know we will take some. What is important is that we will learn, we will adapt, and by doing so we will earn our public's trust. The natural resource management community is closer to agreement than we were a few years ago - so we are making progress.

Ecosystem management will be an exciting and fruitful journey. It is important for us to recognize our shared goals; promote local participation in decisions and activities; and utilize the best knowledge and technology available. Chief Jack Ward Thomas has proposed that our land ethic for the century ahead be sustainable ecosystems. It is a worthy challenge for us all.

Relationship of Research to Management in the Madrean Archipelago Region

Peter F. Ffolliott[1], Leonard F. DeBano[2], and Alfredo Ortega-Rubio[3]

Abstract.—Our purpose is to provide a context for answering the question: How this conference can address the relationship of research to management of ecosystems in the Madrean Archipelago region? We hope that the linkages between research and management, necessary to meet people's needs while maintaining biophysical integrity, will be viewed as a circular process. That is, much effective research is formulated in response to people's desires for implementing better management, and (in turn) better management frequently evolves from the infusion of the new findings. To place the linkages between research and management into a perspective for the participants of this conference, we present a conceptual model of the main sectors of the Madrean Archipelago (population, agriculture, industry, natural resources, and pollution), which are linked by a web of feedback loops representing transfers of knowledge and technology obtained from researchers and managers. We believe this representation provides a useful tool for attempting to understand where we have been, where we currently are, and where we should proceed in the future to ensure that the concerns of people are addressed properly in relation to the unique characteristics of the Madrean Archipelago region. It is imperative that researchers, managers, and all of the other stakeholders work together in developing a mutual trust in understanding and managing the resources in question.

INTRODUCTION

The intent of this conference is bringing together researchers, managers, and all of the other stakeholders in the Madrean Archipelago—the area in the southwestern United States and northwestern Mexico where scattered, isolated mountains are found in a sea of largely evergreen woodlands—to address a wide array of issues relating to conservation and sustainability of the region. One key to the success of the conference, therefore, is adequately addressing the relationship of research to management of the represented ecosystems. That is the purpose of this paper.

Science, as used here, represents the possession of knowledge attained through study (research) and practices (management). Therefore, researchers and managers are scientists. It is our view that scientists should enter into a compact of trust with all the other interested stakeholders in the advancement of knowledge. Unfortunately, researchers, managers, and environmentalists in the Madrean Archipelago are occasionally at odds on the direction that science should take. Much of this disagreement can be traced to differing environmental philosophies that people possess.

A problem from a theoretical standpoint has been the conflict between what have been called the "biocentrism" and "anthrocentrism" schools of thought. The biocentrists assert the need to put nature first, and the dire environmental consequences of putting human needs first (Hays 1992), while anthrocentrists argue that human needs take precedence over environmental concerns. Biocentrists have gained a fair amount of public-

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ity in the popular press, but have not always affected the cause of environmental action to the extent that they have hoped. To protect natural systems from development, they often adopt the pragmatic action of finding ways for public or private bodies to insulate an area from the private market to "save" it.

While the basic philosophical issues of this discussion are important, a more productive approach for this conference may be one advanced by Norton (1991). He believes that the dominant reason for environmental actions should be practical, pragmatic, and focused on problem-solving. He also believes that interested stakeholders waste much time and energy, and foster unneeded tensions, by arguing the merits of the biocentric view as epitomized by John Muir in relation to the use-oriented tradition of conservation exemplified by Gifford Pinchot. It is more important, Norton continues, that all of the stakeholders focus on practical situations in which those who are at odds on some philosophical points can work out mutually acceptable solutions to problems.

ROLES OF RESEARCHERS AND MANAGERS

The roles of researchers and managers in relation to the consumptive and nonconsumptive uses of resources in satisfying human desires have been articulated nicely by Stoltenberg et al. (1970) among others. In general, resource managers assist individual and societal stakeholders in a number of ways. Managers help stakeholders identify and clarify their objectives. They also identify for the stakeholders the alternative approaches to achieving their objectives, and help them to evaluate or compare these alternatives, selecting the most promising opportunities for achieving the stated objectives. Managers frequently spend a disproportionate part of their time supervising subsequent activities to implement these decisions, however, and have insufficient time to emphasize problem-solving efforts. This situation is unfortunate, because managers often are making their most valuable contributions helping stakeholders make decisions.

Just as a manager's contributions are measured by how effectively they help stakeholders satisfy their wants, the value of resource researchers is determined largely by how much their efforts increase the efficiency of the managers (Stoltenberg et al. 1970). One purpose of research is to develop new alternatives (practices, tools, concepts, products, services, etc.) for managers. Another purpose is to answer questions of fact that arise in the management process. A third is to answer questions of fact that arise in conducting research, since all to often these basic questions must be answered satisfactorily before the first two purposes of research can be addressed efficiently.

Many researchers do not provide information directly to managers. Some provide information to solve the problems of other researchers. Research, therefore, can be viewed as a continuum with the manager at one end of the spectrum. Managers are concerned principally with stakeholders' problems. When managers lack the information needed to help evaluate stakeholders' alternatives, they often "experiment" with these alternative approaches until a "satisfactory solution" is obtained; many managers, therefore, become "surrogate" researchers in the process.

Next on the continuum are researchers who are attempting to answer managers' immediate questions of fact, for example those focusing on resource-use trends, prices, and technologies. Following these are the "developmental researchers," who create new alternatives for the managers that will help solve both immediate problems and those yet to be formulated. Further along the spectrum are the researchers who serve a clientele of other researchers. These researchers typically come from the basic disciplines, providing the facts, relationships, and other inputs needed by those who conduct the "more applied" developmental research. Although the ultimate clients for all researchers and managers are the other stakeholders, it can be seen that the intermediate clientele can be managers or other researchers.

Successful problem anticipation and, as a consequence, planning become more difficult as the distance on the spectrum between researchers and managers increases. While researchers focus on their immediate clients in many instances, even their most basic activities usually are intended to help solve management problems. Research planners, therefore, need to anticipate these problems accurately and articulate their contents appropriately. Information necessary for the solutions of the problems comes from managers, environmentalists, and other members of society who are stakeholders in the enterprise. To the extent that information comes from all these sources, it confirms the premise put forth earlier in this paper that research and management should be viewed as a circular process.

A PERSPECTIVE ON THE IMPORTANCE OF RESEARCH AND MANAGEMENT IN THE MADREAN ARCHIPELAGO REGION

A perspective on the importance of effective research and responsive management in the Madrean Archipelago region can be gained, we believe, through a recognition of the dynamic nature of the systems encountered. The conceptual model in figure 1, originally constructed by Meadows et al. (1972) to represent the limits to growth on a world-wide scale, illustrates how population, agriculture, industry, natural resources, and pollution in the Madrean Archipelago are linked together by a web of multiple feedback loops. These feedback loops represent transfers of the "products" of knowledge and technology from one sector to another and, therefore, are largely the combined products of research and management. While other models may apply equally well, this model was selected because it is structured in a format that depicts the Madrean Archipelago region, and contains the sectors important to the people of the region.

Most of the linkages in figure 1 suggest interdependence of the sectors represented (population, agriculture, etc.). Agriculture and population, for example, have an obvious interdependence in that more of one implies more of another. Industry dependents on needed inputs of nonrenewable resources (ore, fuels, etc.), and, therefore, the flows of these resources depend largely upon the level of industrial capital targeted for their exploitation. Industry and agriculture both generate pollution, and severe pollution affects both people (by reducing their health) and their food sources (by reducing agricultural yield). Effective research followed by responsive management are necessary in assuring that all of the feedback loops connecting the sectors are identified properly, the flowlines are comprehensive in content, and the flows into and out of the reservoirs are effective, efficient, and appropriate. Attaining these assurances should be a major goal of researchers and managers in the Madrean Archipelago region. To this end, we hope that this conference provides a forum for the participants to evaluate where we have been, where we currently are, and where we should proceed in the future in meeting this important goal.

The representation shown in figure 1 is a simplified model and not intended to be all encompassing. It is obvious that much has been left out of this simplified version. For example, all of the resources that drive industries (metals, energy, foodstocks, etc.) are amalgamated into a single feedback loop. Similarly, all of the pollutants (human, agricultural, and industrial wastes) are represented by one loop. And, importantly, there is no representation of geographical inference in the model. The peoples in both the

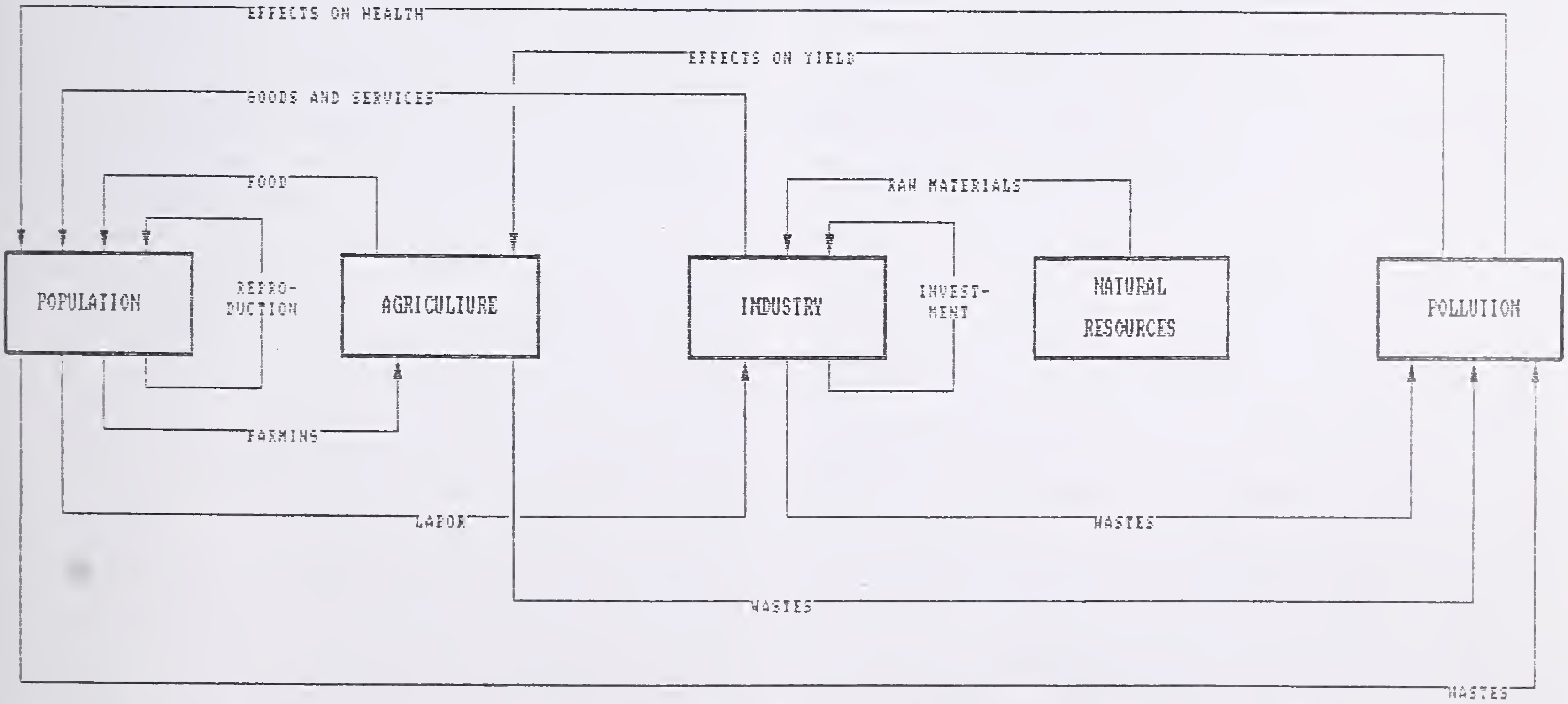

Figure 1.—Linkages of population, agriculture, industry, natural resources, and pollution in the Madrean Archipelago region (adapted from Meadows et al. 1972).

southwestern United States and northwestern Mexico are one—as perhaps they should be considered in this conference.

CONSERVATION AND SUSTAINABILITY IN THE MADREAN ARCHIPELAGO REGION

Researchers and managers in the Madrean Archipelago, along with researchers and managers throughout other regions of the United States and Mexico, face changing expectations on how limited resources should be used to meet people's needs. Managerial strategies, scientific knowledge, and technology necessary for producing the traditional multiple uses of resources only partially satisfy stakeholders' interests in the use of resources in the 1990s. Researchers and managers, therefore, must become increasingly responsive to the more demanding viewpoints that stakeholders have of these resources and their respective roles in meeting people's desires. Such a perspective embraces a stewardship that balances the protection of natural environments and a sustainability of products and services needed by people (Kessler et al. 1992).

There is little question that the multiple use philosophy of management served society reasonably well into the 1980s. Lands were characterized largely in terms of their capacities to yield commodities and amenities. A primary role of research at this time was discovering the factors that limited the realization of these capacities, while a key objective of management was reducing or removing these limitations. Answers to questions about resources required the identification of "optimum yields" among the desired (and often competing) uses (Kessler et al. 1992). However, multiple use is not necessarily the best way to approach management when stakeholders begin to ask far-ranging questions on how to balance a wide range of potential uses and values, which is the situation in the Madrean Archipelago today. An alternative paradigm, one embracing an "ecosystem approach," has been proposed by the National Research Council (1990) for the management of forest lands. We suggest this ecosystem paradigm applies equally well to many of the lands and resources in the Madrean Archipelago.

The ecosystem approach modifies and broadens the multiple use paradigm to one of holistically conceived ecosystem management. It requires one to view lands in a comprehensive context of living systems (including soils, plants, animals, minerals, climate, water, topography, and all of the ecological processes that link them together) that has importance beyond traditional commodity and amenity uses (Kessler et al. 1992). With this view, management practices that optimize the production or use of one or a few resources can compromise the balances, values, and functional properties of the whole. Furthermore, the production or use of individual resources in themselves might not lead to sustainability.

Objectives of the ecosystem approach relate to the ecological and aesthetic conditions of the landscape, and sustainable levels of land uses and resource yields that are compatible with these conditions. In some respects, these objectives reflect the earlier concept of "area-oriented" multiple use management, in which the information needed to describe resource potentials is drawn from "resource-oriented" multiple use. This information is then arranged, analyzed, and evaluated in spatial relation to a given land area's suitabilities for management, and the dynamics of local, regional, and national demands of the people (Ridd 1965).

Current conflicts in resource management indicate that the roles of public participation in relation to endorsing management practices are changing, regardless of the paradigm. Stakeholders' roles in the past have been largely to respond to professionally prescribed alternatives that estimate outputs of management in terms of cords of fuelwood, animal-unit months of grazing, recreational user-days, or breeding pairs of Mexican spotted owls (Kessler et al. 1992). Tradeoffs have been presented as changes in the quantities of one resource use in relation to the others.

The production-oriented multiple use management of the past no longer reflects the thinking of many people in the Madrean Archipelago. People are not only thinking about optimizing the levels of competing uses through management, but also obtaining a harmonious relationship with the rest of the natural system, in contrast to a view favoring people's dominance over nature (Norton 1988). It is important, therefore, that researchers and managers develop approaches that better fit the way people think about land and resources in today's world. Stakeholders must become informed about the conditions, capabilities, and options for their lands and resources, and share the knowledge that professionals accrue through the research and management experience (Kessler et al. 1992). At the same time, researchers and managers must understand and consider the values and needs of people, rather than concluding what is good or bad for society from their own, often technical, perspectives.

It should be obvious that new thinking about resources, people-nature relationships, and sustaining ecosystems is required in the scientific communities of the Madrean Archipelago. The resulting changes, when they occur, will likely be reflected by a trend where the traditional basic and applied disciplines come together in seeking solutions to the problems of conservation, ecosystem sustainability, and people's welfare (Christensen 1989, Murphy 1990). The activities of this conference should encourage such a trend.

CONCLUDING COMMENTS

A frequent debate that we have all heard is whether a big conference such as this is useful and effective in comparison to a smaller symposium that addresses specific topics. We are convinced, however, that this conference, while "big" to some people, will play an important role in planning for the future of the Madrean Archipelago that could not be filled by smaller symposia on more specific, often limited subjects. This conference will highlight many of the recent, continuing, and planned efforts of the research and management communities in the region that will facilitate communication among people of previously diverse interests. The potential will be established for the researchers, managers, environmentalists, and other stakeholders participating in this conference to cooperate in a setting characterized by mutual interests, principles, and knowledge. For this to happen requires a recognition of the ecological characteristics of the resource base, the level of ecological knowledge held by the stakeholders, the varied social and economic objectives involved, the heterogeneity of the stakeholders and organizational structures, and the cultures of the people involved. All of these topics will be considered in the conference.

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Northern Sierra Madre Occidental and Its Apachian Outliers: A Neglected Center of Biodiversity[1]

Richard S. Felger and Michael F. Wilson[2]

Abstract.—The Apachian-Madrean region is a zone of confluence and geographic termini of species and floras from the north and the south. Lower and intermediate elevations support many taxa of tropical plants and animals that are at their northernmost limits. It is a region of tremendous habitat diversity and species richness. Much of the region remains little known, and quantified data are scarce. This report offers brief synopses on the insect fauna, ichthyofauna, herpetofauna, avifauna, mammals, and vegetation and flora of the region. The vascular plant flora is estimated to include approximately 4,000 species, although endemism is not particularly high. A partial listing of endemic plants numbers more than 250 taxa. Likewise there are approximately 250 wild relatives of domesticated crop plants. Land race diversity of native crops is richer than in any other American region north of the tropics. A brief economic assessment, descriptions of environmental threats and conservation measures are included.

INTRODUCTION

In the rush to save the rainforest, other biologically rich natural areas have been neglected. The Sierra Madre Occidental of Mexico and its montane outliers in the southwestern United States constitute such a region. While recognized by the International Union for the Conservation of Nature (IUCN) as one of the global megacenters of plant diversity (Felger et al. in press), this region has received far less critical attention from biogeographers and conservationists than it deserves. The purpose of this work is to direct attention to the unusual and diverse biota of this region and to describe the threats to this diversity.

The Sierra Madre Occidental forms a zone of essentially contiguous montane woodland that stretches from southern Mexico nearly to the international border of the United States. Pacific tropical lowlands fringe the greater portion of the western flank while temperate highlands to the east exert a profound continental influence on the inland portions. Conventional classifications of biotic communities necessarily define regions by virtue of their similarities. In contrast, we are more interested in calling attention to a region that is distinguished by a remarkable heterogeneity of habitats. As such, there are no convenient biotic or, for that matter, political or geographic boundaries that allow us to define the region.

We focus on a 180,000 km^2 area situated largely in northwest Mexico, as far south as the Sinaloa border with Sonora and Chihuahua, and northward along the continental divide, roughly at the Sonora-Chihuahua border, to southwestern New Mexico and southeastern Arizona in the United States (fig. 1). The area is about 300 km from east to west (approximately 111 to 107 degrees west longitude), centered on the continental divide. It is 600 km long, spanning an area from

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the mountains of southeastern Arizona and southwestern New Mexico in the United States to the Río Mayo, Río Fuerte and Río Conchos drainages in Sonora and Chihuahua, Mexico (approximately 25 to 32 degrees north latitude). Elevations in this region range from 400 m to more than 3000 m on the highest peaks.

GEOGRAPHY

The region includes two floristic districts of the Madrean province centered on the Sierra Madre Occidental of northern Mexico. This district includes the sky-island ranges such as the Animas, Baboquivari, Chiricahua, Galiuro, Huachuca, Santa Rita, Santa Catalina, and Pinaleño mountains of the United States and the Sierra de los Ajos, Azul, Buenos Aires, Cananea, la Purica, and Mariquita of Mexico, among others. The Apachian district extends northward to the Mogollon Rim in the southwestern United States. Adjacent areas of mid-elevation and sky island peaks in northwestern Mexico form the southern portion of this district which merges with the northern reaches of the Madrean district. Included is the Deming Bridge in the vicinity of the Chiricahua and Animas mountains which is the lowest place on the continental divide between Mexico and Canada. The Madrean district is characterized by the cordilleran flora which begins at the northernmost edge of the Sierra Madre Occidental proper, lying about 150 km south of the United States border. This district extends southward in western Mexico and eventually merges with tropical Mesoamerican regions.

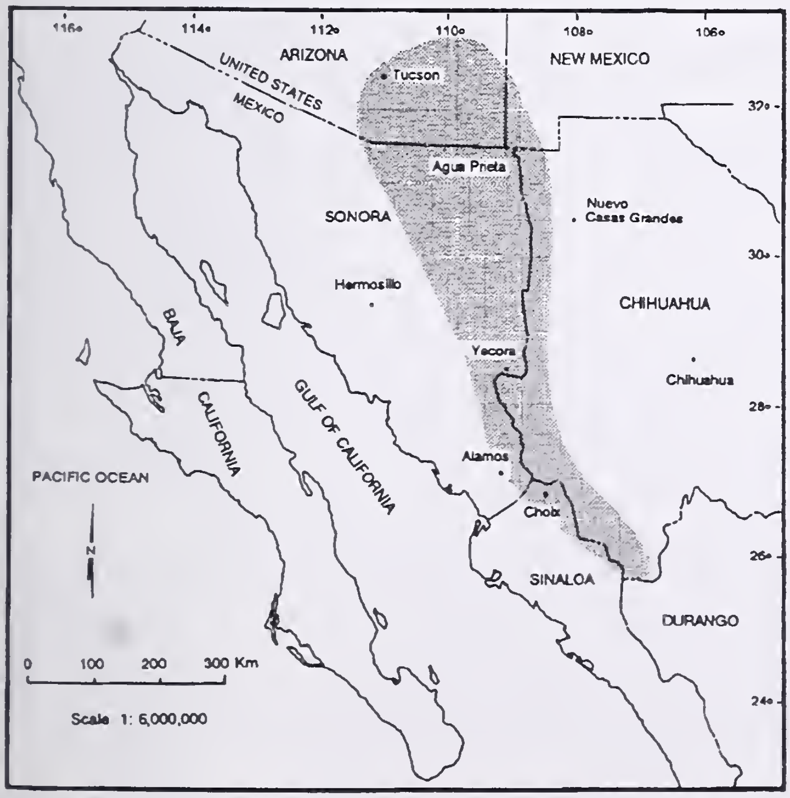

Figure 1.—Northern Sierra Madre Occidental and southern Apachian/Sky Island complex in southwestern North America.

Based upon a land classification study using climatic, geomorphological, and lithological features, Cuanalo et al. (1989) placed the Mexico portion of the Apachian/Madrean Region in the Sierra Madre Occidental Terrestrial Province. Of the 33 subregions distributed in the 10 regions of this province, eight are found in the area covered by the Madrean Region of southwestern North America. They are distinctive enough to warrant special classification: (La1) Arroyo Santísimo; (La6) western portion of the Sierra Madre Occidental; (Lb3) Santiago Papasquiaro; (Lc7) Barranca del Cobre; (Lc8) Yepachic; Tecoragui; (Lf1) Cananea; (Lg2) Nuri; and (Lh5) Chuichupa.

The region is drained primarily by the Río Yaqui, Río Mayo, and Río Fuerte watersheds in the west, and to the east by the Río Bravo (Río Grande) and Río Conchos. The northern outlier archipelago in southeastern Arizona falls largely within the Gila River drainage. Volcanic tuff and Laramide limestones dominate the surface geology.

Precipitation is generally proportional to elevation in the region.Precipitation ranges from roughly 300 to more than 1200 mm/year on the highest peaks, with a summer monsoon predominating in seasonal contribution. The southern portions of the region, particularly at low to mid-elevations, are essentially frost-free, but as one moves northward and upward in elevation, freezing temperatures become common. Moderate to severe winter freezing occurs at the higher elevations.

BIOLOGICAL SIGNIFICANCE

The complex topography and the extreme elevational gradients of the sky island ranges and the northern Sierra Madre Occidental result in a rich flora and fauna (Toledo & Ordóñez 1993). However, it is not merely the individual biotic communities that make the region remarkable, for most of these communities can be found elsewhere and often more extensively. Spanning several degrees of latitude, the character of the region makes for unusual and striking assemblages of habitats. This effect is particularly remarkable for the tropical and subtropical western flanks of the range. The Sierra Madre Occidental acts as a corridor for many taxa. Animals and plants occur here that are more commonly associated with the neotropics than with areas relatively close to the United States border. Species mingle which would otherwise be separated by considerable distance, both geographically and biotically. For example, in canyons of the Río Satachic, near Nacori Chico in northeastern Sonora, maples grow alongside palms and organpipe cacti. In the southern reaches of the region, oaks, pines and alders are host to epiphytic orchids and bromeliads.

With such assemblages of organisms—tropical, temperate, xeric —climatic extremes exert a profound influence, perhaps more often and of a greater magnitude than in more homogeneous communities. Catastrophic frosts occur approximately every ten to fifteen years in portions of the region (Bowers 1980). These events can have devastating effects on animal and plant populations. Areas where subtropical plants show repeated and profound effects of frost are common towards the northern part of the region, and this is visible both locally and on a gross scale. Within a short distance, from cliff-face to arroyo bottom, plant stature and size may change drastically. Pruned by winter frost, shrunken by drought, certain plant species that become formidable trees in tropical lowlands are merely small shrubs in northern Sonora and southern Arizona.

During years of unfavorable weather, frost- or drought-sensitive species may maintain themselves as residual populations in various microhabitats, re-invading neighboring zones during more equitable periods. However, local extinctions during recent times have been well documented for certain groups of organisms, particularly insects (see Bailowitz & Brock 1991). It seems that the generally low level of endemism in most taxa of the region is, in many cases, partially a by-product of a fauna and flora that is in continual ebb and flow between more equitable areas to the south and uncertain habitats to the north. It is not correct to call all these populations "relicts," however, for the more mobile organisms may repeatedly establish, die-off and re-establish themselves. Populations stranded in refugia since the Pleistocene, such as the Mt. Graham red squirrel and the *Tilia* trees at Basaseachic Falls, are indicative of a very different process.

Even so, other phenomena in this region are ultimately unrelated to climate but have effects that are similar and remarkable. On the western side of the sierras, particularly in east-central Sonora, hydrothermally-altered, acidic soils support oaks and pines surrounded by tropical deciduous forest (Goldberg 1982, Búrquez et al. 1992). So well delineated are these zones that one can move from one biotic community to another in but a few steps. These pine-oak or oak communities vary in size from less than one to many hectares in area and are of the same elevation as the surrounding legume-dominated forest. Though they may be several kilometers from the main body of madrean oak woodland, they often have an impressive complement of animals reliant on oaks or pines.

Many species are at the very limit of their ranges within the region. This effect is more striking for tropical organisms than for temperate ones. For while temperate climes and their inhabitants can be found at higher elevations far south of the region discussed here, the tropics of the Americas, under the yoke of winter frost and summer drought, exhaust themselves on the western flank of the northern Sierra Madre Occidental. Consequently, while relatively few animals and plants encounter their southern limits within our region, many more are at their northernmost range here. This phenomenon involves a broad spectrum of organisms - moths as well as birds, trees as well as orchids.

VEGETATION AND FLORA

The evergreen woodlands and forests of the region were derived from more generalized Madro-Tertiary vegetation before the end of the Pleistocene (Axelrod 1979). Despite the commonality of species in genera such as *Pinus*, *Juniperus*, and *Quercus*, there are at least two distinct floristic assemblages of woodland species in the mid- to upper-elevations of the region (McLaughlin 1986). These allied but readily distinguishable floristic elements have been termed the Apachian, designating the northern horseshoe-shaped district rimming the northern Sierra Madre Occidental, but extending as far north as the Mogollon Rim; and the Madrean, designating the more seminal and tropical flora characteristic of the mountains between the Sierra Mohinora and the United States border (McLaughlin 1986, 1989).

Within these two districts, no less than eight physiognomic vegetation types can be found: montane evergreen forest; oak-coniferous (evergreen) woodland; tropical deciduous forest; oak savanna (the oaks mostly drought-deciduous); chaparral; short-grass prairie; subtropical thornscrub; and subtropical desert fringe (Brown 1982, Marshall 1957, Rzedowski 1978). A ninth physiognomic vegetation type (which may be the counterpart of the oak savanna) is the barrancan oak woodland which forms a distinctive, narrow belt on the western slope of the Sierra Madre (Gentry 1942). Three of these types, montane evergreen forest, mixed evergreen woodland, and chaparral, are strongly associated with the Madro-Tertiary flora (Axelrod 1979). The Chiricahua Mountains, the Pinaleños and other northern sky islands have grassland and desert-margin at their bases and coniferous forest including spruce (*Picea*) and fir (*Abies*) at their highest elevations. Two major deserts, the Sonoran and Chihuahuan, reach their limits at the lower flanks of this montane region.

The flora of the Apachian/Madrean Region is the northwestern backbone of the two richest floras of mega-Mexico—which ranks as one of the three top mega-diversity centers of the world. We estimate that there are at least 4,000 vascular plant species within the confines of the region, although no regional summary is available. This estimate is based on the relative size of local and subregional floras (Table 1, also see McLaughlin 1995) and on floristic analyses by Rzedowski (1991, 1993). Most of these local floras fall short of the actual number of species present. For example, in spite of intense investigations over the last half century, the Río Mayo listing is probably only two-thirds to three-quarters complete (Phil Jenkins, pers. comm.). A partial listing of endemic plants in the region totals more than 250 taxa (Appendix 1). New species and infraspecific taxa continue to be discovered as the region becomes better-known botanically.

Table 1. Selected floras from the Apachian-Madrean Region

Area	No. of Species	Reference
Central Sierra Tarahumara	1900	Bye, unpublished
Río Mayo	2100	Martin, in prep.
Parque Nacional, Cascada de Basaseachic	750+	Spellenberg et al., in prep.
Río Bavispe	1100	White 1948
Sierra de los Ajos	est 1000	Fishbein et al., this volume
Chiricahua Mts	1200	Bennett et al., in prep.; Reeves 1976
Huachuca Mts	907	Bowers & McLaughlin, in prep.
Rincon Mts	959	Bowers & McLaughlin 1987
Pinaleño Mts.	786	McLaughlin 1993
Animas Mts	620	Wagner 1977

In terms of species richness per family, the most important families in the region are the Asteraceae (Compositae), Fabaceae (Leguminosae), Poaceae (Gramineae), and Euphorbiaceae. At least 18 families reach their northern limits—at least for western North America—within the region (Appendix 2). Tropical orchids represented by ten genera, including pseudobulb-forming species, also reach their northern limits here as do more than 120 other tropical genera (Appendix 2). Seventy-two percent of the trees of the region are tropical species at the northernmost limit of their range (Felger & Johnson 1995).

The Apachian-Madrean forests contain the largest remaining ponderosa pine ecosystem in southwestern North America that has not suffered fire suppression for most of the twentieth century. Douglas fir and pine tree-ring chronologies from several sites in northern Mexico contain the best known records of the El Niño-Southern Oscillation weather phenomenon (Cleaveland et al. 1992, Stahle & Cleaveland 1993). The El Niño-Southern Oscillation is the most important known cause of interannual variation in the global climate (Folland et al. 1990).

Local extinctions and the status of plants at risk in areas north of the international boundary are relatively well documented (e.g., Folk & Warren 1994), but the status of such plants in Sonora and Chihuahua remains virtually unknown. We can expect loss of biological diversity in the northern Sierra Madre Occidental, in some cases even before taxa are described. For example, the drowning of gigantic and biologically unexplored canyons by the Huites Dam in northeastern Sinaloa will undoubtedly result in extinctions.

USEFUL PLANTS

The region is the richest in wild congeners of domesticated crops of any area north of the Tropic of Cancer. Many of these plants are used and managed by indigenous peoples. Eighteen landraces of pre-Columbian crops occur in the area. Found in native fields, these include endemic domesticates of *Agave, Lepidium* and other mustards, *Hyptis*, and *Panicum*. There are at least 253 wild relatives of domesticated crop plants in the Apachian-Madrean Region (Appendix 3, also see Nabhan 1991, Nabhan & Felger 1985). We estimate that the region supports 700 to 1000 useful wild plants, a few of which are listed in Appendix 4.

Because many communities of the Sierras have persisted in their traditional subsistence activities, much of their extensive botanical knowledge has remained intact. Ethnobotanical inquiries have suggested plant species with potential for economic development. The ethnobotanies of the Guarijio, Mayo, Mountain Pima, Sonoran mestizos and Tarahumara have been studied by Bye (1976), Gentry (1942, 1963), Laferrière (1991), Pennington (1963), Rea (in press), Reina-Guerrero (1993) and Yetman et al. (in prep). To date, we estimate that at least 350 food plants and 600 medicinal plants from this region have been documented ethnographically. These include a considerable number of species belonging to the Agavaceae, Asteraceae (Compositae), Cactaceae, Fabaceae (Leguminosae), Lamiaceae (Labiatae), and Solanaceae.

Important phytochemicals and other properties have been identified from analyses inspired by these ethnobotanies. For instance, the high papain content of *Jarilla chocola* (Tookey & Gentry 1969) has been established, as has the high soluble fiber content of *Hyptis*, *Plantago*, and *Salvia* seed mucilages (Brand et al. 1990). Other utilitarian categories, such as fish poisons used by the Tarahumara, have generated considerable interest (Pennington 1963). The toloache (*Datura lanosa*) of the western barrancas of Chihuahua has the highest content of hyoscine (scopolamine), an alkaloid in great demand by the pharmaceutical industry, of any Mexican species studied (Bye et al. 1991).

Among the regional floras in arid and semiarid southwestern North America, it is estimated that 18 percent of the species have been utilized by people for food and 20 percent for medicinal purposes (Baker et al. in prep., Felger & Nabhan 1978). About 10 percent of the edible species, or 1.8 percent of the flora, served as major food resources (Felger 1979). These estimates, based on compilation of known data, are in line with results from individual ethnobotanical studies (e.g. Bye 1976, 1985; Felger & Moser 1985; Gentry 1942, 1963; Laferrière 1991; Rea in press). For example, the Tarahumara utilized at least 220 species of plants for food. Their pharmacopoeia includes about 300 plant species (Bye 1985) of which 47 are collected and sold in the urban markets of northern Mexico (Bye 1986).

Several potentially important relatives of domesticated crops are endemic to the Sierras, yet the germplasm resources of the region remain undercollected. *Agave, Cucurbita, Phaseolus, Prunus,* and *Solanum* are well-represented in the region, with more than 50 species found here. At Nabogame (near Sierra Mohinora), Chihuahua, the northernmost population of teosinte is disjunct several hundred kilometers from the tropical range of these wild and weedy relatives of maize, where they infrequently introgress with cultivated corn (Doebley & Nabhan 1989). The 21 wild *Phaseolus* taxa in the Sierra Madre Occidental constitute a richer assemblage than found anywhere else north of the Tropic of Cancer (Nabhan 1990a). The maintenance of gene flow between wild and cultivated plants by Tarahumara agroecological practices, which include the management of nearby forest, may be responsible for the development of a productive scarlet runner bean that is adapted to high mountain areas with short growing seasons. In fact, the mosaic of wild montane vegetation and Indian fields has provided ideal settings for studying introgression between wild and domesticated *Capsicum, Cucurbita, Phaseolus,* and *Zea*.

MAMMALS

Approximately 104 mammal species are found in the Apachian district of the Sierra Madre Occidental. The mammalian fauna is a product of a combination of climatic and elevational factors with contributions from two large biogeographic areas. Within this region several species such as the long-tailed vole (*Microtus longicaudus*) and the red squirrel (*Tamasciuris hudsonicus,* as subsp. *grahamensis*) reach the southern limits of their distributions, while species like the Nayarit squirrel (*Sciuris nayaritensis*) and the painted spiny pocket mouse (*Liomys pictus*) reach their northern limits. Some northern species are replaced by southern ones in this area. For instance, the montane shrew (*Sorex monticolus*) of central Arizona is replaced by the Arizona shrew (*Sorex arizonae*) in the sky island complex and the long-eared myotis (*Myotis evotis*) is replaced by the southwestern myotis (*Myotis auriculus*).

This region also functions as a corridor for the continued northward and westward expansion of subtropical species like javelina (*Tayassu tajacu*), coati (*Nasua narica*), "Mexican" opossum (*Didelphis virginiana californicus*) and cotton rats (*Sigmodon* spp.). Recent reports of jaguar (*Panthera onca*) (Girmendonk 1994) indicate continued use of this area as a conduit for occasional northward movement of this animal. The status of the jaguarundi (*Felis yagouaroundi*) in the region is more uncertain. Despite continuing reports of these animals there are still no specimens from Arizona, Sonora or Chihuahua (David Brown, pers. comm.).

Although bat species richness increases further south, our area is well represented with 29 species. Subtropical species include the funnel-eared bat (*Natalis*), naked-backed bat (*Pteronotus davyi*), mustached bat (*Pteronotus pernilli*) and ghost-faced bat (*Mormoops megalophylla*) which reach their northern limits here, while the silver-haired bat (*Lasionycteris noctivagans*) only reaches as far south as the Chiricahua Mountains. Nectar-feeding bats (*Leptonycteris* and *Chaeronycteris*) depend on the nectar and pollen of agaves and other plants in their annual migrations. Other bats take advantage of the area for hibernals or foraging during the tempered winter months.

The construction of dams, declining groundwater levels, clearcutting of forests, farming and grazing has had a profound effect on the mammals of the region. *Cynomys ludovicianus*, the black-tailed prairie dog, was extirpated in Arizona prior to 1940, largely as a result of efforts by ranchers (Hoffmeister 1986). This species still "occurs in large numbers in the Valle de Carretas and other areas in northern Chihuahua and Sonora. In fact their abundance can only be described as awesome, at least periodically" (David Brown, pers. comm.). Some small areas serve as refugia for threatened species such as the southern river otter (*Lutra longicaudis*). The fate of the Mexican wolf (*Canis lupus baileyi*), however, is not clear. This animal is now probably extirpated in Sonora and Chihuahua and reports of individuals in Arizona should be regarded with skepticism (David Brown, pers. comm.). If current trends in land use continue these animals, severely threatened in their natural habitat, will follow the fate of the region's extirpated grizzly bear (*Ursus arctos*).

AVIFAUNA

Approximately 260 to 295 breeding birds are found in the Madrean center and its Apachian outliers. This estimate includes breeding birds in both the valleys and mountains, concentrating on the northern and middle Sierra Madre Occidental, the archipelago of sky islands in the United States, and portions of biotic communities at the bases of montane zones such as tropical deciduous forest.

Over half of the bird species in North America, including Greenland, are found in the Chiricahua Mountains (Kunzman et al. in prep.). As in other groups, many of the bird species of the region are not limited to the northern Sierra Madre Occidental. Many birds of madrean habitats are also found in the southern and eastern sierras as well as lowland tropical areas. In the United States, mountains with oak or pine-oak woodland in southern Arizona, New Mexico and the Chisos Mountains of Texas include several famous locales for sighting madrean bird species. The avifauna of the area is rich. The Madrean region has not been well studied as a migration corridor. However, over a hundred species are known visitants and migrants and the adjacent Pacific lowlands provide a crucial link for various species of hummingbirds and other migrants to their breeding grounds in northwestern North America.

Despite the generally wide area over which madrean habitats can be found, the "middle" Sierra Madre Occidental (sensu Escalante et al. 1993) is a center of bird endemism in Mexico. While there are no endemic bird families in the region, there is endemism at the generic, specific and subspecific levels. At least thirteen bird species are endemic to the northern Sierra Madre Occidental. Four species—the thick-billed parrot (*Rhynchopsitta pachyrhyncha*), Beechy's or purplish-backed jay (*Cissilopha beechii*), tufted jay (*Cyanocorax dickeyi*) and Mexican chickadee (*Parus sclateri*)—reside predominantly within the region. Extensive areas of forest are home to "specialty" birds of the pine-oak regions such as the thick-billed parrot, Mexican spotted owl (*Strix occidentalis mexicanus*), Arizona woodpecker (*Dendrocopos arizonae*), snowy-bellied martin (*Progne dominicensis*), Mexican chickadee, red-faced warbler (*Cardellina rubrifrons*), painted and slate-throated redstarts (*Myioborus picta* and *M. minatus*) and black-headed siskin (*Spinus notatus*).

Several bird families of Eurasian origin encounter their southern limits of distribution either in the northern Sierra Madre or just south of our area—these include the Paridae (titmice and chickadees), Aegithalidae (bushtits), Sittidae (nuthatches), Laniidae (shrikes), and Alaudidae (larks). The northern limits of at least five southern families are found in the region or nearby—these include the Psittacidae (parrots), Cracidae (chachalacas), Momotidae (motmots), Tinamidae (tinamous) and Trogonidae (trogons) with over a dozen other families terminating just south of the area. The Sierra Madre Occidental is the probable center of radiation for jays, woodpeckers, wrens, and ground sparrows (*Melazone*).

Habitat loss is the single most important element affecting bird populations in the Sierra Madre Occidental. The pet trade and hunting are also detrimental, particularly where bird populations have already been compromised by destruction of natural areas. The magnificent imperial woodpecker (*Campephilius imperialis*), which once inhabited mature mountain forests from Sonora to Michoacán, is extinct. Like the ivory-billed woodpecker of the United States, imperial woodpeckers were primarily victims of habitat loss, although unlike the former, hunting by local peoples may have sealed its fate (David Brown, pers. comm.).

ICHTHYOFAUNA

The ichthyofauna of the region, while relatively low in numbers of species in comparison with streams to the east and north, has an interesting and complex biogeographic history. Distributions of fishes with northern affinities, such as the roundtail chub or *charalito aleta redonda* (*Gila robusta*), suckers (*matalotes*) of the *Catostomus insignis/bernardini/conchos* clade, Yaqui catfish or *bagre Yaqui* (*Ictalurus pricei*), longfin dace or *charalito aleta larga* (*Agosia chrysogaster*), and Mexican stoneroller (*Campostoma ornatum*), appear to have been derived, at least in part, through interbasin connections and fragmentations in large, north-south oriented structural troughs which are part of a southerly extension of the Basin and Range Physiographic Province (Hendrickson et al. 1980, Minckley et al. 1986).

The Sonora topminnow or *guatopote de Sonora* (*Poeciliopsis occidentalis*), with southern affinities, has a distribution very similar to that of the longfin dace, ranging from the Río Fuerte to the Gila River. There is high diversity in this genus at lower elevations of the Fuerte and Mayo drainages, where a number of species and a complex of unisexual clones of hybrid origins have been the focus of many important studies in genetics, evolutionary and ecological theory, and conservation biology (e.g., Quattro et al. 1992, Vrijenhoek 1993, Leberg & Vrijenhoek 1994). These topminnows are among the most abundant fishes in low elevation streams where they often occur with the region's only other native freshwater fish of tropical origin, the Sinaloan cichlid or *mojarra de Sinaloa* (*Cichlasoma beani*).

Numerous species of the Yaqui, Mayo and Fuerte drainages were transferred across the continental divide when the headwaters of these rivers eroded into and captured former tributaries of the Rio Grande or endorheic (without outlet to the sea) drainages in Chihuahua (Minckley et al. 1986, Smith & Miller 1986). These include the Mexican stoneroller, beautiful shiner or *sardinita hermosa* (*Cyprinella formosa*), ornate minnow (*Codoma ornata*), Conchos chub or *charalito Conchos* (*Gila pulchra*) and undescribed relatives, Yaqui catfish, fleshylip sucker (*Catostomus leopoldi*), Cahita sucker (*C. cahita*), Rio Grande sucker or *matalote del Bravo* (*C.* [*Pantosteus*] *plebeius*), and an undescribed pupfish or *cachorito* (*Cyprinodon* sp.).

Several species that are found at high elevations apparently evolved by fragmentation of wide ancestral distributions. The presence of trouts in the region during ancient times is indicated by the occurrence of the Mexican golden trout or *trucha dorada Mexicana* (*Oncorhynchus chrysogaster*) in headwaters of the Ríos Fuerte and Culiacán (Needham & Gard 1964, Smith & Miller 6). This species is the apparent sister species of all other trout and salmon of the genus (Stearley & Smith 1993, Stearley 1992). Mountain suckers (subgenus *Pantosteus* of the genus *Catostomus*) likely have similar biogeographic histories (Smith 1992).

The Gila River basin of extreme northern Sonora, southern Arizona and western New Mexico is noteworthy for having a large number of endemic fishes, many of which are now endangered. Two trouts, both listed as threatened in the United States, Gila mountain-sucker (*Catastomus* [*Pantosteus*] *clarki*), and the Sonora sucker (*Catostomus insignis*) are endemic there, as are two small, endangered minnows, the loachminnow or *charalito locha* (*Rhinichthys cobitis*) and the spikedace or *charalito espina* (*Meda fulgida*). The basin also had a suite of Colorado River basin endemics (Minckley et al. 1986). Many of these once occurred in the mainstream Gila and San Pedro rivers of eastern and southeastern Arizona and northern Sonora which flow around the bases of sky islands such as the Pinaleño and Huachuca Mountains. All of these, Colorado squawfish or *salmon blanco* (*Ptychocheilus lucius*), bonytail chub or *charalito elegante* (*Gila elegans*), razorback sucker (*Xyrauchen texanus*), flannelmouth sucker (*Catostomus latipinnis*) and woundfin (*Plagopterus argentissimus*), have been extirpated in the Gila River basin and are critically endangered elsewhere (Minckley & Deacon 1991). Sonora topminnow and desert pupfish (*Cyprinodon macularius*), once both abundant in the middle and lower Gila River, remain as natural populations at only a few springs.

Unfortunately, the destruction of river basins of the western United States (Rinne & Minckley 1991, Moyle & Williams 1990) is being repeated in Mexico. The construction of dams, channeling and diversions is fragmenting populations of the primary freshwater fishes and threatening secondary marine fauna once common to the lower reaches of all major drainages to the Gulf of California. Non-native fishes, primarily sunfishes, catfishes and cichilds, invariably stocked in reservoirs. These exotics, which have had severe effects on native faunas elsewhere in western North America, have spread far from release sites. Some introduced species have hybridized with related native species so that genetically "pure" stock of certain species is now rare. Other threats include grazing and logging which can alter discharge, erosion and sedimentation in ways often detrimental to native fishes far downstream (Hendrickson & Minckley 1985). Unfortunately, lists of endangered, threatened, and extinct Mexican fishes (Williams et al. 1989, Contreras-Balderas & Lozano-Vilano 1994, Secretaría de Desarrollo Social 1994) are already long, are growing rapidly, and include many taxa from our region.

HERPETOFAUNA

This northern portion of the Sierra Madre Occidental, with associated tropical areas to the south and desert areas to the north, is rich in total herpetofaunal diversity although low in numbers of salamander species. There are at least 136 species of amphibians and reptiles in the region (3 salamanders, 29 frogs and toads, 11 turtles, 37 lizards, and 56 snakes) (Bogert & Oliver 1945, Flores-Villela 1993, Heringhi 1969, Stebbins 1985). Eight of those species are endemic to our region.

In this region several genera, a few families and a number of species are at the very northern limits of their distribution in the Americas. The northern casque-headed frog (*Pternohyla fodiens*), Mexican leaf frog (*Pachymedusa dacnicolor*), spiny-tailed iguana (*Ctenosaura hemilopha*), brown vine snake (*Oxybelis aeneus*) and *Boa constrictor* are representatives of genera found at their northern limits in this region. Other notable reptiles and amphibians that are at their northern limits here are the *pichicuate* (*Agkistrodon bilineatus*), green rat snake (*Elaphe triaspis*), spotted box turtle (*Terrapene nelsoni*), ridge-nosed rattlesnake (*Crotalus willardi*), and Mexican beaded lizard (*Heloderma horridum*).

Several species commonly thought of as desert dwellers actually occur in the tropical deciduous forest at their southernmost limits, but extend into arid desertlands in the southwestern United States. These species include the Sonoran desert toad (*Bufo alvarius*), regal horned lizard (*Phrynosoma solare*), zebra-tailed lizard (*Callisaurus draconoides*), western banded gecko, (*Coleonyx variegatus*), tiger rattlesnake (*Crotalus tigris*), saddled leaf-nosed snake (*Phyllorhynchus browni*), and desert tortoise (*Gopherus agassizi*).

Little is known about the status of amphibian populations in our region, especially in Mexico. Declines have been documented in populations of native ranid frogs in Arizona, with some leopard frog species severely affected by introduced predators such as bullfrogs and certain fishes (Clarkson & Rorabaugh 1989, Rosen et al. 1995). The Tarahumara frog (*Rana tarahumarae*) is extinct in the United States and has declined in some populations in northern Sonora, a decline that seems to be related to toxic fallout from copper smelters (Hale et al. in press). However, the greatest threat to the herpetofauna of the region is the clearing and conversion of tropical deciduous forest habitats for buffelgrass pasture.

INSECTS

In contrast to the eastern and southern states of Mexico, the northwestern Mexican states of Sonora, Chihuahua and Sinaloa are poorly known entomologically. It has been only recently that species lists have been produced for areas in the northern Sierra Madre Occidental. On the other hand, the insect faunas of Arizona and New Mexico are comparatively well known. As is most always the case with arthropod surveys, the first species lists generated deal with the more popular and manageable groups of insects, such as the Lepidoptera and Coleoptera.

While few insect families reach the northern limits of their range within the region, dozens of insect genera and hundreds or perhaps thousands of species reach the limits of their distributions here. Expansion and contraction of range is a relatively common phenomenon for a number of species in the region, consequently endemism seems to be rather low for most insect groups in the northern Sierra Madre Occidental. For example, there have been many well-known disappearances of insect species from the sky islands of southeastern Arizona (see Bailowitz & Brock 1991), e.g. Lepidoptera such as *Apodemia* *phyciodoides, Hylesia coinopus, Speyeria nokomis coerulescens,* which in certain cases have been followed by apparent re-establishment of viable populations, e.g. *Gloveria howardi, Heliconius charitonius, Syssphinx raspa.* All these species are resident and abundant to the south. Still others are occasional interlopers from tropical areas, perhaps never able to survive in marginal habitats.

Many prominent tropical lepidopteran genera reach the northern limits of their ranges within our area: *Doxocopa, Heliconius, Hamadryas, Marpesia, Morpheis, Myscelia, Parides, Siproeta,* and many others. The large number of tropical plants found in the region insure that many associated insects are also present. For example, the tropical Brassolid genus, *Opsiphanes,* can be found as far north as the vicinity of Magdalena, Sonora, where the larvae feed upon palms (James Brock, pers. comm.). The Madrean region, specifically the more arid zones of the international border region, has the richest bee fauna in the world (Ayala et al. 1993). Certain epiphytic orchids are dependent upon Euglossine bees for pollination (Dressler 1993). Eluding discovery in the region until recently, *Euglossa* was found near Alamos, Sonora, in 1994 (Andrew Salywon, pers. comm.). The six species of Sonoran *Ficus* trees are accompanied by their obligate pollinators, minute wasps of the Agaonidae (Smith 1994). Trees of the Bombacaceae are at their northern limits in Sonora, as are the saturniid genera *Caio* and *Dysdaemonia* and the giant buprestid *Euchroma,* all of which are dependent upon these plants (Wolfe & Pescador 1994, Hespenheide 1983).

Fifty-two percent of the Sphingidae and approximately 79 percent of the Saturniidae confirmed for the state of Sonora are not found north of our region (Smith 1993, Peigler & Opler 1993). The northernmost populations of leaf-cutter ants (*Atta*) occur in southwestern Arizona (Byars 1949) and can be common in the more subtropical areas of the region, where their nests and middens are often host to passalid and scarabid beetles, various roaches and other commensal insects. The gregarious larvae of the pierid butterfly, *Eucheira socialis,* inhabit silk-pouches which are suspended from the foodplant, madrone (*Arbutus* spp.). The larvae and pupae have served as food for native peoples since prehistoric times (Castelló 1987). The silk of the larval pouches, which resembles chamois, has been used for a variety of utilitarian purposes in Mexico (Peigler 1993). Yaqui, Mayo and other tribes use the cocoons of *Rothschildia cincta* and a few other saturniid moths (Felger & Moser 1985, Peigler 1994) to make rattles which are used for ceremonial purposes. The large paper nests of honey wasps, *Brachygastra,* can be found on rock walls at least as far north as the vicinity of Nacori Chico, Sonora (Peter Jump, pers. comm.). The nests are harvested in Mexico as a wild source of honey.

With the striking examples of principally mesoamerican arthropods in the region, one might expect the presence of species of economic importance. Metallic-green *Haemagogus* mosquitoes, notorious yellow-fever vectors elsewhere (Hogue 1983), are present as are chiggers, fleas, ticks, Simuliid and Tabanid flies, Triatomine bugs, and other potential vectors of disease. While important vector-borne diseases, such as bubonic plague (Hoffmeister 1986) and malaria, are or have been present in Arizona, little work of medical or veterinary concern has been done in the neighboring Mexican portion of the region. Fruit-flies of the genera *Anastrepha* and *Ceratitis* are able to establish themselves on the wide variety of both cultivated and wild fruits. These serious pests are a principal cause of restrictions placed upon international commerce in fruits.

ECONOMIC ASSESSMENT

Although only a few non-timber resources have been investigated for economic potential, cottage industries based on sustainable harvests of wild plants are possible. For example, it has been estimated that during a "dry" year roughly 20 tons of dry fruits of wild chiltepines (*Capsicum annuum* var. *aviculare*) are harvested in the state of Sonora, and that as much as 50 tons might be harvested during a "wet" year (De Witt 1991). The total export to the United States is about 6 tons, where the retail price in 1990 was $72 per pound (Nabhan 1990b).

An important medicinal plant of this region is chuchupate (*Ligusticum porteri, = L. madrensis*). The Tarahumara value the aromatic roots for medicinal and ritual purposes. Its popularity in the medicinal herb markets has increased to the point that over-collection has diminished or driven local populations to extinction. This moisture-and shade-loving species declines as forests are cleared and arroyo heads are eroded. Nevertheless, a local business is based upon the medicinal preparation called "COPANGEL," 2/5 of which is the ground root of this perennial herb. Based upon the retail value of this commercial product, one hectare of chuchupate is worth about $75,000. The roots are currently exported to the United

States, Japan, and Germany. Clinical studies by the Mexican national health program have determined that it is an effective treatment for peptic ulcers (Mundo et al. in press).

Emory Oak (*Quercus emoryi*) acorns, locally called *bellotas*, are wild-harvested each summer in northeastern Sonora and southeastern Arizona. A favorite of Sonorans and many Arizonans, the seeds are eaten fresh. They are sold locally, and in Sonoran markets and in Tucson they can be purchased for about $3.50 kg. Unlike many other kinds of acorns, they are palatable with no preparation due to a relatively low tannin content. These acorns have recently been shown to have an extremely high glycemic index value (Brand et al. 1990). Various other Madrean oaks likewise have "sweet" acorns and represent a potentially significant resource. The current price of acorn meal can be as high as $10 per pound in Korea, and the supply falls far short of the demand.

Several species of columnar cacti in the lowland, subtropical zones in Sonora and Chihuahua yield highly desirable fruits which can be eaten directly, dried or prepared as juice, condiments or wine. They are harvested for local consumption and occasionally reach marketplaces in nearby cities, such as Hermosillo, Sonora. The demand is high, and the vendors usually sell out very early on mornings when the fruit is available. Desirable species include the mountain organpipe or *saguira* (*Stenocereus montanus*) and the organpipe or *pitaya* (*Stenocereus thurberi*). Organpipe jam sells for $15/kg retail. Ten kg of fresh fruit yield one kg of jam. In some regions of northern Sonora, the local Indian people harvest 30 kg of fruit per person. Harvesting of columnar cactus fruit from wild populations by native peoples, at least in a subsistence economy, seems to have virtually no effect on the cactus populations (Felger & Moser 1985, Hastings & Turner 1965).

In recent years eco-tourism has provided a major economic resource for the region. This usually non-destructive industry is growing and expanding rapidly. The Tarahumara region in southwestern Chihuahua is especially popular, as is the Alamos area in southeastern Sonora. Birdwatching brings many people to the region, providing significant income for southeastern Arizona businesses.

THREATS

The remoteness of the rugged Sierras in Mexico with their relatively low human population densities and cultural conservatism have allowed the region to retain much of its ecosystem in a rather natural state. However, in the Sierra Madre Occidental, as in the rest of the world, an ever increasing human population is placing more demands on the environment. While many areas in Arizona and New Mexico are protected for the foreseeable future, certain Arizona mountains and many northern Mexico ranges are in a precarious situation.

Livestock exports to the United States are an important source of revenue for Mexican ranchers. Today, there are few places in northern Mexico free of cattle and goats. Overgrazing has reduced plant cover, hastened soil erosion and aggravated local flooding, with similar problems occurring in areas north of the international boundary. The wholesale clearing and replacement of native vegetation in Sonora and Sinaloa began about 30 years ago. Mexican ranchers continue to seed African buffelgrass (*Pennisetum ciliare*) over large tracts of cleared land. This practice constitutes the most serious cause of desertification in northern Mexico. While the land area devoted to buffelgrass pastures has not been adequately measured, estimates vary between 382,000 and 500,000 hectares for Sonora (Aguirre-Murrieta 1994). Comparable figures are probable for Sinaloa. The conversion to buffelgrass pastures has widespread support by Mexican state and federal governmental agencies and the practice is accelerating. In Sonora alone, government programs call for as much as 6 million additional hectares to be cleared and planted with this grass (Búrquez in press). Buffelgrass is well-suited to areas with little or no frost and a pronounced hot and dry season, therefore tropical deciduous forests are particularly at risk. If this conversion continues, only the most inaccessible tracts of this vegetation will remain in Mexico. Tropical deciduous forests are globally threatened.

Soil erosion has increased where native vegetation has been cleared and converted to farm lands. In subtropical regions there is a long history of slash and burn agriculture for milpas or rozas (cornfields) (Gentry 1942). Unlike large-scale commercial agriculture which is confined mostly to lowlands and valleys, damage caused by slash and burn practices is typical of rural areas and is often evident only in isolated regions. Many milpas occupy slopes of 45 degrees or more. Likewise, the selective cutting of hardwood legumes and other trees and shrubs for cooking fuel, home-heating and other purposes is not without environmental consequences. The cutting of *vara* *prieta* (*Croton* cf. *niveus*) of southeastern Sonora for tomato stakes has made this once common tree scarce (Steinmann & Felger in press.).

Extensive over-harvesting of mesquite (*Prosopis velutina* and *P. glandulosa* var. *torreyana*) and desert ironwood (*Olneya tesota*), for charcoal exported primarily to the United States, threatens lowlands throughout the region (Nabhan & Carr 1994). Many of the subtropical hardwood trees such as amapa (*Tabebuia impetiginosa* and *T. chrysantha*) yield highly prized lumber for roof beams (*vigas*) and fine cabinet-making. The great sabinos or bald cypress (*Taxodium mucronatum*) yield a durable wood which commands a high price. These and many other species are legally protected by the Mexican forestry department but, as in many other remote regions of the world, enforcement is often difficult.

The ever-present demand and shortage of fresh water in nearby desert communities puts a serious strain on the water resources of the region. Every river system in the region has been dammed, and all river deltas have been seriously damaged. The construction of a large dam near Huites, Sinaloa, will create a large reservoir on the middle Río Fuerte, backing up water into the lower reaches of the Barranca del Cobre. Thousands of hectares of riparian habitat will be flooded and much of the remaining tropical deciduous forest and coastal thornscrub are being cleared downstream for concomitant irrigation districts. Other major canyons will certainly be considered as sites for reservoirs.

Northern Mexico's mining history is famous. Spaniards began operation of mines as long ago as 1620. Open pit copper mines at Cananea and Nacozari have been expanded, while others in Sonora are being developed, such as northeast of Cucurpe, the vicinity of Mulatos, and at Piedras Verdes near Alamos. These activities pose a continuing threat to the environment. Air pollution from smelters, such as at Cananea and Nacozari in northeastern Sonora have serious effects on certain animals (Hale et al. in press).

Cultivation of marijuana and opium poppies, usually considered a legal problem, poses a major ecological, social and economic threat. The presence of an armed group of drug cultivators, buyers and distributors is a danger to the local inhabitants, tourists and scientists. Native peoples in the Sierra Madre Occidental have been forced to cultivate and harvest drug crops by criminals from outside the mountain communities. Failure to cooperate with druglords and their underlings has resulted in injury and death (Weisman 1994). Aerial spraying of herbicides by law enforcement agencies to eliminate drug plantations has caused extensive but undocumented and unstudied damage to the native vegetation and flora, and may be a human health hazard. The application of herbicides on Sierra Alamos and elsewhere threatens unique populations of tropical species.

The most dire threats to the sierras are the logging and pulping industries. The heartland of the Sierra Tarahumara presently contains only two percent old growth stands of conifers (Burns et al. 1994). Almost all of the coniferous forests of northern Mexico have been cut one to four times during the twentieth century. Large-scale financing is supporting clear-cutting, harvesting and destruction of understory trees and plants, and pulping of diverse species. A major forestry development project for Chihuahua and Durango proposed by the World Bank (Seedhead News 1991) has been scrapped, but similar projects are likely to be instigated. A large pulp mill at Anahuac, Chihuahua, has been expanded and renovated with a US $350 million loan from the Chase Manhattan Bank. The 1993 North American Free Trade Agreement (NAFTA) will undoubtedly encourage increased exploitation of Mexican raw materials. It will be an international challenge to avert the inevitable environmental problems including loss of biological diversity.

Recently, there have been changes in governmental policy which may counter the increasing awareness of environmental concerns in Mexico. In 1992, Article 27 of the Constitution of Mexico was modified in order that ejidos (communal land-holding organizations) have the option to disincorporate. Ejidos have controlled 70 percent of the land in the northern Sierra Madre since the 1930s. Disincorporation can lead to privatization and sale of forested lands to large corporations. Similarly, Indian ancestral land claims appear to be weakened by recent constitutional changes.

Revision of Mexico's forestry laws have been made that allow "long term leases of forested land to foreign companies. It also would eliminate requirements for environmental impact studies, allow transnational corporations to replace native vegetation with commercial agroforestry plantations of exotic species, and eliminate extraction authorization requirements that provide monitoring of forestry projects and environmental conditions. All of the major NGO and environmental organizations in Mexico have opposed these revisions, maintaining they invade the rights of indigenous peoples and diminish economic benefits to ejidos, indigenous communities, and small forest proprietors." (Burns et al. 1994)

CONSERVATION

Most of the sky island mountains of southeastern Arizona and New Mexico are administered by the United States National Forest Service, which is faced with the conflicting responsibilities of conservation, generating revenue from timber sales, providing leases for grazing and development, and furnishing recreational areas. Interest in development of mountain areas for housing and resorts is of recurrent concern for environmentalists and scientists. The construction of telescopes on Mt. Graham, in the Pinaleño Mountains, has been a source of tremendous dissension among conservationists, U.S. federal agencies and the University of Arizona. A substantial portion of the Huachuca Mountains is protected by incorporation into the Ft. Huachuca Military Reservation. The Gray Ranch in southwestern New Mexico, which includes the Animas Mountains, was purchased by The Nature Conservancy in 1990 and protection continues under the Animas Foundation to which this property has been transferred. The Atascosa, Baboquivari, Chiricahua, Dragoon, Huachuca, Peloncillo, Rincon, Santa Rita, Santa Catalina, and other smaller mountain ranges are protected as Coronado National Forest, U.S. National Monuments, state parks, or a combination of these or other protected designations.

Conservation efforts in Mexico have suffered from underfunding and neglect. Although several areas in northwestern Mexico have special conservation status, enforcement of environmental policy and protection of natural areas has been lax or nonexistent. For instance, in Sonora the Sierra Bavispe, Sierra de los Ajos and the nearby Sierra de la Purica and Sierra Buenos Aires were granted protection during the 1930s. However these areas have not been managed as preserves and, like many other areas that have been given special status, they have not escaped logging or cattle ranching (Búrquez in press).

Mexico, however, maintains a bulwark of governmental agencies that could be very effective in the conservation of natural areas. Many of the mountainous areas in Mexico are under the control of the Mexican federal government, either that of the Secretary of Agriculture (SARH) which manages forest refuges and national parks, or the Subsecretary of Ecology, of the Secretary of Social Development (SEDESOL), which manages the national system of protected areas. Mexico does not lack in its pool of talented and educated individuals who could effect change in environmental policy. Various institutions have been active in attempting to gain or increase protection for new and existing nature preserves.

Preservation of important natural areas can be complemented by land management programs involving local communities. In diverse parts of the region, *in situ* conservation by indigenous and other rural people has been informal but often effective. Some of these activities are becoming formalized. The Arizona Rainforest Alliance, Forest Guardians, the Advisory Council of the Sierra Madre, and the Regional Confederation of the Tepehuan and Tarahumara People are working with a number of Tarahumara and Northern Tepehuan communities to set up a series of community-managed bioreserves in the Sierra Madre Occidental. Many of the indigenous ejidos want to protect their ancestral forests but lack the official mechanism to achieve such measures. Gaining official protection for these areas needs support from all concerned organizations.

The northern Sierra Madre has a few small areas that have been granted special protection such as the Cascada de Basaseachic National Park. There are several designated National Forest Reserves in the four-state area of the northern Sierras, including those at Campo Verde, Papigochic, and Tutuaca, in Chihuahua; the Sierras de los Ajos, Buenos Aires, La Purica and others, in Sonora; and El Centenaria, in Durango. There are also more than a dozen nominally protected forest zones in these states, but these remain areas for multiple use or for recovery after severe overharvesting.

Important areas which have been proposed to receive protection are the Barranca del Cobre with the Barranca Sinforosa, and Sierra Mohinora, Chihuahua; the Sierra Mazatán, Sierra la Mariquita, Mesa El Campañero, Arroyo el Reparo near Yécora, the Sierra Alamos with the upper Río Cuchujaqui region southeast of Alamos, and other areas in Sonora; and the Sierra San Luis on the Sonora-Chihuahua border (Búrquez in press, Felger et al. in press). In addition to the Biosphere reserve at La Michilia, Durango, there are other areas that are worthy of this designation. Notable areas under consideration by local governments for conservation include: Cañón la Cruz del Diablo east of Guasabas, Sonora; the Sierra el Tigre near Huachinera, Sonora; Cañón de Tepoca, Sonora; Laguna de Babichic, Chihuahua; the Llanos de Carretas, Chihuahua; the Sierra Mohinora, Durango; and the Barrancas of the Río Verde.

CONCLUSION

The rugged Madrean region of northern Mexico is complex. Its forests are the largest terrestrial oxygen-biomass producing ecosystems remaining in southwestern North America. The nature of the region is largely one of endpoints, meeting places and overlap—a peculiar combination of xeric, temperate and tropical elements determined by unique combinations of geography, topography, and climate. Remarkable assemblages of biotic communities are frequent here and many organisms are at the very limits of their ranges. Such places are not common on our planet. Our hope is to encourage interest in an area that has often been overlooked by researchers.

Scientific interest in the region will have important ramifications for conservation, for it will be through documentation and publicizing

that protection will be forthcoming. The future of many areas is tenuous. Development is exacting an enormous toll and this is particularly true of the southern portion of the region. We hope that all involved parties—government, business, conservation organizations and the local populace—will have the opportunity and wisdom to act with careful deliberation in their future endeavors.

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Appendix 1. Some Apachian-Madrean endemic or near-endemic plants.

ACANTHACEAE - ACANTHUS FAMILY
Stenandrium pilosulum (Blake) T.F. Daniel
Tetramerium abditum (Brandegee) T.F. Daniel

AGAVACEAE - CENTURY PLANT FAMILY
Agave bovicornuta Gentry
A. jaiboli Gentry
A. palmeri Engelm.
A. parryi Engelm. var. *huachucensis* (Baker) Little
A. parviflora Torr. subsp. *flexiflora* Gentry
A. parviflora subsp. *parviflora*
A. polianthiflora Gentry
A. shrevei Gentry subsp. *magna* Gentry
A. shrevei subsp. *shrevei*
Hesperaloe nocturna Gentry
H. tenuifolia G. Starr ined.
Yucca grandiflora Gentry
Y. madrensis Gentry
Y. schottii Engelm.

ALLIACEAE - ONION FAMILY
Allium plummerae S. Watson

AMARYLLIDACEAE - AMARYLLIS FAMILY
Hymenocallis pimana Laferrière

APIACEAE (UMBELLIFERAE) - CARROT FAMILY
Arracacia edulis S. Watson
Eryngium lemmoni Coult. & Rose
Prionosciadium madrense S. Watson
P. townsendi Rose
Tauschia alloides Bye & Const.
T. bicolor Const. & Bye
T. tarahumara Const. & Bye

APOCYNACEAE - DOGBANE FAMILY
Amsonia grandiflora Alexander
A. kearneyana Woods.
Macrosiphonia brachysiphon (Torr.) A. Gray
M. woodsoniana Standl.

AQUIFOLIACEAE - HOLLY FAMILY
Ilex rubra S. Watson

ASCLEPIADACEAE - MILKWEED FAMILY
Asclepias mirifica Woods.
Cynanchum wigginsii Shinners
Gonolobus gonoloboides (Greenm.) Woods.
Metastelma latifolium Rose

ASPLENIACEAE - SPLEENWORT FAMILY
Woodsia cochisensis Windham

ASTERACEAE (COMPOSITAE) - ASTER FAMILY
Acourtia dieriergeri Cabrera
Alomia stenolepis Blake
Ageratina palmeri (A. Gray) Gage
A. paupercula (A. Gray) R.M. King & H. Robins.
A. sandersii B.L. Turner
A. stricta (A. Gray) R.M. King & H. Robins.
A. yecorana B.L. Turner
A. venulosum (A. Gray) King & Robins.
Berlandiera lyrata A. Gray var. *monocephala* B.L. Turner
Bidens gentryi Sherff
Brickellia betonicifolia A. Gray
B. floribunda A. Gray
B. lemmoni A. Gray
B. lewisii B.L. Turner
B. simplex A. Gray
Carphochaete pringlei (S. Watson) B.L. Turner
Circium basaseachense Nesom
C. rothrockii (A. Gray) Petrak
Cosmos palmeri B.L. Robins.
Erigeron basaseachensis Nesom
E. byei Sundberg & Nesom
E. circulis Nesom
E. dactyloides (Greenm.) Nesom
E. eruptens Nesom
E. fundus Nesom
E. jenkinsii Nesom
E. heliographis Nesom
E. kuschei Eastw.
E. lemmonii A. Gray
E. macdonaldii Nesom
E. mayoensis Nesom
E. mohinorensis Nesom
E. naroiensis Nesom
E. podophyllus Nesom
E. rhizomactus Nesom
E. sceptrifer Nesom
E. strigulosus Greene
Heterotheca rutteri (Rothr.) Shinners
Hieraceum carneum Greene
H. lemmoni A. Gray
Hymenothrix palmeri A. Gray var. *glandulosa* (S. Watson) B.L. Turner
Hymenoxys quinquesquamata Rydb.
Iostephane madrensis (S. Watson) Strother
Laennecia chihuahuana Nesom
L. eriophylla (A. Gray) Nesom
L. pimana Nesom & Laferrière
Lasianthaea podocephala (A. Gray) K. Beeker
Leibnitzia occimadrensis Nesom
Melampodium longicorne A. Gray
Pectis imberbis A. Gray
P. pimana Laferrière & Keil
Perityle batopilensis A.M. Powell
P. cochisensis (Niles) A.M. Powell
P. gentryi A.M. Powell
P. microcephala A. Gray
Pinaropappus junceus A. Gray
P. pooleana B.L. Turner
Plummera ambigens Blake
P. floribunda A. Gray
Senecio mayoensis B.L. Turner
S. tepopana B.L. Turner
Stevia martinii B.L. Turner
Tagetes lemmoni A. Gray
T. palmeri A. Gray
Tomentaurum niveum (S. Watson) Nesom
Tridex erecta A. Gray
Verbesina callilepis Blake
V. gentryi Standl.
V. joyaliae B.L. Turner
Viguiera montana A. Gray
V. ovalis Blake
V. triloba (A. Gray) Olsen
Wedelia chihuahuana B.L. Turner
W. gentryi B.L. Turner
W. pimana B.L. Turner

Xanthocephalum gymnospermoides (A. Gray) Benth. & Hook. var. *eradiatum* M.E. Lane

BERBERIDACEAE - BARBERRY FAMILY

Berberis longipes La Ferr.
B. pimana Laferrière & Marr.

BORAGINACEAE - BORAGE FAMILY

Lithospermum obovatum MacBride

BRASSICACEAE (CRUCIFERAE) - MUSTARD FAMILY

Arabis microsperma Rollins
A. tricornuta Rollins
Draba petrophila Greene var. *petrophila*
D. petrophila var. *viridis* (A.A. Heller) C.L. Hitchc.
D. rubicaulis A.A. Heller
Romanschulzia correllii Rollins
Thelypodiopsis byei Rollins
T. wootonii (Robins.) Rollins var. *parviflora* Rollins
T. wootonii var. *wootonii*

BROMELIACEAE - PINEAPPLE FAMILY

Tillandsia cretacea L.B. Smith
T. elizabethae Rauh

CACTACEAE - CACTUS FAMILY

Coryphantha recurvata (Engelm.) Britt. & Rose
C. robbinsorum (W.H. Earle) A.D. Zimmerm.
Echinocereus adustus Engelm. var. *adustus*
E. bristolii W.T. Marsh.
E. lauii G.R.W. Frank
E. ledingii Peebles
E. rigidissimus (Engelm.) Hort. F. A. Hodge var. *rigidissimus*
E. rigidissimus var. *rubispinosus* (G.R.W. Frank & Lau) N.P. Taylor
E. scheeri (Salm-Dyck) Scheer var. *gentryi* (Clover) N.P.Taylor
E. scheeri var. *obscuriensis* A. Lau
E. stoloniferus W.T. Marsh. var. *stoloniferus*
E. stoloniferus var. *tayopensis* (W.T. Marsh.) N.P. Taylor
Ferocactus alamosanus Britt. & Rose
F. pottsii (Salm-Dyck) Backeb.
Mammillaria barbata Engelm.
M. bocensis Craig var. *movasana* Reppenhagen
M. lindsayi Craig
M. macdougalii Rose
M. meigiana H. Earle
M. saboae Glass var. *goldii* (Glass & Foster) Glass & Foster
M. saboae var. *haudeana* (A. Lau & Wagner) Glass & Foster
M. saboae var. *saboae*
M. sonorensis Craig
M. standleyi (Britt. & Rose) Orcutt var. *standleyi*
M. wrightii Engelm. var. *wilcoxii* W.T. Marsh.
Opuntia santa-rita Griffiths & Hare

CAMPANULACEAE - CAMPANULA FAMILY

Lobelia cordifolia Hook. & Arn.
L. endlichii (F. Wimmer) Ayers
L. knoblochii Ayers

CAPRIFOLIACEAE - HONEYSUCKLE FAMILY

Lonicera cerviculata S.S. White

CARYOPHYLLACEAE - PINK FAMILY

Silene thurberi S. Watson

CHENOPODIACEAE - GOOSEFOOT FAMILY

Atriplex griffithsii Standl.

CISTACEAE - ROCK ROSE FAMILY

Helianthemum chihuahuense S. Watson

CONVOLVULACEAE - MORNING GLORY FAMILY

Ipomoea arborescens (Humb. & Bonpl.) G. Don var. *pachylutea* Gentry
I. thurberi A. Gray
I. chilopsidis Standl
I. tenuiloba Torr. var. *lemmonii* (A. Gray) Yatsk. & C. Mason

CRASSULACEAE - STONECROP FAMILY

Echeveria chihuahuensis von Pollnitz
E. craigiana E. Walther
Graptopetalum bartramii Rose
G. occidentalis Rose & Walther
Sedum lumholtzii Robins. & Fernald
S. madrense S. Watson
S. mellitulum Rose
Tacitus bellus Moran & Meyran

EBENACEAE - PERSIMMON FAMILY

Diospyros sonorae Standl.

EUPHORBIACEAE - SPURGE FAMILY

Croton sp. "Yécora"
Tragia laciniata (Torr.) Müll. Arg.

FABACEAE (LEGUMINOSAE)- LEGUME FAMILY

Acacia millefolia S. Watson
Astragalus gentryi Standl.
A. hypoxylus S. Watson
A. thurberi A. Gray
Coursetia barrancana Lavin
C. glabella (A. Gray) Lavin
Dalea lumholtzii B.L. Robins. & Fernald
D. pinetorum Gentry var. *anilantha* Barneby
D. pinetorum var. *pinetorum*
D. pringlei A. Gray var. *oxyphyllidia* Barneby
D. pringlei var. *pringlei*
D. tentaculoides Gentry
D. tomentosa (Cav.) Willd. var. *mota* Barneby
Lotus alamosanus (Rose) Gentry
Lupinus huachucanus M.E. Jones
L. lemmoni C.P. Smith
Marina alamosana (Rose) Barneby
M. goldmanii (Rose) Barneby
Mimosa grahami A. Gray var. *prolifica* (S. Watson) Barneby
Mimosa guiracobensis Gentry
M. pauli Barneby
Nissolia gentryi Rudd
Phaseolus parvulus Greene
P. salicifolius Piper
P. supinus Wiggins & Rollins
Zapoteca formosa (Kunth) H. Hern. subsp. *formosa*

FAGACEAE - BEECH FAMILY

Quercus tarahumara Spellenb., Bacon & Breedl.
Q. toumeyi Sarg.

GENTIANACEAE - GENTIAN FAMILY

Centaurium gentryi Broome
Gentianella microcalyx (Lemmon) J.M. Gillett

HYDROPHYLLACEAE - WATERLEAF FAMILY

Phacelia arizonica A. Gray

LAMIACEAE (LABIATAE) - MINT FAMILY
Agastache breviflora (A. Gray) Epling
A. mearnsii Woot. & Standl.
A. pallida (Lindley) Kory var. *coriacea* A. Sanders
Hedeoma dentatum Torr.
H. floribundum Standl.
H. oblongifolium (A. Gray) A.A. Heller var. *mexicanum* Irving
Hyptis seemannii A. Gray
Salvia alamosana Rose
S. goldmanii Fernald
S. lemmonii A. Gray

MALVACEAE - MALLOW FAMILY
Anoda succulenta Fryxell
Kosteletzkya thurberi A. Gray
Sida hyalina Fryxell

NOLINACEAE - BEARGRASS FAMILY
Nolina matapensis Wiggins

OLEACEAE - OLIVE FAMILY
Fraxinus gooddingii Little

PASSIFLORACEAE - PASSIFLORA FAMILY
Passiflora quercetorum Killip

POACEAE (GRAMINEAE) - GRASS FAMILY
Bouteloua alamosana Vasey
B. eludens Griffiths
Muhlenbergia capillipes (M.E. Jones) Peterson & Annable
M. dubioides C.O. Goodding
M. xerophila C.O. Goodding
Setaria arizonica Rominger

POLEMONIACEAE - PHLOX FAMILY
Ipomopsis macombii (Torr.) V. Grant
I. thurberi (Torr.) V. Grant
Polemonium glabrum J.F. Davidson
Polemonium sp. (Basaseachic)

POLYGALACEAE - MILKWORT FAMILY
Polygala orthotrica Blake
P. piliophora Blake

PRIMULACEAE - PRIMROSE FAMILY
Primula rusbyi Greene

RANUNCULACEAE - BUTTERCUP FAMILY
Delphinium andesicola Ewan

ROSACEAE - ROSE FAMILY
Potentilla albiflora L.O. Williams
Prunus gentryi Standl.
P. zinggii Standl.

RUBIACEAE - MADDER FAMILY
Crusea wrightii A. Gray var. *wrightii*
Hedyotis spellenbergii Nesom & Vorobik

SCROPHULARIACEAE - SNAPDRAGON FAMILY
Brachystigma wrightii (A. Gray) Pennell
Limosella pubiflora Pennell
Mabrya geniculata (Robins. & Fernald) Elisens subsp. *geniculata*
M. geniculata subsp. *lanata* Elisens
Mimulus pallens Greene
Penstemon fasciculatus A. Gray
P. discolor Keck

SOLANACEAE - NIGHTSHADE FAMILY
Browallia eludens R. VanDevender & P. Jenkins

TILIACEAE - LINDEN FAMILY
Triumfetta chihuahuensis Standl.

VALERIANACEAE - VALERIAN FAMILY
Valeriana apiifolia A. Gray

VERBENACEAE - VERBENA FAMILY
Lippia gentryi Standl.

Appendix 2. Selected, southern (tropical) plant families and genera at their northern limits in western North America.

FAMILIES (genera)

Begoniaceae (*Begonia*)
Bombacaceae (*Ceiba*, *Pseudobombax*)
Bromeliaceae (*Pitcairnia*, *Tillandsia*)
Caricaceae (*Jarilla*)
Clethraceae (*Clethra*)
Cochlospermaceae (*Amoreuxia*, *Cochlospermum*)
Eriocaulaceae (*Eriocaulon*)
Erythroxylaceae (*Erythroxylum*)
Gesneriaceae (*Achimenes*)
Magnoliaceae (*Magnolia*)
Meliaceae (*Cedrella*, *Trichilia*)
Melastomataceae (*Clidemia*)
Myrsinaceae (*Ardisia*, *Myrsine*)
Myrtaceae (*Psidium*)
Olacaceae (*Schoepfia*)
Opiliaceae (*Agonandra*)
Piperaceae (*Piper*)
Zamiaceae (*Dioon*)

GENERA

ACANTHACEAE - ACANTHUS FAMILY
Blechum
Elytraria
Henrya
Pseuderanthemum
Tetramerium

APOCYNACEAE - DOGBANE FAMILY
Mandevilla
Plumeria
Stemmadenia

AMARYLLIDACEAE - AMARYLLIS FAMILY
Sprekelia

ARALIACEAE - GINSENG FAMILY
Oreopanax

ARECACEAE (PALMAE) - PALM FAMILY
Brahea
Sabal

ASCLEPIADACEAE - MILKWEED FAMILY
Pherotrichis

ASTERACEAE (COMPOSITAE) - ASTER FAMILY
Ageratum
Alloispermum
Blumea
Calea

Dahlia
Elephantopus
Jaegeria
Lagascea
Lasianthaea
Milleria
Montanoa
Perymerium
Sclerocarpus
Tithonia
Tridax
Trigonospermum
Wedelia

BIGNONIACEAE - BIGNONIA FAMILY
Tabebuia

BORAGINACEAE - BORAGE FAMILY
Cordia

CACTACEAE - CACTUS FAMILY
Pilosocereus

CELASTRACEAE - STAFF-TREE FAMILY
Schafferia
Wimmeria

CISTACEAE - ROCK ROSE FAMILY
Lechea

COMMELINACEAE - SPIDERWORT FAMILY
Gibasis
Tripogondra

CRASSULACEAE - STONECROP FAMILY
Echeveria

CUCURBITACEAE - GOURD FAMILY
Cremastopus
Cyclanthera
Sechiopsis

EUPHORBIACEAE - SPURGE FAMILY
Dalechampia
Drypetes
Sebastiana

FABACEAE (LEGUMINOSAE) - LEGUME FAMILY
Albizia
Bauhinia
Brongniartia
Conzattia
Leucaena
Lonchocarpus
Lysiloma
Piscidia
Platymiscium

HYDRANGEACEAE - HYDRANGEA FAMILY
Hydrangea

IRIDACEAE - IRIS FAMIY
Tigridia

LAURACEAE - LAUREL FAMILY
Cinnamomum
Persea

LYTHRACEAE - LOOSESTRIFE FAMILY
Cuphea

MALPIGHIACEAE - MALPIGHIA FAMILY
Aspicarpa
Bunchosia
Callaeum

MORACEAE - MULBERRY FAMILY
Chlorophora
Dorstenia
Ficus
Trophis

ONAGRACEAE - EVENING PRIMROSE FAMILY
Gongylocarpus
Lopezia

OPILIACEAE - OPILIA FAMILY
Agonandra

ORCHIDACEAE - ORCHID FAMILY
Bletia
Brassovola
Cattleya
Cuitlauzinia
Cyrtopodium
Encyclia
Govenia
Laelia
Oncidium
Stanhopea

PAPAVERACEAE - POPPY FAMILY
Bocconia

POACEAE (GRAMINEAE) - GRASS FAMILY
Chaetium
Lasiacis
Pennisetum
Pereilema
Otatea

RUBIACEAE - RUE FAMILY
Chiococa
Hintonia
Hamelia
Psychotria
Randia

SAPINDACEAE - SOAPBERRY FAMILY
Paulinia
Serjania
Thouinia

SCROPHULARIACEAE - SNAPDRAGON FAMILY
Buchnera
Escobedia
Lamourouxia
Russelia
Seymeria

SIMAROUBACEAE - SIMAROUBA FAMILY
Alvaradoa

SOLANACEAE - NIGHTSHADE FAMILY
Cestrum
Jaltomata

STERCULIACEAE - STERCULIA FAMILY
Guazuma
Melochia

TILIACEAE - LINDEN FAMILY
Corchorus
Heliocarpus
Triumfetta

ULMACEAE - ELM FAMILY
Aphananthe

URTICACEAE - NETTLE FAMILY
Pouzolzia
Urea

VERBENACEAE - VERBENA FAMILY
Priva
Vitex

VIOLACEAE - VIOLET FAMILY
Hybanthus

Appendix 3. Genetic resources for crop improvement: wild relatives of domesticated, or economically valuable plants.

ACERACEAE - MAPLE FAMILY
Acer glabrum Pursh
A. grandidentatum Nutt.
A. negundo L.

AGAVACEAE - CENTRY PLANT FAMILY
Agave angustifolia Haw. var. *angustifolia*
A. bovicornuta Gentry
A. jaiboli Gentry
A. multifilifera Gentry
A. ocahui Gentry
A. palmeri Engelm.
A. parryi Engelm.
A. parviflora Torr.
A. polianthiflora Gentry
A. schottii Engelm.
A. shrevei Gentry
A. vilmoriniana Berger
A. wocomahi Gentry
Yucca arizonica McKelvey
Y. grandiflora Gentry
Y. madrensis Gentry
Y. schottii Engelm.

ALLIACEAE - ONION FAMILY
Allium cernuum Roth.
A. glandulosum Link & Otto.
A. gooddingii Ownbey
A. kunthii G. Don
A. plummerae S. Watson

AMARANTHACEAE - AMARANTHUS FAMILY
Amaranthus fimbriatus (Torr.) Benth.
A. hybridus L.
A. palmeri S. Watson

ASTERACEAE (COMPOSITAE) - ASTER FAMILY
Helianthus annuus L.
Porophyllum coloratum (H.B.K.) DC.
P. macrocephalum DC.

BRASSICACEAE (CRUCIFERAE) - MUSTARD FAMILY
Lepidium densiflorum Schrader
L. lasiocarpum Nutt.
L. medium Greene
L. thurberi Woot.
L. virginicum L.

CACTACEAE - CACTUS FAMILY
Opuntia engelmannii Engelm.
O. durangensis Britt. & Rose
O. karwinskiana Salm-Dyck
O. robusta Pfeiff.
O. wilcoxii Britt. & Rose

CHENOPODIACEAE - GOOSEFOOT FAMILY
Chenopodium album L.
C. ambrosioides L.
C. incisum Poir.
C. neomexicanum Standl.
C. pratericola Rydb.

CONVOLVULACEAE - MORNING GLORY FAMILY
Ipomoea alba L.
I. ancisa House
I. arborescens (Humb. & Bonpl.) G. Don
I. aristolochiaefolia (H.B.K.) G. Don
I. barbatisepala A. Gray
I. bracteata Cav.
I. cairica (L.) Sweet
I. capillacea (H.B.K.) G. Don
I. cardiophylla A. Gray
I. chilopsidis Standl.
I. costellata Torr.
I. cristulata Hallier
I. fistulosa (Mart.) D. Austin
I. hederacea Jacq.
I. imperati (Vahl.) Griseb.
I. jalapa (L.) Pursh
I. lactescens Benth.
I. laeta A. Gray
I. x*leucantha* Jacq.
I. leptotoma Torr.
I. meyeri G. Don
I. minutiflora (Mart. & Gal.) House
I. muricata (L.) Jacq.
I. nil (L.) Roth.
I. pedatisecta Mart. & Gal.
I. pedicellaris Benth.
I. plummerae A. Gray
I. pubescens Lam.
I. pulchella Roth.
I. purpurea (L.) Lam.
I. quamoclit L.
I. scopulorum Brandegee
I. tenuiloba Torr. var. *lemmonii* (A. Gray) Yatsk. & Mason
I. tenuiloba var. *tenuiloba*
I. turbinata Lag.
I. thurberi A. Gray
I. triloba L.
I. wrightii A. Gray

CUCURBITACEAE - GOURD FAMILY
Cucurbita argyrosperma Huber subsp. *argyrosperma* var. *palmeri* (L.H. Bailey) Merrick & Bates
C. foetidissima H.B.K.
Luffa operculata (L.) Cogn.

DIOSCOREACEAE - YAM FAMILY
Dioscorea remotiflora Kunth
Dioscorea sp.

EBENACEAE - PERSIMMON FAMILY
Diospyros sonorae Standl.

ERICACEAE - HEATHER FAMILY
Vaccinium caespitosum Michx.
V. confertum H.B.K.
V. oreophyllum Rydb.

ERYTHROXYLACEAE - COCA FAMILY
Erythroxylum mexicanum H.B.K.

EUPHORBIACEAE - SPURGE FAMILY
Manihot aesculifolia (H.B.K.) Pohl.
M. angustiloba (Torr.) Müll.Arg.
M. davisiae Croiz.
M. rubicaulis I.M. Johnst.
Manihot sp. (tree)

FABACEAE (LEGUMINOSAE) - LEGUME FAMILY
Canavalia villosa Benth.
Indigofera densiflora Mart. & Gal.
I. macilenta Standl.
I. suffruticosa Mill.
Leucaena lanceolata S. Watson
Phaseolus acutifolius A. Gray var. *acutifolius*
P. acutifolius var. *tenuifolius* A. Gray
P. coccineus L. subsp. *formosus* (Kunth) M.M.& S.
P. coccineus subsp. *glabellus* (Piper) Delgado
P. leptostachyus Benth.
P. falciformis Piper
P. leptostachyus Benth. var. *leptostachyus*
P. leptostachyus var. *micranthus* (Hook. & Arn.) Delgado
P. lunatus L. var. *silvester* Baudet
P. maculatus Scheele subsp. *maculatus* Freytag
P. maculatus subsp. *ritensis* (M.E. Jones) Freytag
P. microcarpus Mart.
P. parvulus Greene
P. pauper Standl.
P. pauciflorus Ses. & Moç.
P. pedicellatus Benth. var. *grayanus* (Woot. & Standl.) A. Delgado
P. pedicellatus var. *polymorphus* (S. Watson) Delgado
P. pluriflorus Mareschal et al.
P. salicifolius Piper
P. sempervirens Piper
P. xantotrichus Piper

GROSSULARIACEAE - GOOSEBERRY FAMILY
Ribes cf. *brandegeii* Eastw.
R. ceriferum Cov. & Rose
R. pinetorum Greene

JUGLANDACEAE - WALNUT FAMILY
Juglans major (Torr.) Heller

LAMIACEAE (LABIATAE) - MINT FAMILY
Hyptis emoryi Torr.
H. mutabilis (Rich.) Briq.
H. seemannii A. Gray
H. septentrionale Epling
H. stellulata Benth.
H. suaveolans (L.) Poit.
Salvia alamosana Rose
S. azurea Lam.
S. betuliifolia Epling
S. cinnabarina Mart. & Gal.
S. elegans Vahl var. *sonorensis* Fernald
S. fluviatilis Fernald
S. goldmanii Fernald
S. greggii A. Gray
S. hispanica L.
S. lasiosepala Hook. & Arn.
S. lemmoni A. Gray
S. melissodora Lag.
S. mexicana L.
S. monantha Brandegee
S. muscaroides Fernald
S. palmeri A. Gray
S. reptans Jacq. var. *glabra* (A. Gray) K.M. Peterson
S. riparia Kunth
S. roscida Fernald
S. seemannii Fernald
S. setosa Fernald
S. tiliaefolia Vahl

LAURACEAE - LAUREL FAMILY
Cinnamomum sp.
Persea podadenia Blake

MALPIGHIACEAE - MALPIGHIA FAMILY
Malpighia emarginata DC.

MALVACEAE - Mallow Family
Gossypium thurberi Todaro

MELIACEAE - CHINA-BERRY FAMILY
Cedrela odorata L.

MORACEAE - MULBERRY FAMILY
Ficus cotinifolia H.B.K.
F. insipida Willd.
F. maxima Mill.
F. pertusa L. f.
F. petiolaris H.B.K.
F. trigonata L.
Morus microphylla Buckl.

MYRTACEAE - MYRTLE FAMILY
Psidium sartorianum (Berg.) Ndzu.

PINACEAE - PINE FAMILY
Abies bifolia A. Murr.
A. concolor (Gordon & Glend.) Hildebr.
A. durangensis Martínez
Pinus cembroides Zucc.
P. douglasiana Martínez
P. durangensis Martínez
P. edulis Engelm.
P. englemannii Carr.
P. herrerae Martínez
P. leiophylla Scheide & Deppe var. *chihuahuana* (Engelm.) Shaw
P. lumholtzii Robins. & Fernald
P. maximinoi H.E. Moore
P. oocarpa Scheide
P. ponderosa Laws. & C. Laws. var. *arizonica* (Engelm.) Shaw
P. ponderosa var. *scopulorum* Engelm.
P. strobiformis Engelm.
Pseudotsuga menziesii (Mirb.) Franco var. *glauca* (Mayr) Franco

PIPERACEAE - PEPPER FAMILY
Piper hispidum Sw.
P. jaliscanum S. Watson

PLANTAGINACEAE - PLANTAIN FAMILY
Plantago alismatifolia Pilger
P. australis Lam. var. *hirtella* (H.B.K.) Rahn
P. argyrea Morris
P. cf. *lanceolata* L.
P. linearis H.B.K.
P. patagonica Jacq.

POACEAE (GRAMINEAE) - GRASS FAMILY
Eragrostis ciliaris (L.) R. Br.
E. erosa Scribn.
E. intermedia Hitchc.
E. maypurensis (H.B.K.) Steud.
E. mexicana (Hornem.) Link subsp. *mexicana*
E. pectinacea (Michx.) Nees var. *miserrima* (Fourn.) J. Reeder
E. pectinacea var. *pectinacea*
Hordeum pusillum Nutt.
Pennisetum karwinskii Schrader
Setaria arizonica Rominger
S. grisebachii Fourn.
S. leucopila (Scrib. & Merr.) K. Schum.
S. liebmannii Fourn.
S. longipila Fourn.
S. pumila (Poiret) Roemer & Schultes
Zea mays L. subsp. *mexicana* (Schrad.) Iltis

RHAMNACEAE - BUCKTHORN FAMILY
Ziziphus amole (Ses. & Moç.) M.C. Johnst.
Z. obtusifolius (Torr. & A. Gray) A. Gray var. *canescens* (A. Gray) M.C. Johnst.

ROSACEAE - ROSE FAMILY
Fragaria ovalis (Lehm.) Rydb.
F. vesca L. subsp. *bracteata* (Heller) Staudt.
Prunus serotina Ehrh. subsp. *capuli* (Cav.) McVaugh
P. serotina subsp. *virens* (Woot. & Standl.) McVaugh
P. emarginata (Dougl.) D. Dietr.
P. gentryi Standl.
P. zinggii Standl.
Rubus arizonensis Focke
R. neomexicanus A. Gray
R. parviflorus Nutt.
R. strigosus Michx.

SOLANACEAE - NIGHTSHADE FAMILY
Capsicum annuum L. var. *aviculare* (Dierb.) D'Arcy & Eshb.
Nicotiana obtusifolia Mart. & Gal.
N. plumbaginifolia Viviani
Physalis acutifolia (Miers) Sandw.
P. angulata L. var. *lanceifolia* (Nees) Waterf.
P. caudella Standl.
P. hederaefolia A. Gray var. *puberula* A. Gray
P. hypophila Standley
P. lagascae Roem. & Schult.
P. leptophylla Robins. & Greenm.
P. pruinosa L.
P. viscosa subsp. *mollis*
Solanum adscendens Mill.
S. americanum Mill.
S. azureum Fernald
S. candidum Lindl.
S. erianthum D. Don
S. fendleri A. Gray
S. ferrugineum Mart. & Gal.
S. geminiflorum Mart. & Gal.
S. grayi Rose var. *grayi*
S. jamesi Torr.
S. heterodoxum Dunal var. *heterodoxum*
S. lumholtzianum Bartlett
S. nigrescens Mart. & Gal.
S. refractum Hook. & Arn.
S. seaforthianum Andrews
S. tridynamum Dunal
S. umbellatum Mill.

VITACEAE - GRAPE FAMILY
Vitis arizonica Engelm.

Appendix 4. Examples of commonly used plants of economic importance.

AGAVACEAE - CENTURY PLANT FAMILY
Agave angustifolia Haw. var. *angustifolia*
A. palmeri Engelm.
A. vilmoriniana Berger
Dasylirion wheeleri S. Watson var. *durangense* (Trel.) Laferrière
D. wheeleri var. *wheeleri*
Hesperaloe nocturna Gentry
Nolina microcarpa S. Watson

APIACEAE (UMBELLIFERAE) - CARROT FAMILY
Eryngium heterophyllum Engelm.
Ligusticum porteri Coult. & Rose

ARECACEAE (PALMAE) - PALM FAMILY
Brahea aculeata (Brandegee) H. E. Moore
Sabal uresana Trel.

ASTERACEAE (COMPOSITAE) - ASTER FAMILY
Acourtia thurberi (A. Gray) Reveal & R.M. King
Cosmos parviflorus (Jacq.) Pers.
C. pringlei Robins. & Fernald
Iostephane heterophylla (Cav.) Hemsl.
I. madrensis (S. Watson) Strother
Lasianthaea podocephala (A. Gray) K. Becker
Parthenium tomentosum DC. var. *stramonium* (Greene) Rollins
Pectis stenophylla A. Gray
Psacalium decompositum (Robins. & Fernald) Robins. & Brett.
Senecio (*Packera*) *candidissimus* Greene
S. (*Roldana*) *sessilifolius* (Hook. & Arn.) Hemsl.
Tagetes filifolia Lag.
T. lucida Cav.
T. micrantha Cav.

BIGNONIACEAE - BIGNONIA FAMILY
Tabebuia chrysantha (Jacq.) Nichols.
T. impetiginosa (A. DC.) Standl.

BOMBACACEAE - SILK-COTTON FAMILY
Ceiba aesculifolia (H.B.K.) Britt. & Baker

BURSERACEAE - FRANKINCENSE FAMILY
Bursera penicillatus (DC.) Engler

CACTACEAE - CACTUS FAMILY
Opuntia engelmannii Engelm.
Opuntia spp.
Pachycereus pecten-aboriginum (Engelm.) Britt. & Rose
Stenocereus montanus (Britt. & Rose) Buxb.
S. thurberi (Engelm.) Buxb.

CARICACEAE - PAPAYA FAMILY
Jarilla chocola Standl.

CHENOPODIACEAE - GOOSEFOOT FAMILY
Chenopodium ambrosioides L.
C. graveolens Willd.

COCHLOSPERMACEAE - COCHLOSPERMUM FAMILY
Amoreuxia gonzalezii Sprague & Riley
A. palmatifida Ses. & Moç.

CONVOLVULACEAE - MORNING GLORY FAMILY
Ipomoea bracteata Cav.

CUCURBITACEAE - GOURD FAMILY
Cucurbita foetidissima H.B.K.

CUPRESSACEAE - CYPRESS FAMILY
Cupressus arizonica Greene
Juniperus deppeana Steud.
J. durangensis Martínez
Taxodium mucronatum Tenn.

EBENACEAE - PERSIMMON FAMILY
Diospyros sonorae Standl.

ERICACEAE - HEATHER FAMIY
Arbutus arizonicus (A. Gray) Sarg.
A. xalapensis Sarg.
Arctostaphylos pungens H.B.K.

EUPHORBIACEAE - SPURGE FAMILY
Croton cf. *niveus* Jacq.

FABACEAE (LEGUMINOSAE) - LEGUME FAMILY
Acacia cochliacantha Willd.
A. farnesiana (L.) Willd.
A. pennatula (Cham. & Schlecht.) Benth.
Brongniartia alamosana Rydb.
Caesalpinia platyloba S. Watson
Erythrina flabelliformis Kearney
Haematoxylum brasiletto Karst.
Lysiloma microphyllum Benth.
Phaseolus maculatus Scheele subsp. *maculatus* Freytag
P. maculatus subsp. *ritensis* (M.E. Jones) Freytag
P. salicifolius Piper
Pithecellobium dulce (Roxb.) Benth.
Platymiscium trifoliata Benth.
Prosopis glandulosa Torr. var. *torreyana* (L.D. Benson) M.C. Johnst.
P. velutina Woot.
Senna atomaria (L.) Irwin & Barneby
Zornia reticulata J.E. Smith

FAGACEAE - BEECH FAMILY
Quercus albocincta Trel.
Q. emoryi Torr.

LABIATAE (LAMIACEAE) - MINT FAMILY
Hedeoma patens M.E. Jones
Mentha arvensis L. var. *villosa* (Benth.) Stewart
Monarda citriodora Lag. subsp. *austromontana* (Epling) Scora

LAURACEAE - LAUREL FAMILY
Cinnamomum sp.

MELIACEAE - CHINABERRY FAMILY
Cedrela odorata L.

MORACEAE - MULBERRY FAMILY
Chlorophora tinctoria (L.) Benth. & Hook. f.
Ficus pertusa L. f.

MYRTACEAE - MYRTLE FAMILY
Psidium sartorianum (O. Berg) Ndzu.

PINACEAE - PINE FAMILY
Abies concolor (Gordon & Glend.) Hildebr.
A. durangensis Martínez
Pinus cembroides Zucc.
P. douglasiana Martínez
P. durangensis Martínez
P. edulis Engelm.
P. englemannii Carr.
P. herrerae Martínez
P. lumholtzii Robins. & Fernald
P. oocarpa Scheide
P. ponderosa Laws. & C. Laws. var. *arizonica* (Engelm.) Shaw
P. ponderosa var. *scopulorum* Engelm.
P. strobiformis Engelm.
Pseudostsuga menziesii (Mirb.) Franco var. *glauca* (Mayr) Franco

POACEAE (GRAMINEAE) - GRASS FAMILY
Bouteloua spp.
Eragrostis spp.
Hordeum pusillum Nutt.
Pennisetum karwinskii Schrader
Setaria spp.
Zea mays L. subsp. *mexicana* (Schrad.) Iltis

POLYGONACEAE - BUCKWHEAT FAMILY
Eriogonum atrorubens Engelm.
E. tenellum Torr.

ROSACEAE - ROSE FAMILY
Potentilla thurberi A. Gray
Prunus gentryi Standl.
P. serotina Ehrh. subsp. *capuli* (Cav.) McVaugh
P. serotina subsp. *virens* (Woot. & Standl.) McVaugh
P. zinggii Standl.

RUBIACEAE - RUE FAMILY
Hintonia latiflora (Ses. & Moç.) Bullock
Randia echinocarpa Ses. & Moç.

SAPINDACEAE - SOAPBERRY FAMILY
Sapindus saponaria L.

SAPOTACEAE - SAPOTE FAMILY
Sideroxylon capiri (A. DC.) Pitt. subsp. *tempisque* (Pitt.) T.D. Penn.
S. persimile (Hemsl.) T.D. Penn. subsp. *subsessiliflorum* (Hemsl.) T.D. Penn.
S. tepicense (Standl.) T.D. Penn.

SOLANACEAE - NIGHTSHADE FAMILY
Capsicum annuum L. var. *aviculare* (Dierb.) D'Arcy & Eshb.
Datura lanosa Bye
Jaltomata procumbens (Cav.) Gentry
Solanum fendleri A. Gray
S. jamesii Torr.

STERCULIACEAE - STERCULIA FAMILY
Guazuma ulmifolia Lam.

VERBENACEAE - VERBENA FAMILY
Lippia graveolens H.B.K.
L. palmeri S. Watson
Vitex mollis H.B.K.

An Overview of the Flora of the Sky Islands, Southeastern Arizona: Diversity, Affinities, and Insularity

Steven P. McLaughlin[1]

Abstract.—The "sky-island" region of southeastern Arizona is roughly coincident with the Apachian District of the Madrean Floristic Province. The region extends to the Pinaleño and Santa Teresa Mountains in the north and to the Baboquivari Mountains in the west. The total flora of this region includes approximately 2100 species of which 166 are exotics. The largest mountain ranges within the sky-island region of southeastern Arizona have local floras possessing about 1/3 to ½ of the regional flora. For their size and elevational range, the Rincon and Huachuca Mountains are comparately rich in species while the Pinaleño Mountains are comparatively depauperate. Based on their distributions within the western United States, the native species of southeastern Arizona can be classified as Madrean (57%), Cordilleran (17%), Sonoran (15%), Californian (6%), and Intermountain (5%). The Madrean element is a heterogenous group of species found mostly south of the international border and reaching their northern limits in southern Arizona; included are species with Chihuahuan, Sierra Madrean, and Neotropical affinities as well as Apachian (sky-island) endemics. Over half of the Madrean species from southeastern Arizona extend to Durango, and about 1/5 reach southern Mexico. In comparison to true insular floras, those of the sky-island region display high species diversity, comparatively low degree of local and regional endemism, and low percentage of exotic species.

INTRODUCTION

Flora refers to the plant species present in a region, irrespective of their importance in the landscape. In other words, flora refers only to the presence of species, not to their dominance or abundance. The study of flora is referred to as floristic plant geography. The purpose of this paper is to discuss the flora of the sky-island region, particularly that of southeastern Arizona, in terms of its diversity, affinities, and insularity.

STUDY AREA

The sky-island region refers to an area consisting of portions of southeastern Arizona, southwestern New Mexico, northeastern Sonoran, and northwestern Chihuahua. This region is characterized by its many small, isolated mountain ranges (fig. 1), covered with oak woodland and, on the higher ranges, pine-oak forest and coniferous forest. These ranges are separated from one another other by plains and valleys covered with desert and desert grassland.

Included in the sky-island region are all the mountain ranges in southeastern Arizona from the Santa Teresa Mountains in the north to the Baboquivari Mountains in the west; the Animas Mountains of southwestern New Mexico are also part of this region. The isolated mountain ranges of northern Mexico display clear physiographic and floristic continuity with those of the southwestern United States. Mountains of northern Mexico that are part of the sky-island system include the Sierra de San Luis, Sierra el Tigre, Sierra de los Ajos, Sierra San Jose, Sierra Cananea, Sierra

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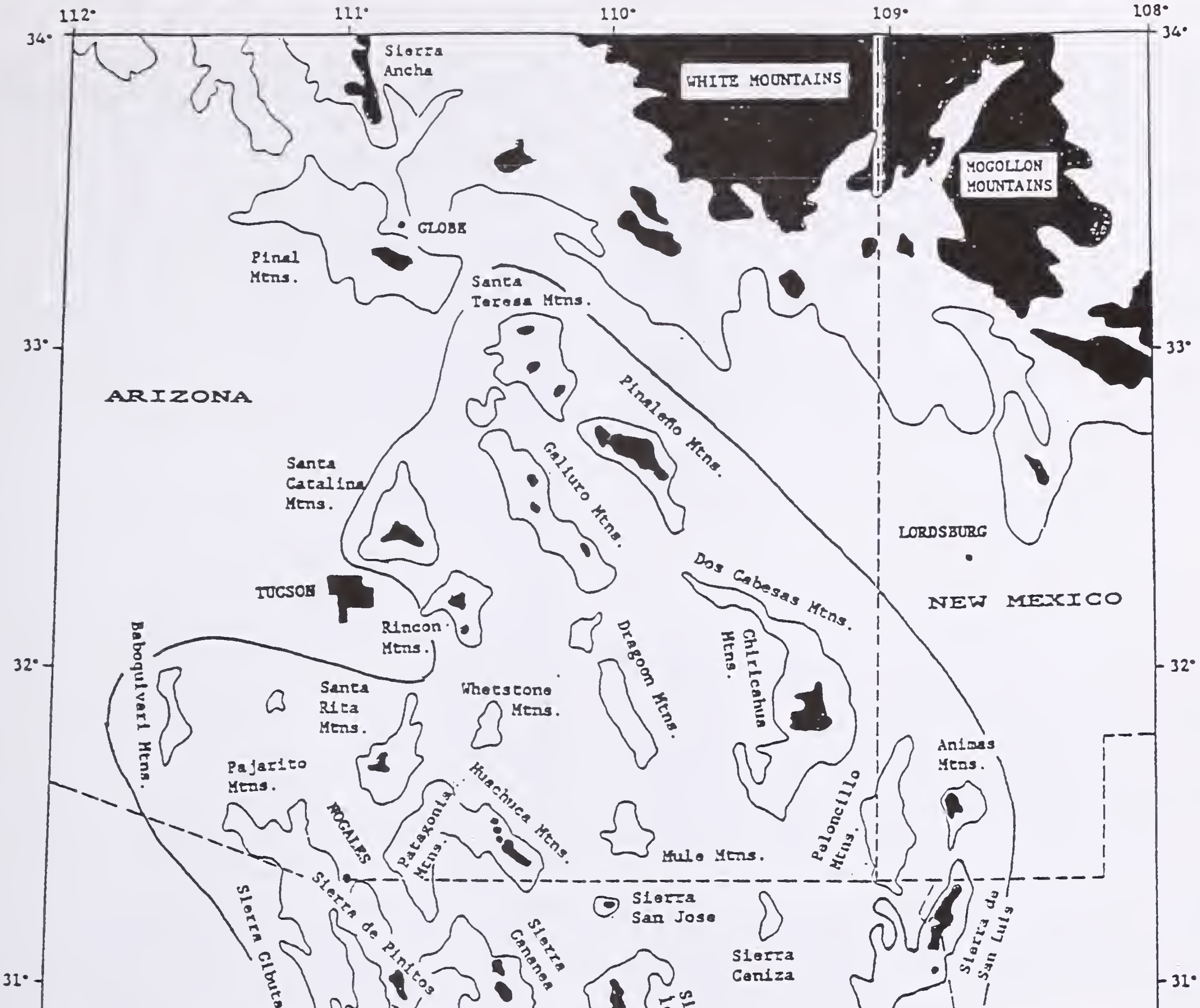

Figure 1.—Map of the sky-island region, southwestern United States and northwestern Mexico. The boundaries for the mountain ranges correspond to the lower elevational limits of the oak woodlands; shaded areas are coniferous forests (after Brown and Lowe, 1980). The approximate boundaries of the Apachian Floristic District are shown; the dashed line in Mexico indicates greater uncertainty in the exact placement of this boundary.

Azul, and Sierra de Pinitos (fig. 1). It is not clear, however, exactly where the southern boundary of the sky-island region should be placed on floristic grounds. I separate it at the point where woodland and forest vegetation form a continuous cover in the northern Sierra Madre Occidental (fig. 1).

The sky-island region has a semi-arid climate with biseasonal precipitation. Percent summer rainfall increases from northwest to southeast across the region. Total annual precipitation generally decreases from west to east in southeastern Arizona (McLaughlin, 1992b, 1993).

DIVERSITY

Diversity refers to the number of species in a particular area. Diversity can be analyzed on several scales (Whittaker, 1977): (1) *alpha* diversity, the number of species in a plot or community, generally 10-100 species; (2) *gamma* diversity, the number of species in a landscape, usually 100-1000 species; and (3) *epsilon* diversity, the number of species in a region, generally more than 1000 species. I apply Whittaker's (1977) concept of *epsilon* diversity to that of areas the size of floristic districts and larger, and *gamma* diversity to that of local floras. In the case of the sky-island region, *epsilon* diversity refers to the diversity of the entire region, while *gamma* diversity refers to the diversity of the individual mountain ranges (or other comparable areas) making up the sky-island region. In addition to these inventory diversities, *beta* diversity and *delta* diversity refer to change in species composition between plots or communities within a landscape, and between landscapes within a region, respectively (Whittaker, 1977).

Diversity (*Alpha*) of Plant Communities

Whittaker and Niering (1975) examined species diversity over the elevational gradient of the Santa Catalina Mountains. They found that the highest diversities were not in the most mesic, highest-productivity forests, but in the open communities at mid elevations—in woodlands, grasslands, and the spinose-suffrutescent desert (Table 1). Lowest *alpha* diversity was found in ponderosa pine forest and in the lower bajada (creosote bush) desert. Wentworth (1982), working in the Mule Mountains, also recorded maximum species diversity in oak woodlands and grasslands. The patterns of species diversity on southwestern mountain ranges have been interpreted as an example of high diversity at intermediate productivity. It is more likely that gradients of decreasing diversity with increasing aridity (downslope) and decreasing area (upslope) interact to produce high diversities at midslope.

Table 1.—Plant-community diversity (0.1 ha plots) in the Santa Catalina Mountains (from Whittaker and Niering, 1975).

Community-type	Elev. (m)	No. of Species
Corkbark fir forest	2720	15
Douglas fir-white fir forest	2640	16
Douglas fir forest	2650	10
Ponderosa pine-white pine forest	2740	13
Ponderosa pine forest	2470	8
Ponderosa pine-silverleaf oak forest	2180	12
Pine-oak woodland	2040	18
Pygmy conifer-oak scrub	2040	20
Open oak woodland	1310	58
Desert grassland	1220	46
Spinose-suffrutescent desert	1021	41
Upper Bajada desert	870	33
Lower Bajada desert	760	6

Plant ecologists often measure *alpha* diversity in 0.1 ha plots. Temperate North American sites typically average 20-30 species/0.1 ha (Whittaker, 1977; Gentry, 1988). Oak woodlands and grasslands in the sky-island region display comparatively high *alpha* diversity (40-60 species/0.1 ha plot) while forest communities have comparatively low *alpha* diversity (10-20 species/0.1 ha). Plant communities from neotropical sites typically have *alpha* diversities of 100-250 species/0.1 ha plot (Gentry, 1988).

Diversity (*Gamma*) of Local Floras

Patterns of *gamma* diversity can be investigated by examining the numbers of species in local floras. Many biogeographers have noted that the number of species increases in a regular manner as a function of the amount of area sampled. A log-log plot of the number of species vs. area is generally a straight line. Bowers and McLaughlin (1982) compared species diversity in 20 local floras from throughout Arizona. They found that elevation range, rather than area, provided the best predictor of species diversity. Species diversity increases with increasing habitat diversity, which, in mountainous areas, is more closely related to elevation range than to areal extent.

A number of local floras have been compiled (or are in progress) for different sites in southeastern Arizona (Table 2), including four of the larger ranges—the Pinaleño Mountains, Huachuca Mountains, Rincon Mountains, and Sierra el Tigre. Number of species in this discussion refers to the number of native species only—naturalized exotic species are excluded. Patterns in *gamma* diversity within the sky islands region are shown in fig. 2, which displays species number vs. elevation range for the 13 local floras listed in Table 2. There is a stronger relationship between species number and elevational range (r = 0.653, p = .016) than between log species and log area (r = 0.514, p. = .072), as previously observed by Bowers and McLaughlin (1982).

Of the four large ranges, the Rincon Mountains (Bowers and McLaughlin, 1987) and Sierra el Tigre (White, 1948) have the largest floras. The compilation of the Huachuca Mountains flora is still in progress (Bowers and McLaughlin, this symposium). The Huachucas have a lower total elevation range than the Rincons and their flora is correspondingly smaller. The Pinaleño Mountains (McLaughlin, 1993) have the greatest elevation range, yet their flora is smaller than those of the three other large ranges. Shreve (1919) pointed out that in the Pinaleños there are few sharply cut and well-watered canyons. Bennett and Kunzmann (1992) found an association between topographic "roughness" and plant-species richness among 6 mountain ranges from the southwest. In comparison to other sky-island ranges, the Pinaleños also seem to be somewhat drier (Martin and Fletcher, 1943; McLaughlin, 1993).

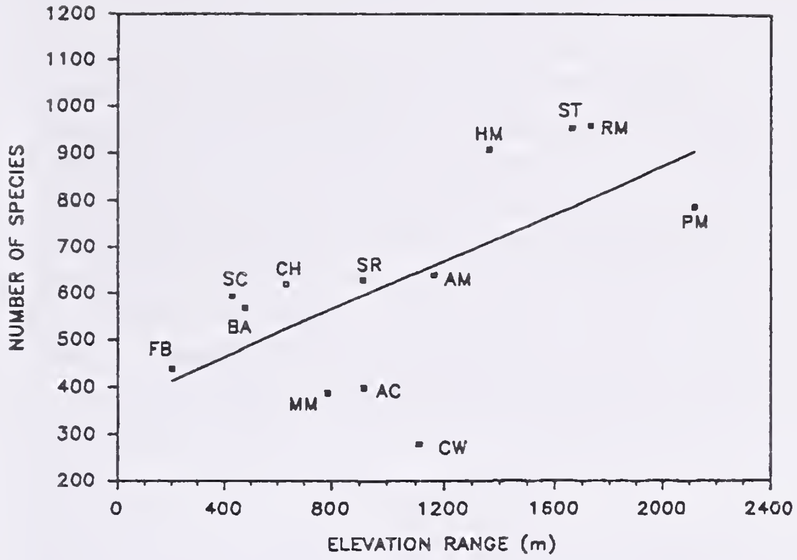

Figure 2.—Relationship between number of native species and elevation range for 13 local floras from the sky-island region. Abbreviations are: AC, Aravaipa Canyon; AM, Animas Mountains; BA, Buenos Aires National Wildlife Refuge; CH, Chiricahua National Monument; CW, Chiricahua Wilderness; FB, Fort Bowie National Historic Site; HM, Huachuca Mountains; MM, Mule Mountains; PM, Pinaleño Mountains; RM, Rincon Mountains; SR, Northern Santa Rita Mountains; SC, Sycamore Canyon; and ST, Sierra el Tigre.

Sycamore Canyon Natural Area (Toolin et al., 1980) and the Buenos Aires National Wildlife Refuge (McLaughlin, 1992b) have relatively large floras for their narrow elevation ranges. Both are situated in the relatively wet southwestern section of southeastern Arizona. The Sycamore Canyon flora illustrates the high *gamma* diversity of major canyon environments with their varied array of microhabitats. Chiricahua National Monument (Reeves, 1976) also contains several major canyons. While Buenos Aires National Wildlife Refuge does not span a great elevational range, it does have a large areal extent with many scattered aquatic and wetland habitats.

The floras for Fort Bowie National Historic Site (Warren et al., 1992), the northern Santa Rita Mountains (McLaughlin and Bowers, 1990), and

Table 2.—Local floras from the Apachian Floristic District.

Flora	Number of species	Elevations High	Low	Range
Rincon Mountains	959	2643	915	1728
Sierra el Tigre	953	2360	700	1660
Huachuca Mountains	907	2887	1525	1362
Pinaleño Mountains	786	3267	1150	2117
Animas Mountains	638	2597	1433	1164
Northern Santa Rita Mountains	628	1919	1006	913
Chiricahua National Monument	619	2230	1598	632
Sycamore Canyon Natural Area	593	1464	1037	427
Buenos Aires National Wildlife Refuge	568	1401	926	475
Fort Bowie National Historic Site	438	1600	1400	200
Aravaipa Canyon	398	1678	763	915
Mule Mountains	387	2248	1464	784
Chiricahua Wilderness	287	2988	1876	1112

the Animas Mountains (Wagner, 1977) all lie approximately on the regression line of fig. 2. The Mule Mountains (Wentworth, 1982) and Aravaipa Canyon (Warren and Anderson, 1980) appear to be somewhat species poor; both floras are probably under-collected. The notable outlier in fig. 2 is the flora for the Chiricahua Wilderness (Leithliter, 1980), which covers the upper elevations of the Chiricahua Mountains. The high elevations of the sky islands are notably depauperate at the community level (Whittaker and Niering, 1975) and apparently at the landscape level, also.

The *gamma* diversity of sky-island floras is compared with those from other floristic districts in the western United States in figs. 3-4. McLaughlin (1992a) used a data base of 101 floras from the western United States to identify 20 floristic districts (see FLORISTIC AFFINITIES, below). In fig. 3 the average number of native species is plotted as a function of average area for each district; in fig. 4 average species number is plotted against average elevation range. Five floras from the sky-island region (the Apachian District) were included in this analysis. The plot of average species number vs. average area (fig. 3) for this sample shows a weak species-area relationship. The Apachian floras have the second highest diversity in fig. 3 despite representing a comparatively small average area.

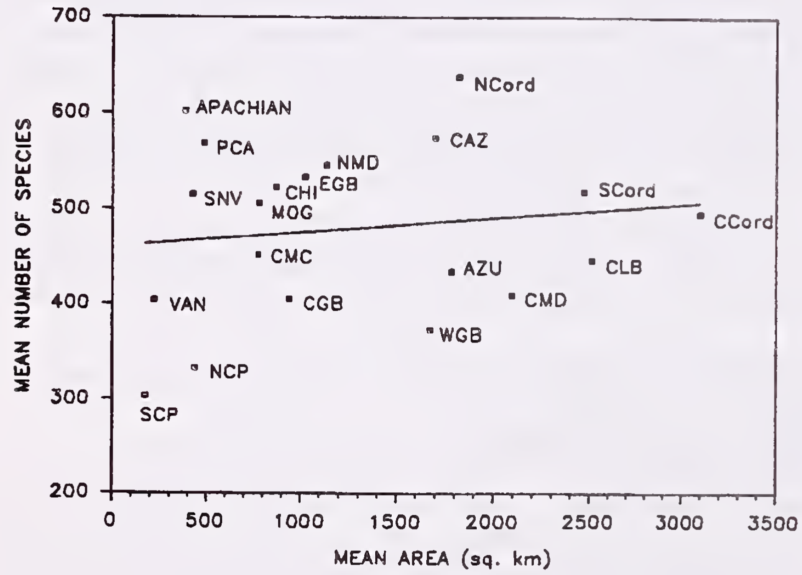

Figure 3.—Relationship between average number of native species and average area of local floras in 20 floristic districts from the western United States. Abbreviations are: AZU, Arizona Upland; CAZ, Central Arizonan; CCord, Central Cordilleran; CGB, Central Great Basin; CHI, Chihuahuan; CLB, Columbia Basin; CMC, Cismontane California; CMD, Colorado-Mojave Desert; EGB, Eastern Great Basin; MOG, Mogollon; NCord, Northern Cordilleran; NCP, Northern Colorado Plateau; NMD, Northern Mojave Desert; PCA, Peninsular California; SCord, Southern Cordilleran; SCP, Southern Colorado Plateau; SNV, Sierra Nevada; VAN, Vancouverian; and WGB, Western Great Basin.

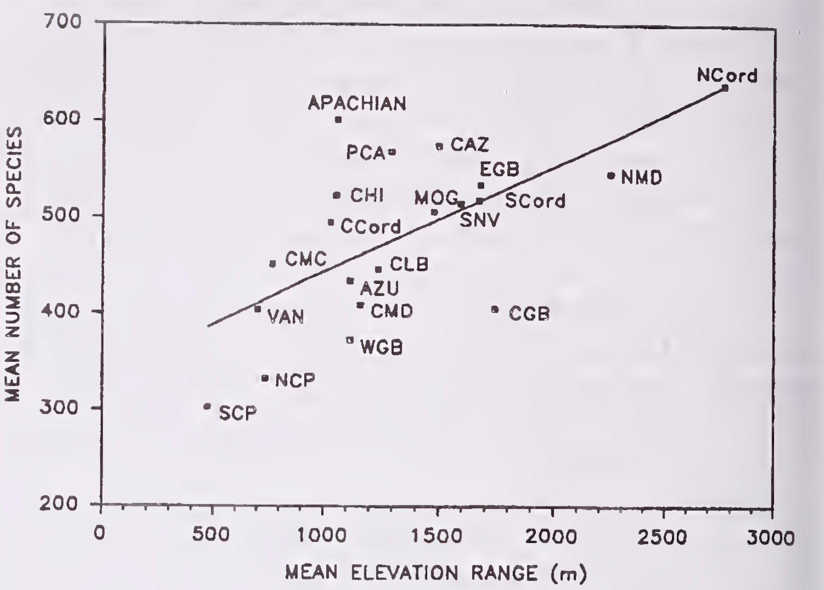

Figure 4.—Relationship between average number of native species and average elevation range of local floras in 20 floristic districts from the western United States. *Abbreviations are as in fig. 3.*

The plot of average species number vs. average elevation range (fig. 4) shows a much stronger relationship. The group of 5 Apachian floras stands out as being farthest above the regression line. This figure shows that Apachian local floras have the highest average diversity, when corrected for elevation range, of all floristic districts from the western United States. The 5 floras included in this analysis had an average of 602 species and an elevation range of 1056 m; the sample of 13 Apachian floras in Table 2 spans a similar average elevation range (1038 m) but has somewhat higher average diversity (627 species).

The high *gamma* diversity in the sky-island region is a consequence of both the high *alpha* diversity of some of its plant communities (Table 1) and high *beta* diversity. Temperature and precipitation change rapidly over short map distances on mountain ranges in the sky-island region, leading to rapid species turnover and community change. Stated in another way, the region has very high ecosystem-level diversity.

Total Diversity (*Epsilon*) of the Sky-island Region

The flora of the sky-island region within the United States is reasonably well known. I have compiled a preliminary checklist of this flora, based both on written works (local floras, regional treatments, monographs) and collections housed at the University of Arizona herbarium. The total flora of the sky-island region in southeastern Arizona, an area of approximately 40000 km^2, consists of approximately 1940 native and 166 exotic species (Table 3). The largest families are the Asteraceae (308 native spp.), Poaceae (204 native spp.), Fabaceae *sensu lato* (161 native spp.), Cyperaceae (71 native spp.), Euphorbiaceae (57 native spp.), and Scrophulariaceae (52 native spp.).

Southeastern Arizona represents only about half of the sky-island region (fig. 1). The size of the entire flora of the region is not known. There are 225 species in the flora of the Bavispe region (White, 1948) that do not occur in the sky-island region of southeastern Arizona. The total number of sky-island species not found in Arizona is likely to be between 2 and 4 times this number, giving an estimate for the regional flora of ca. 2300-2800 species.

FLORISTIC AFFINITIES

Affinity refers to the geographical relationships of the flora. Species may be either endemic (restricted to the area under consideration) or occur both within and outside the area. In a local or regional flora endemics generally constitute a small proportion of the total number of species. The nonendemics can be classified, either subjectively or objectively, into floristic elements — groups of species with more or less coincident ranges. It is then possible to determine which floristic elements make up a significant proportion of any particular flora and how the spectrum of floristic elements varies with latitude, longitude, elevation, substrate, and other environmental factors. Such an analysis of floristic affinities using floristic elements simplifies the comparison of floras within and between regions. It may also be helpful in understanding the phytogeographic history of a region.

Table 3.—Summary of the flora of the Apachian Floristic District in southeastern Arizona.

Taxon	Native Spp.	Exotic Spp.	Total Spp.
Ferns and Fern Allies	67	0	67
Gymnosperms	17	0	17
Flowering Plants			
Dicotyledons	1477	108	1585
Monocotyledons	377	58	435
TOTAL	1938	166	2104
Largest Families:			
Asteraceae	308	20	328
Poaceae	204	56	260
Fabaceae	161	10	171
Cyperaceae	71	1	72
Euphorbiaceae	57	2	59
Scrophulariaceae	52	8	60
Cactaceae	42	0	42
Malvaceae	39	1	40
Lamiaceae	35	5	40
Boraginaceae	35	0	35
Convolvulaceae	34	1	35
Brassicaceae	33	10	43

Shreve (1915) was the first to discuss the affinities of the flora of southeastern Arizona in any detail. He noted that the plants of the desert have strong affinities with the floras of the Sonoran and Chihuahuan deserts and almost no relationship to those of the Mojave and Great Basin deserts. The flora of the encinal (oak woodland) region of the Santa Catalinas appeared to Shreve to be related to that of the Sierra Madre of northwestern Mexico and the Great Plains. The forest flora appeared to have affinities both with the Rocky Mountains to the north and the mountains of Mexico to the south. Shreve also noted that there was a distinct endemic element in the forest flora, i.e. species restricted to the isolated ranges of southern Arizona and New Mexico.

The phytogeography of the higher elevations of the sky islands has received much attention. Moir and Ludwig (1979) felt that the floristic affinities of the mixed-conifer and spruce-fir forests of Arizona and New Mexico were primarily with the northern Cordillera (Petran) region, i.e., the Rocky, Cascade, and Sierra Nevada mountains. Muldavin and DeVelice (1987) classified all plant species found in their montane habitat-type plots as Petran, Madrean, Southwest Endemics, or other; they found that spruce-fir and white fir forests are strongly Petran in floristic composition, Douglas fir and ponderosa pine forests contain a mix of Petran and Madrean species, and Apache pine and Chihuahua pine forests (i.e., the pine-oak woodlands), are strongly Madrean.

Robinson (1968) noted that Madrean species (taxa with southern affinities) form an important element in the high-elevation flora of the Chiricahua Mountains, particularly on south-facing slopes. In the lower-lying Rincon Mountains, species with Madrean affinities predominate at all elevations (Bowers and McLaughlin, 1987); even above 2300 m species with northern affinites account for less than half of the flora.

Whittaker and Niering (1964) were the first to attempt to define a comprehensive set of floristic categories for southeastern Arizona. Using regional manuals and herbarium records, they grouped species into "areal types" as a means of analyzing the floristic affinities of the plants of the Santa Catalina Mountains. These areal types group species by pattern of geographic distribution, i.e., they are essentially geographic elements. This subjective classification has been used in other studies (Bowers, 1980; Wentworth, 1982, 1985).

Whittaker and Niering (1965) found, in agreement with Shreve (1915), that their Rocky Mountain, Temperate, Northern, and Holarctic areal types—those with northern affinities—were best represented at high altitudes. Their Madrean areal type was most abundant at mid-latitudes in the oak and pine-oak woodlands, and their Sonoran and Latin American areal types predominated at low elevations. Endemics appeared to be uniformly distributed at all elevations above 915 m (Table 4).

Whittaker and Niering (1965) stated that the affinities of the desert grassland were with the short-grass plains east of the Rocky Mountains. They placed relatively few species in their Plains areal type, however, and although these were most abundant in the desert grassland, the overall affinities of the desert grasslands were similar to those of the open oak woodlands.

The Chihuahuan areal type was not well-represented in the flora on the south side of the Santa Catalinas. Whittaker and Niering (1968) found more species with Chihuahuan affinites on limestone on the northern side of the range between 1830-2135 m. Wentworth (1981) compared the floras of granite and limestone substrates in the Mule Mountains and found an even stronger pattern. Granite slopes had a high percentage of Madrean species while limestone slopes had a high proportion of Chihuahuan species. Wentworth concluded that the Mules represented the northwesternmost extent of Chihuahuan desert vegetation and flora. Wentworth (1985), however, found relatively small proportions of Chihuahuan species on higher-elevation limestone sites in the Huachuca Mountains.

McLaughlin (1992a) developed a hierarchical system of floristic elements and floristic areas using factor analysis, an ordination technique, with presence-absence data from 101 local floras from the western United States. This data base was divided into three subsets: narrow species, those occurring in 9 or fewer local floras; regional species, those occurring in 10-19 local floras; and widespread species, those occurring in 20 or more local floras. Five floristic areas were defined for the widespread species, nine for regional species, and 20 for narrow species. The floristic areas defined at these different scales were nested in a hierarchical manner, and corresponded to traditional phytogeographic categories—provinces, subprovinces, and districts, respectively, for widespread, regional, and narrow species. Floristic elements corresponding to each floristic area can be determined indirectly from the ordination of floras (McLaughlin, 1994).

The 5 floristic provinces in the western United States are the Cordilleran Province, including the Rocky Mountains, Cascade Mountains, the higher ranges of the central Great Basin, and the northwestern part of California; the Intermountain Province, including most of the Great Basin, the Columbia Plateau, the Colorado Plateau, and the Wyoming Basin; the Sonoran Province, including both the Sonoran and Mojave desert areas; the Californian Province, including the cismontane portions of California exclusive of the northwestern coastal area, and the Madrean Province. The

Table 4.—Floristic affinities of vegetation zones within the Santa Catalina Mountains (Whittaker and Niering, 1965). Data in the table are the total numbers of species found in all study plots of each vegetation type over the elevation al gradient. The spruce-fir forests are actuall from the Pinaleño, not the Catalina Mountains. Abbreviations for areal types are: RM, Rocky Mountain; W, Western; H, Holarctic; N, Northern; T, Temperate; MA, Madrean; SW, Southwestern; P, Plains; CH, Chihuahuan; LA, Latin American; SO, Sonoran; and End, Endemic.

Vegetation	Elev. (m)	RM	W	H	N	T	MA	SW	P	CH	LA	S0	End	Total
Spruce-fir	2950-3260	13	5	2	3	3	2	4					2	35
Mixed-conifer	2740-2920	11	13	4	4	2	2	7			1		3	47
Pine forest	2440-2740	11	9	1	1	5	11	11	1				5	55
Pine-oak forest	2130-2440	9	6	1	1	3	17	18	1		1		2	59
Pine-oak woodland	1830-2130	6	3	1		1	19	19	1	1	2		3	56
Pygmy conifer-oak	1520-1830	2	3				23	28	1	1	4	1	3	66
Open oak woodland	1400-1700	1	4	1		1	22	38	4	2	9	6	4	92
Desert Grassland	1220-1700	1	2	1		1	17	39	6	5	13	15	5	105
Spinose Desert	915-1220		1	1		1	4	33	2	4	12	21	3	82
Upper Bajada Desert	850		1					20	1	6	5	11		44
Lower Bajada Desert	760		1					12		1	4	4		22

Table 5.—Floristic affinities of the flora of the sky-islands region of southeastern Arizona. Numbers are percentages of the total flora of each area. Abbreviations for floristic elements are: MAD, Madrean; CORD, Cordilleran; SON, Sonoran; INT, Intermountain; CAL, Californian; APA, Apachian; CHI, Chihuahuan; AUP, Arizona Upland; and MOG, Mogollon.

Flora	All Species:						Narrow Species:		
	MAD	CORD	SON	CAL	INT	APA	CHI	AUP	MOG
Total Flora of Sky-island Region in SE Arizona	57.2	17.4	15.1	5.6	4.7	30.9	9.2	6.4	5.5
Pinaleños, above 2745 m	20.8	74.3	0.0	1.2	3.7	9.0	0.4	0.0	14.7
Chiricahua Wilderness	57.0	36.6	0.7	3.9	1.8	30.5	2.1	0.0	10.8
Pinaleño Mountains (all)	52.7	27.2	10.7	4.8	4.6	20.9	2.4	2.0	5.6
Huachuca Mountains	69.9	18.0	5.0	3.6	3.5	38.8	6.4	0.7	6.1
Animas Mountains	72.4	12.9	6.6	3.4	4.7	28.1	8.9	0.9	5.0
Rincon Mountains	61.5	10.6	19.4	5.6	2.9	31.6	4.3	6.9	2.1
No. Santa Rita Mtns	71.9	4.0	16.8	4.1	3.2	31.8	6.6	4.8	1.1
Fort Bowie NHS	72.6	4.6	15.9	2.3	4.6	19.8	9.7	2.8	1.6
Buenos Aires NWR	61.0	3.0	23.0	9.4	3.6	27.7	5.3	8.9	0.4
Mule Mountains	85.8	2.6	9.3	0.5	1.8	37.6	13.4	1.0	0.5

Madrean Province in the United States includes a single subprovince with 3 floristic districts: the Apachian District in southeastern Arizona and southwestern New Mexico; the Chihuahuan District in southern New Mexico and west Texas; and a Central Arizona District occurring across the center of the state below the Mogollon Rim and above the lower deserts (McLaughlin, 1992a).

In this classification, the sky-island region is coextensive with the Apachian District of the Madrean Floristic Province. The Arizona Upland District of the Sonoran Floristic Province lies to the west, the Central Arizona District to the northwest, the Mogollon District of the Cordilleran Province to the northeast, and the Chihuahuan District to the east and southeast.

Although this system consists of 34 floristic elements, only a few elements are important in any particular region. In southeastern Arizona, Madrean elements account for over half (57%) of the species in the flora (Table 5). Cordilleran and Sonoran elements are also important, accounting for 17% and 15% of the total flora.

The affinities of selected local floras are also given in Table 5. The flora of the Pinaleño Mountains above 2745 m, i.e., within the mixed-conifer and spruce-fir forests, has a flora with mostly Cordilleran affinities. The flora of the Chiricahua Wilderness area, which lies mostly at high elevations, is primarily Madrean, however, with a large Cordilleran component. The Mogollon element is well represented in the high-elevation flora of the Pinaleño Mountains and in the Chiricahua Wilderness. The Sonoran elements constitute a high percentage of the floras of Buenos Aires Wildlife Refuge and the Rincon Mountains. The Chihuahuan element is best represented in the floras of the Mule Mountains, Fort Bowie National Historic Site, and the Animas Mountains. The percentage of Apachian species is particularly high in the Huachuca and the Mule mountains.

The Madrean elements include widespread and regional species and narrowly distributed species in the Apachian, Chihuahuan, and Central Arizonan elements. "Narrowly distributed" refers to the distribution of species in the western United States. Many of the Madrean species that are narrowly distributed in the western US are much more widespread south of the international border. In order to better characterize these Madrean elements, I tabulated the number of species classified as Madrean that also occur in the floras of Durango (González et al., 1991), Valle de Tehuacan (Dávila et al., 1993), and Chiapas (Breedlove, 1986) (Table 6). A higher percentage of species with widespread and regional distributions extend to Durango than species with narrow distributions. In other words, species that are more widely distributed north of the international border are also more widely distributed south of the border. However, a similar percentage of widespread and regional Madrean and Chihuahuan species extend to the Tehuacan Valley, and a higher percentage of Apachian species extend to Chiapas. The high proportions of all elements (except for Central Arizonan) reaching Durango indicate that the majority of the taxa from south-

Table 6.—Percentages of Madrean elements represented in the flora of southeastern Arizona also found in the floras of Durango (González et al., 1991), Valle de Tehuacan (Dávila et al., 1993), and Chiapas (Breedlove, 1986).

Element	Durango	Tehuacan	Chiapas
Widespread and Regional	63	23	14
Apachian	49	18	23
Chihuahuan	59	24	9
Central Arizonan	17	5	2

eastern Arizona that are classified as Madrean are distributed throughout the northern Sierra Madre Occidental. Approximately 17% of all the species classified as Madrean reach Chiapas; this group can best be characterized as a widespread Neotropical element.

Almost 600 species, nearly a third of the flora of southeastern Arizona, is classified as Apachian. This means that their distribution in the western United States in concentrated in the Apachian Floristic District. Only a small proportion of these--54 species, or less than 10%--appear to be endemic to the Apachian District (Table 7). The number of Apachian endemics is likely to shrink—not grow—with further study. Although additional rare taxa are likely to be discovered from within the area, others will prove to be more widespread, and some (*Plummera ambigens*?, *Polygala piliophora*?) may not prove to be good species.

Table 7.—Sky-island endemics in the flora of southeastern Arizona.

Family	Species
Aspleniaceae	*Woodsia cochisensis* Windham
Apocynaceae	*Amsonia grandiflora* Alexander, *A. kearneyana* Woodson
Asteraceae	*Brickellia floribunda* Gray, *B. lemmoni* Gray, *Cirsium rothrockii* (Gray) Petrak, *Erigeron heliographis* Nesom, *E. kuschei* Eastw., *E. lemmoni* Gray, *E. scopulinus* Nesom & Roth, *Hieracium carneum* Greene, *H. lemmoni* Gray, *Hymenoxys quinquesquamata* Rydb., *Plummera ambigens* Blake, *P. flori bunda* Gray, *Tagetes lemmoni* Gray, *Viguiera triloba* (Gray) Olsen
Brassicaceae	*Arabis tricornuta* Rollins, *Draba petrophila* Greene
Cactaceae	*Coryphantha recurvata* (Engelm.) Britt. & Rose, *Cochiseia robbinsorum* W. H. Earle, *Echinocereus ledingii* Peebles
Caryophyllaceae	*Silene thurberi* S. Wats.
Chenopodiaceae	*Atriplex griffithsii* Standl.
Crassulaceae	*Graptopetalum bartramii* Rose
Euphorbiaceae	*Tragia laciniata* (Torr.) Muell.-Arg.
Fabaceae	*Acacia millefolia* S. Wats., *Astragalus hypoxylus* S. Wats., *A. thurberi* Gray, *Dalea tentaculoides* Gentry, *Lupinus lemmoni* C. P. Smith, *Phaseolus supinus* Wiggins & Rollins
Hydrophyllaceae	*Phacelia arizonica* Gray
Lamiaceae	*Agastache breviflora* (Gray) Epling, *Hedeoma dentatum* Torr., *Salvia lemmoni* Gray
Polygalaceae	*Polygala orthotricha* Blake, *P. pili ophora* Blake
Ranunculaceae	*Delphinium andesicola* Ewan
Rosaceae	*Potentilla albiflora* L. O. Williams
Rubiaceae	*Hedyotis greenei* (Gray) W. H. Lewis
Rutaceae	*Choisya arizonica* Standl., *C. mollis* Standl.
Scrophulariaceae	*Limosella pubiflora* Pennell, *Penstemon discolor* Keck
Agavaceae	*Agave palmeri* Engelm., *A. parviflora* Torr., *Yucca schottii* Engelm., *Y. thornberi* McKelvey
Liliaceae	*Allium plummerae* S. Wats.
Poaceae	*Bouteloua eludens* Griffiths, *Muhlenbergia dubioides* C. O. Goodding, *M. xerophila* C. O. Goodding, *Setaria arizonica* Rominger

The endemics account for just 2% of the estimated regional flora.

INSULARITY

The names "sky-island region" and "Madrean Archipelago" imply that the biota of the region has characteristics similar to that found on true islands.

Certain floristic attributes of the sky islands can be compared with those from two oceanic archipelagos, the Hawaii Islands (Wagner et al., 1990) and Galapagos Islands (Wiggins and Porter, 1971) (Table 8). There are similarities in the inter-island distributions of species. The larger ranges in the sky-island region each contain about 35-45% of the total regional flora, similar to the percentages for the larger islands in Hawaii (39-47%). The larger islands in the Galapagos have a higher percentage (46-71%) of the flora of the entire archipelago. The inter-island similarity is approximately the same in the sky islands (62%) as in the Galapagos (65%), both of which are higher than in the Hawaiian Islands (54%). However, the regional flora of the Apachian Districts has fewer endemics (2-3%) than either the Hawaiian (89%) or Galapogos (30%) floras; the sky-island region also has a much lower percentage of exotic species (ca. 8%) than either the Hawaiian (47%) or Galapogos (15%) floras. Total floras are known from too few of the sky-island region mountains to compare their species-area relationships with those of true archipelagos. The larger ranges in the sky-island region are much smaller in area than the larger Hawaiian and Galapagos islands, but the floras of the mountains in the sky-island region are much larger (780-950 native species) than those of the larger islands of

Table 8.—Floristic comparison of Hawaiian, Galápagos, and "Sky" Islands.

	Hawaii	Galápagos	Sky Islands
Islands Included	Hawai'i Kaua'i Maui O'ahu	Isabela San Cristobal San Salvador Santa Cruz	Huachucas Pinaleños Rincons
Mean island Size (km^{2})	3886	1675	488
Mean Island Altitude (m)	2521	1048	1736
Mean Number of Native Species	421	278	884
Percentage Endemic Species (of total native species in archipelago)	88.8	29.9	2.9
Percentage Exotic Species (of total species in archipelago	47.31	4.8	8.2
Mean Inter-Island Similarity (Otsuka's Index)	.538	.654	.620

either the Hawaiian (370-450 native species) or Galapagos (220-390) archipelagos. Thus, in terms of endemism, percentage exotics, and overall diversity, the floras of the mountains of the sky-island region appear to differ substantially from those of true islands.

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Trees of the Northern Sierra Madre Occidental and Sky Islands of Southwestern North America

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Abstract.—This report covers the naturally occurring montane tree flora of the northern Sierra Madre Occidental of eastern Sonora and western Chihuahua and the sky islands extending into southeastern Arizona and southwestern New Mexico. This flora is comprised of 233 species in 130 genera and 61 families, which represents approximately 5 percent of the total flora of the region. The region is a meeting place of the temperate North American and Neotropical tree floras with intrusions of Sonoran and Chihuahuan desert at lower elevations. The legume (Fabaceae), oak (Fagaceae), and pine (Pinaceae) families are the most diverse, and the oaks *(Quercus)* and pines *(Pinus)* are the largest genera. This is the first comprehensive listing of the trees of the northern Sierra Madre Occidental. Extensive areas of tropical deciduous forest (TDF) cover the lower elevations of the southern part of the region in Sonora and Chihuahua and harbor 60 percent of the regional tree flora. Oak woodland and pine-oak woodland occur at higher elevations and mixed conifer forest at the highest elevations, and support 43, 33, and 11 percent respectively of the regional tree flora. The Madrean forest once stretched unbroken into the American tropics but accelerating deforestation is leading to fragmentation of the keystone species populations.

INTRODUCTION

This publication covers the trees of the sky island mountains of southeastern Arizona, southwestern New Mexico, northeastern Sonora, and northwestern Chihuahua, and the contiguous northern Sierra Madre Occidental in western Chihuahua and eastern Sonora. The northern limit of this bioregion is marked by the Pinaleño Mountains (Mt. Graham) in Arizona. Out of practicality we have set the southern limit of this study at the Sonora-Sinaloa border and adjacent mountains of southwestern Chihuahua. The mountains just east of the Cascada de Basaseachic in southern Chihuahua form the southeastern point, and the Sierra de Alamos in southern Sonora marks the southwestern point. The sky island ranges in Arizona include the Chiricahua, Galiuro, Huachuca, Pinaleño, Rincon, Santa Catalina, Santa Rita mountains, and in New Mexico the Animas and southern Peloncillo mountains. A land of extremes, it is topographically and geologically complex.

We are including all of the tree species known to us in the montane regions at elevations above the deserts and grassland in the north, and above tropical thornscrub in the south. The northern sky islands, especially at higher elevations, have a continental and temperate makeup. Many north temperate tree species penetrate far southward in the interior of Mexico at intermediate or higher elevations in areas such as the Central Plateau. Fourteen percent of the tree flora, or 33 tree taxa (species and a few subspecies or varieties) reach their southern limits in the region (Table 1, p. 78-83).

Overall, the region is arid to semi-arid except at the highest elevations. The lower elevations in the northern part of the region are bounded by the Sonoran Desert on the western flanks and the Chihuahuan Desert and grassland on the eastern flanks. The southern mountains, especially at lower and intermediate elevations, support tropical and subtropical biota. This southern flora, in southeastern Sonora and southwestern Chihuahua, consists largely of a flora that is continuous with the American tropics. As one moves northward through our region, there is a tendency towards a reduction in stature and an attrition of tropical species and genera. Seventy-two percent

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of the tree flora, or 164 species of southern or tropical origin reach their northern limits in the region (Table 1; also see Felger et al., this volume). Nine plant families represented by trees here do not extend farther north in western North America, i.e., Bombacaceae, Clethraceae, Cochlospermaceae, Erythroxylaceae, Magnoliaceae, Myrsinaceae, Myrtaceae, Olacaceae, and Opiliaceae.

The total annual precipitation generally decreases from south to north, but increases with elevation. Precipitation is largely bi-seasonal. The monsoon-like, summer rainy season is most pronounced and dependable towards the south, while winter precipitation increases in importance northward. Soil moisture is the principal limiting factor in this dry region. The northward expansion of many of the more tropical or subtropical species is blocked by an invisible "frost-line" of freezing weather coupled with increasing aridity. Frosts are infrequent or virtually absent towards the southern part of the region at lower to intermediate elevations. Increasing aridity northward tends to raise the lower elevational limits of the tropical/subtropical trees while the frost-line descends in elevation. This results in narrowing elevational distributions or bands of tropical/subtropical species northward and fragmentation of frost-sensitive and drought-intolerant populations into specific microhabitats. There is often somewhat of a paradox, because microhabitats with the most favorable moisture conditions (riparian bottomlands and north-facing slopes) tend to experience the most severe freezing temperatures (see Búrquez et al., in press).

The total flora for the region is estimated to include at least 4,000 species of vascular plants (Felger et al., this volume). Within this rich flora we have documented 233 species of trees (Table 1), which represent about 5 percent of the total flora. These tree species are distributed in 130 genera and 61 families (Table 2). In our opinion this tree flora is approximately 95 percent complete, with additional records likely to be found in the remote mountains and canyons in southwestern Chihuahua and adjacent Sonora. The largest families of trees are the legume (Fabaceae), oak (Fagaceae), and pine (Pinaceae) families, and the most diverse genera are the oaks (*Quercus*; fig. 1) and pines (*Pinus*) (Table 2).

There are about seven tree species and one variety endemic to the region: *Fraxinus gooddingii, Ilex rubra, Nolina matapensis, Opuntia thurberi* var. *thurberi, Prunus gentryi, P. zinggii, Yucca schottii,* and *Y. grandiflora* (Table 1). However, it would not be surprising to find the *Ilex* and the two Prunus species in northern Sinaloa. A number of others occur only in the southern part of our region and in northern Sinaloa, e.g., *Albizia sinaloensis, Brongniartia alamosana, Diospyros sonorae, Opuntia thurberi* var. *alamosenses, O. wilcoxii, Quercus albocincta, Q. tarahumara,* and *Sabal uresana*. In fact, the flora of northern Sinaloa flora is not separable from that of southern Sonora and southwestern Chihuahua (Gentry 1946a, 1946b, 1982).

The characters, including size, that constitute a "tree" are often highly subjective but useful for indicating trends, and important for considering keystone or habitat-modifying organisms. The demarcation between the larger shrubs and smaller trees is especially subjective. We have chosen a height of 5 m as the artificial limit between shrubs and trees, and when in doubt have favored including woody plants and excluding the more herbaceous species with seasonal die-back. We have also decided that if a plant is classified as a tree one should be able to climb up into it, or theoretically climb it if the spines are removed, without causing it to collapse. Many have a single trunk at least 10 cm in diameter at about 1 m above ground level. Some species included in this listing have multiple trunks arising at or near the ground and could be classified as shrubs rather than trees. In some cases a particular species may be a shrub across most of its distribution in the region, but in favorable habitats such as moist tropical canyons it may develop into a sizeable

Table 2.—Summary of tree species of the northern Sierra Madre Occidental and the Sky Islands including the seven largest families and five largest genera.

	No. of families	No. of genera	No. of species
Gymnosperms	2	7	26
Dicotyledons	56	119	198
Monocotyledons	3	4	9
Total	61	130	233
Families:			
Fabaceae		23	36
Fagaceae		1	21
Pinaceae		4	18
Moraceae		4	9
Euphorbiaceae		7	8
Cupressaceae		3	8
Burseraceae		1	8
Salicaceae		2	7
Cactaceae		4	6
Largest genera:			
Quercus			21
Pinus			12
Bursera			8
Acacia			6
Ficus			6
Juniperus			5

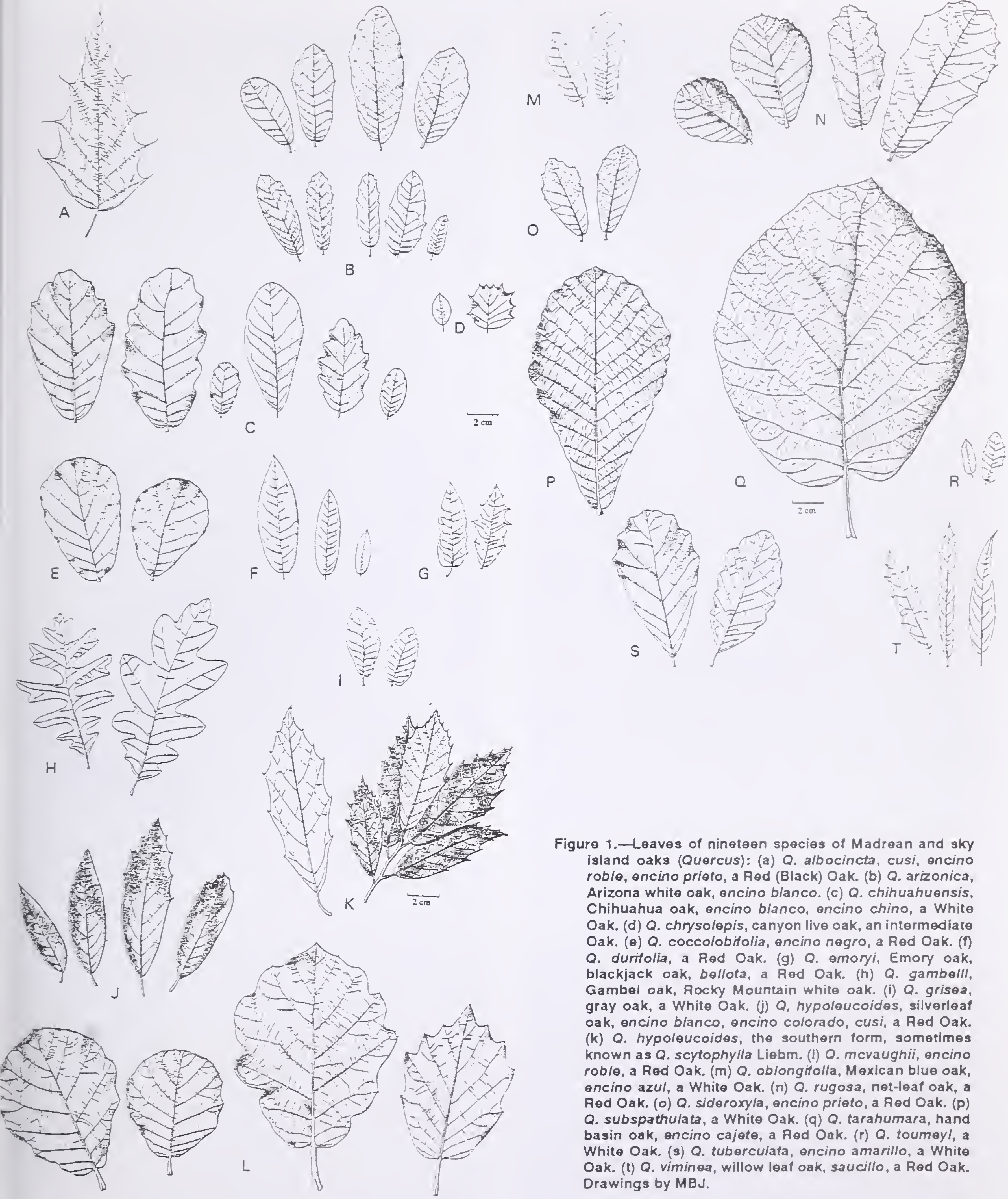

Figure 1.—Leaves of nineteen species of Madrean and sky island oaks (*Quercus*): (a) *Q. albocincta*, *cusi*, *encino roble*, *encino prieto*, a Red (Black) Oak. (b) *Q. arizonica*, Arizona white oak, *encino blanco*. (c) *Q. chihuahuensis*, Chihuahua oak, *encino blanco*, *encino chino*, a White Oak. (d) *Q. chrysolepis*, canyon live oak, an intermediate Oak. (e) *Q. coccolobifolia*, *encino negro*, a Red Oak. (f) *Q. durifolia*, a Red Oak. (g) *Q. emoryi*, Emory oak, blackjack oak, *bellota*, a Red Oak. (h) *Q. gambelii*, Gambel oak, Rocky Mountain white oak. (i) *Q. grisea*, gray oak, a White Oak. (j) *Q, hypoleucoides*, silverleaf oak, *encino blanco*, *encino colorado*, *cusi*, a Red Oak. (k) *Q. hypoleucoides*, the southern form, sometimes known as *Q. scytophylla* Liebm. (l) *Q. mcvaughii*, *encino roble*, a Red Oak. (m) *Q. oblongifolia*, Mexican blue oak, *encino azul*, a White Oak. (n) *Q. rugosa*, net-leaf oak, a Red Oak. (o) *Q. sideroxyla*, *encino prieto*, a Red Oak. (p) *Q. subspathulata*, a White Oak. (q) *Q. tarahumara*, hand basin oak, *encino cajete*, a Red Oak. (r) *Q. toumeyi*, a White Oak. (s) *Q. tuberculata*, *encino amarillo*, a White Oak. (t) *Q. viminea*, willow leaf oak, *saucillo*, a Red Oak. Drawings by MBJ.

tree (e.g., *Aralia humilis* and *Stemmadenia tomentosa*). Other species are shrubs at higher elevations and in the northern part of the region (due to repeated freeze-damage or drought-stress) and trees in the more tropical southern regions (e.g., *Erythrina flabelliformis, Fouquieria macdougalii,* and *Lysiloma watsonii*).

The summary of information in Table 1 calls for some comment. In reality the vegetation is not as simple as the classification presented. Many trees may extend into neighboring vegetation zones along riparian habitats or in other special situations. Extraordinary "shifts" in vegetation types occur on limestone (Whitaker & Niering 1965) and hydrothermically altered soils (Goldberg 1982, Búrquez et al. 1992). The size-classes in Table 1 refer to the larger trees within any given taxon across the entire region. Fire and human mischief have eliminated most of the largest trees from many regions. In certain situations many common trees that are usually small or at most medium-sized may develop into large trees, e.g., *Lysiloma watsonii* and *Vitex mollis* along the Río Guajaray north of Alamos, and *Quercus tarahumara* in the vicinity of Mulatos in east-central Sonora. Perhaps the large number of extraordinarily large trees in the Guarijio Indian region of the Guajaray is related to local conservation or management practices.

There are, or were, trees virtually everywhere in the montane areas—most of the region is or was forested. But man is the enemy of the tree. The forests are receding rapidly. Human population in the region remained low and major roads few until the middle or latter part of the twentieth century. Much diversity of near natural habitats remains, but assaults on trees are escalating. Major threats include dams, logging, firewood cutting, charcoal-making, clearing for agriculture, mining, urbanization, and replacement of the forests with buffelgrass (*Pennisetum ciliare*) at lower elevations in the southern part of the region.

This summary is largely derived from our study of the trees of Sonora which will be treated in depth in a forthcoming book (Felger & Johnson in press). Selected references dealing with trees of our region or adjacent areas include Benson & Darrow (1981), Flora North America (1993), Gentry (1942), Hastings et al. (1972), Kearney & Peebles (1960), Little (1950), Marshall (1957), Mearns (1907), Pennington & Sarukhan (1968), Powell (1988), Shreve (1951), Spellenberg et al. (in prep.), Standley (1920-1926), Steinmann & Felger (in prep.), Turner et al. (in press), Vines (1960), Wiggins (1964), and White (1948). The nomenclature used here results from our interpretation of the taxonomic literature and our work on the flora of the region. The major vegetation types of the region and their tree floras are briefly summarized below.

TROPICAL DECIDUOUS FOREST

Tropical deciduous forest (TDF) is characteristic of the dry tropics worldwide. Increase in human population is leading to global devastation of this habitat. De-forestation and the resulting desertification has contributed to subtropical belts of misery circling the globe. TDF is the least studied of the major vegetation types of the world. Because it is hardly fashionable to save poorly-known, scrawny and often thorny trees in hot, uncomfortable climates, world conservation efforts have largely overlooked TDF. The magnificent tropical deciduous forest of the northern Sierra Madre Occidental is seriously threatened.

The TDF in Sonora and adjacent southwestern Chihuahua is the dry, northern arm of the great TDF swath which sweeps northward in western Mexico. Sonoran-Chihuahuan TDF is sandwiched between tropical thornscrub at lower elevations to the west and the oak zone at higher elevations to the east. Northward, along the east side of the Sonoran Desert, TDF merges into a kind of inland subtropical thornscrub (Felger & Lowe 1976, Búrquez et al. in press) which in turn merges into desertscrub (Shreve 1951). Paul Martin and Chuck Bowden referred to TDF in Sonora as the Secret Forest (Bowden et al. 1993). Howard Scott Gentry (1942) called it the Short-tree Forest, and David Brown (1982) called it Sinaloan Deciduous Forest. Felger & Lowe (1976) and Búrquez et al. (in press) call it tropical deciduous forest. In its natural condition in Sonora, Chihuahua, and northern Sinaloa, there is essentially 100 percent ground cover of forest often 10-15 m tall made up of trees of tropical affinity.

Summers are long and hot and winters short and mild. Freezing weather within the forest is rare and apparently most of the TDF species are highly frost-sensitive. May and June days grow hotter and hotter, building up to the beginning of the long-awaited summer rains. Afternoon clouds increase day by day, and finally, when the violent thunderstorms begin, the leafless trees and vines and undergrowth burst forth in a blaze of green (Gentry 1942). The monsoon rains begin soon after summer solstice, celebrated on June 24 as El Día de San Juan. The rains typically continue through August and into early September. Some trees, such as *Bursera* spp., *Cochlospermum, Erythrina, Jatropha, Ipomoea,* and *Pseudobombax,* defoliate very soon after the rains cease. However, most of the trees defoliate more gradually. Midwinter rains may delay leaf-fall of certain species. Drought-induced deciduating leaves produce a virtually unique but ephemeral display of highly varied pastel colors (Bowden et al. 1993). Spring drought brings on final defoliation to most of the TDF trees. As the weather turns hotter and dryer from March and April to June, even the tree chollas (*Opuntia thurberi*) and prickly pears (e.g., *O. wilcoxii*) become flaccid and droopy from water loss. Cicadas call loudly and writers visiting the Sonoran TDF during the height of the pre-summer drought tell of skeleton forests and the lack of greenery. It is awesome to witness the sudden transformation to luxuriant tropical green with the start of the summer monsoon.

Flowering trees can be found at virtually any time of the year but there are some significant peaks of color display. Mid-winter brings the *amapas* (*Tabebuia* spp.), the *palo santo* (*Ipomoea arborescens*), and then the *echo* (*Pachycereus pecten-aboriginum*). Later in spring the *cuajilote* (*Pseudobombax palmeri*) and *rosa amarilla* (*Cochlospermum vitifolium*) bring forth floral displays. When fallen leaves are dry and crackling underfoot in the searing pre-monsoon heat the hillsides blaze with the dark blue of *gauyacán* (*Guaiacum coulteri*) and rose-purple of *nesco* (*Lonchocarpus hermannii,* = *Willardia mexicana*). These are just a few of the more conspicuous flowering trees. By and large the timing of fruit ripening and seed-fall coincides with the beginning of the summer rains.

Sixty percent (140 species) of the tree species of the region occur in TDF. Legumes rule the tropical-derived TDF as well as the regional thornscrub and Sonoran desertscrub. The fast-growing *mauto* (*Lysiloma microphyllum*) and many other legumes account for the vast majority of the TDF vegetative cover. Biological diversity is high. No single species or small number of species dominates—the forest is shared by a horde of species. Prominent arborescent members of TDF in our region include the following:

- *Bursera* spp.
- *Caesalpinia platyloba*
- *Ceiba aesculifolia*
- *Conzattia multiflora*
- *Fouquieria macdougalii*
- *Haematoxylum brasiletto*
- *Ipomoea arborescens*
- *Lonchocarpus hermannii*
- *Lysiloma microphyllum*
- *L. watsonii*
- *Pachycereus pecten-aboriginum*
- *Pithecellobium leucospermum*
- *Senna atomaria*
- *Stenocereus montanus*
- *S. thurberi*
- *Tabebuia chrysantha*
- *T. impetiginosa*
- *Wimmeria mexicana*

OAK WOODLAND

Oak woodland vegetation is widely distributed at elevations above desert, grassland, thornscrub, or tropical deciduous forest, but below pine-oak woodland or pine forest. The species composition and tree density in oak woodland changes both with elevation and latitude. Although these oak zones have been called Madrean Evergreen Woodland (Brown 1982), many of the oaks and associated species are drought-deciduous during the late spring dry season. Autumn colors associated with falling leaves in temperate regions are seen in our region during the pre-summer drought.

Extensive areas in the northern part of the region are dominated by open woodlands of Emory oak or *bellota* (*Quercus emoryi*). The acorns are harvested in considerable quantity in northern Sonora in early summer and sold locally. This is one of the few remaining commercial, wild food harvests in the region. The acorns are eaten fresh and are often consumed in cantinas—the floors becoming littered with the empty shells. Emory oak, Mexican blue oak (*Q. oblongifolia*), and Arizona oak (*Q. arizonica*) are the most common low-elevation oaks in the northern part of the our region. At lower elevations these oak zones border grassland or desertscrub. There is sometimes a broad ecotone between oak woodland and grassland where the oaks become widely spaced and grasses predominate. Such areas have been termed oak-grassland or oak-savanna. In mountains in southeastern and east-central Sonora oak woodland sometimes occurs as islands on acidic, hydrothermically altered soils within tropical deciduous forest. The ecotone between these two plant communities is often only a few meters.

Oak woodland in southeastern Sonora and southwestern Chihuahua, called Oak Forest by Gentry (1942), shows considerable tropical affinity. At its lower limits it borders tropical deciduous forest. Their boundaries are often remarkably well defined, apparently maintained by fire. Across the Río Mayo and Río Fuerte mountain drainages it is common to see low fires creeping almost harmlessly through dry grasses, forbs, and leaf litter among the barren oaks in May and June. These fires destroy small TDF trees and shrubs but not the oaks and their associated vegetation.

The southern oak woodland is host to a rich array of subtropical or Mexican oak species. There is considerable elevational and habitat zonation among the diverse oaks. Many of the oaks in southeastern Sonora and nearby southwestern Chihuahua are strikingly large-leaved (e.g., the hand-basin oak, *Q. tarahumara*) as compared to those of the northern part of the region. The southern oaks often support tropical epiphytes such as bromeliads (*Tillandsia* spp.) and orchids (e.g., *Encyclia microbulbon, Laelia autumnalis,* and *Oncidium cebolleta*).

PINE-OAK WOODLAND

Extensive areas of pine-oak woodland occur along the east side of the continental divide in western Chihuahua. Along the western slope of the Sierra Madre Occidental the climate is generally somewhat wetter, with presumably milder winter temperatures, resulting in a more diverse flora with more tropical elements including Apache pine (*Pinus engelmannii*), Durango pine (*P. durangensis*), egg-cone pine (*P. oocarpa*), *pino chino* (*P. herrerae*), and Mexican tropical-montane oaks. Towards southeastern Sonora and adjacent Chihuahua the pine-oak woodland is floristically and structurally akin to the Mexican pine-oak woodland of central and southern Mexico.

Pine-oak woodland is continuous with oak woodland at lower elevations. In pine-oak woodland the pines form the overstory while the oaks generally form an understory. There are extensive areas of pine-oak woodland in the mountains of our region. Pine-oak woodland is included within the concept of Madrean Evergreen Woodland (Brown 1982), and the pine forest has been called Madrean Montane Conifer Forest (Brown 1982). For our purposes of this study it is not practical to distinguish pine-oak woodland from pine forest. Especially in the southern part of our region oaks are a major part of the forests containing pines. The abundance of oaks may be in part a consequence of overharvesting of pines. However, especially in the northern part of the region a distinctive pine forest is distinguishable. In these communities Douglas Fir (*Pseudotsuga menziesii*) is often locally common in an otherwise pine-dominated forest, thus blurring the boundary with mixed conifer forest.

At higher elevations within the pine-oak zones the pines become increasingly conspicuous and the tree density increases so that the vegetation could be called forest rather than woodland. Pine forest is characteristically dominated by one species of pine, usually Arizona pine (*Pinus ponderosa* var. *arizonica*), ponderosa pine (*P. ponderosa* var. *scopulorum*), or white pine (*P. strobiformis*), with scattered individuals or small groups of oaks, especially Gambel oak (*Q. gambelii*) and net-leaf oak (*Q. rugosa*). Gambel oak is the only winter-deciduous oak in our region. Pine forest is more widespread in Chihuahua and Durango than in Sonora. Ponderosa pine replaces Arizona pine at the higher elevations in Chihuahua and on the northernmost sky islands. These closely-related pines can be found intermixed in the Santa Catalina Mountains in southern Arizona. Mountains ranges to the south have only Arizona pine, while the ranges to the north have only ponderosa pine.

MIXED CONIFER FOREST

Mixed conifer forest is restricted to the highest mountain tops. Winters are cold and summers cool and moist. It is most extensive in the northern sky islands and at the highest elevations in Chihuahua. Southward in Sonora, mixed conifer forest occurs in extremely limited areas on north-facing slopes and riparian canyons on north slopes. Northeastern Sonora and adjacent Chihuahua support mixed conifer forests at elevations mostly above 2135 m (7000 ft). Mixed conifer forest barely extends into southeastern Sonora from Chihuahua above 2100 m (6890 ft) in the upper reaches of the Río Mayo Drainage. Because there are more extensive areas of higher elevation in Chihuahua the mixed conifer forest is more common there.

Three coniferous genera, *Abies* (fir), *Pinus,* and *Pseudotsuga* (Douglas fir), define this vegetation. These trees are commercially valuable for lumber. Most of the old growth forest has been logged, but in some places it is recovering from extensive logging in the mid-twentieth century. Most of the broadleaf (dicot) trees found here are winter-deciduous, e.g., Gambel oak (*Quercus gambelii*), *capulín* or wild cherry (*Prunus serotina*), ash (*Fraxinus papillosa*), aspen (*Populus tremuloides*), and New Mexico locust (*Robinia* *neomexicana*). Riparian canyons are shaded with tall forests that may include big-tooth maple (*Acer grandidentatum*) and alder (*Alnus oblongifolia*) sometimes towering to 20 meters or more in height. The two highest sky island peaks, the Pinaleño and Chiricahua mountains in southeastern Arizona, support spruce-fir forest (*Picea* and *Abies*) as do a few localities on cold, north-facing slopes at the highest elevations in southwestern Chihuahua.

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Table 1.— Montane tree flora of the northern Sierra Madre Occidental and the Sky Islands.

Geographic distributions: G = "General" distributions, found both north and south of the region; T = "Tropical" or "southern" taxa at the northern limits of their geographic ranges; N = "Northern" taxa at the southern limits of their ranges; R = occuring elsewhere within approximately the same latitudes as our region; E = endemic to our region.
Tree size classes: S = small trees, 5-8 m tall; M = medium-sized trees, 9-18 m; L = large trees, 19 or more m.
Habitats: TD = tropical deciduous forest; OK = oak woodland; PN = pine-oak woodland or forest; MX = mixed conifer forest.
Non-native species are indicated with an asterisk (*).

	G	T	N	R	E	S	M	L	TD	OK	PN	MX
GYMNOSPERMS (CONIFERAE - Conifers)												
CUPRESSACEAE - CYPRESS FAMILY												
Cupressus arizonica Greene var. arizonica	G	-	-	-	-	-	M	L	-	OK	PN	-
C. lusitanica Mill.		T	-	-	-	-	-	L	-	OK	PN	MX
Juniperus coahuilensis (Martínez) R.P. Adams	G	-	-	-	-	S	-	-	-	OK	PN	-
J. deppeana Steud.	G	-	-	-	-	-	-	-	-	OK	PN	-
J. durangensis Martínez	-	T	-	-	-	S	-	-	-	OK	PN	-
J. flaccida Schldl. var. flaccida	-	T	-	-	-	S	-	-	-	OK	PN	-
J. scopulorum Sarg.	-	-	N	-	-	S	-	-	-	-	PN	-
Taxodium mucronatum Ten.	-	T	-	-	-	-	-	L	TD	-	-	-
PINACEAE - PINE FAMILY												
Abies bifolia A. Murr.	-	-	N	-	-	-	-	L	-	-	-	MX
A. concolor (Gord. & Glend.) Hildebr.	-	-	N	-	-	-	-	L	-	-	-	MX
A. durangensis Martínez	-	T	-	-	-	-	-	L	-	-	-	MX
Picea chihuahuana Martínez	-	T	-	-	-	-	-	L	-	-	-	MX
P. engelmannii Engelm. var. engelmannii	-	-	N	-	-	-	-	L	-	-	-	MX
Pinus cembroides Zucc.	-	T	-	-	-	S	-	-	-	OK	PN	-
P. douglasiana Martínez	-	T	-	-	-	-	-	L	-	-	PN	-
P. durangensis Martínez	-	T	-	-	-	-	-	L	-	OK	PN	-
P. edulis Engelm.	-	-	N	-	-	S	-	-	-	OK	PN	-
P. engelmannii Carr.	-	T	-	-	-	-	-	L	-	OK	PN	-
P. herrerae Martínez	-	T	-	-	-	-	-	L	-	-	PN	-
P. leiophylla Schiede & Deppe var. chihuahuana (Engelm.) Shaw	-	T	-	-	-	-	-	L	-	OK	PN	-
P. lumholtzii Robins. & Fern.	-	T	-	-	-	-	-	L	-	-	PN	-
P. maximinoi H.E. Moore	-	T	-	-	-	-	-	L	-	-	PN	-
P. oocarpa Schiede var. oocarpa	-	T	-	-	-	-	-	L	-	-	PN	-
P. ponderosa Laws. & C. Laws. var. arizonica (Englm.) Shaw	-	T	-	-	-	-	-	L	-	-	PN	MX
P. ponderosa var. scopulorum Engelm.	-	-	N	-	-	-	-	L	-	-	PN	MX
P. strobiformis Engelm.	G	-	-	-	-	-	-	L	-	-	PN	MX
Pseudotsuga menziesii (Mirb.) Franco var. glauca (Mayr) Franco	G	-	-	-	-	-	-	L	-	-	PN	MX
MONOCOTYLEDONS												
AGAVACEAE - AGAVE FAMILY												
Yucca arizonica McKelv.	-	-	N	-	-	S	-	-	-	OK	-	-
Y. grandiflora Gentry	-	-	-	-	E	S	-	-	-	OK	-	-
Y. schottii Engelm.	-	-	-	-	E	S	-	-	-	OK	PN	-
ARECACEAE (PALMAE) - PALM FAMILY												
Brahea aculeata (Brandeg.) H.E. Moore	-	T	-	-	-	S	-	-	TD	OK	-	-
B. dulcis (H.B.K.) Mart.	-	T	-	-	-	S	(M)	-	TD	OK	PN	-
B. elegans (Becc.) H.E. Moore	-	T	-	-	-	S	(M)	-	TD	-	-	-
B. nitida André	-	T	-	-	-	S	(M)	-	TD	OK	-	-
Sabal uresana Trel.	-	T	-	-	-	-	M	-	TD	OK	-	-
NOLINACEAE - BEAR-GRASS FAMILY												
Nolina matapensis Wiggins	-	-	-	-	E	S	-	-	TD	OK	-	-
DICOTYLEDONS												
ACERACEAE - MAPLE FAMILY												
Acer glabrum Torr.	-	-	N	-	-	S	-	-	-	-	-	MX
A. grandidentatum Nutt.	-	-	N	-	-	-	-	L	-	OK	PN	MX
A. negundo L.	-	-	N	-	-	-	M	-	-	-	PN	MX

APOCYNACEAE - DOGBANE FAMILY												
Plumeria rubra L.	-	T	-	-	-	S	-	-	TD	-	-	-
Stemmadenia tomentosa Greenm. var. palmeri (Rose & Standl.) Woodson	-	T	-	-	-	S	(M)	-	TD	-	-	-
Vallesia glabra (Cav.) Link	-	T	-	-	-	S	-	-	TD	-	-	-
AQUIFOLIACEAE - HOLLY FAMILY												
Ilex rubra S. Wats.	-	-	-	-	E	-	M	-	-	OK	PN	MX
I. tolucana Hemsl.	-	T	-	-	-	-	M	-	-	-	PN	MX
ARALIACEAE - GINSENG FAMILY												
Aralia humilis Cav.	-	T	-	-	-	S	(M)	-	TD	OK	PN	-
Oreopanax peltatum Linden	-	T	-	-	-	S	(M)	-	TD	OK	PN	-
ASTERACEAE (COMPOSITAE) - ASTER OR COMPOSITE FAMILY												
Montanoa rosei Robins. & Greenm.	-	T	-	-	-	S	-	-	TD	-	-	-
Parthenium tomentosum DC. var. stramonium (Greene) Rollins	-	T	-	-	-	S	-	-	TD	OK	-	-
BETULACEAE - BIRCH FAMILY												
Alnus incana (L.) Moench ssp. tenuifolia (Nutt.) Breit.	-	-	N	-	-	-	M	-	-	-	-	MX
A. oblongifolia Torr.	-	-	N	-	-	-	-	L	-	OK	PN	MX
Ostrya virginiana (P. Mill.) C. Koch	G	-	-	-	-	-	-	L	-	OK	PN	MX
BIGNONIACEAE - BIGNONIA FAMILY												
Chilopsis linearis (Cav.) Sweet ssp. arcuata (Fosberg) Henricks.	-	-	N	-	-	S	-	-	-	OK	-	-
Tabebuia chrysantha (Jacq.) Nichols. ssp. chrysantha	-	T	-	-	-	-	M	(L)	TD	-	-	-
T. impetiginosa (A. DC.) Standl.	-	T	-	-	-	-	M	(L)	TD	-	-	-
BOMBACACEAE - SILK-COTTON FAMILY												
Ceiba aesculifolia (H.B.K.) Britt. & Baker	-	T	-	-	-	-	M	-	TD	-	-	-
Pseudobombax palmeri (S. Wats.) Dugand	-	T	-	-	-	-	M	-	TD	-	-	-
BORAGINACEAE - BORAGE FAMILY												
Cordia sonorae Rose	-	T	-	-	-	S	-	-	TD	-	-	-
BUDDLEJACEAE - BUTTERFLY-BUSH FAMILY												
Buddleja cordata H.B.K. var. cordata	-	T	-	-	-	S	(M)	-	-	-	PN	-
B. parviflora H.B.K.	-	T	-	-	-	S	-	-	-	OK	PN	-
BURSERACEAE - FRANKINCENSE FAMILY												
Bursera arborea (Rose) Riley	-	T	-	-	-	-	-	L	TD	-	-	-
B. fagaroides (H.B.K.) Engl. var. elongata McVaugh	-	T	-	-	-	S	-	-	TD	-	-	-
B. grandifolia (Schldl.) Engl.	-	T	-	-	-	-	M	-	TD	-	-	-
B. lancifolia (Schldl.) Engl.	-	T	-	-	-	S	-	-	TD	-	-	-
B. laxiflora S. Wats.	-	T	-	-	-	S	-	-	TD	-	-	-
B. penicillata (DC.) Engl.	-	T	-	-	-	-	M	-	TD	-	-	-
B. simaruba (L.) Sarg.	-	T	-	-	-	-	-	L	TD	-	-	-
B. stenophylla Sprauge & Riley	-	T	-	-	-	-	M	-	TD	-	-	-
CACTACEAE - CACTUS FAMILY												
Opuntia thurberi Engelm. var. thurberi	-	-	-	-	E	S	-	-	TD	-	-	-
O. thurberi var. alamosenses (Britt. & Rose) Bravo	-	T	-	-	-	S	-	-	TD	-	-	-
O. wilcoxii Britt. & Rose	-	T	-	-	-	S	-	-	TD	-	-	-
Pachycereus pecten-aboriginum (Engelm.) Britt. & Rose	-	T	-	-	-	S	(M)	-	TD	-	-	-
Pilosocereus alensis Weber	-	T	-	-	-	S	-	-	TD	-	-	-
Stenocereus montanus (Britt. & Rose) Buxb.	-	T	-	-	-	S	(M)	-	TD	-	-	-
S. thurberi (Engelm.) Buxb.	-	T	-	-	-	S	(M)	-	TD	-	-	-
CAPRIFOLIACEAE - HONEYSUCKLE FAMILY												
Sambucus mexicana Presl	-	-	N	-	-	S	-	-	-	OK	PN	-
CELASTRACEAE - STAFF-TREE FAMILY												
Wimmeria mexicana (DC.) Lundell	-	T	-	-	-	S	-	-	TD	-	-	-

CLETHRACEAE - CLETHRA FAMILY												
Clethra mexicana DC.	-	T	-	-	-	-	M	-	-	OK	PN	-
COCHLOSPERMACEAE - COCHLOSPERMUM FAMILY												
Cochlospermum vitifolium (Willd.) K. Spreng.	-	T	-	-	-	-	M	-	TD	-	-	-
CONVOLVULACEAE - MORNING-GLORY FAMILY												
Ipomoea arborescens (Humb. & Bonpl.) G. Don var. pachyleuta Gentry	-	T	-	-	-	S	(M)	-	TD	(OK)	-	-
CORNACEAE - DOGWOOD FAMILY												
Cornus disciflora DC.	-	T	-	-	-	S	-	-	-	OK	PN	-
EBENACEAE - PERSIMMON FAMILY												
Diospyros sonorae Standl.	-	T	-	-	-	-	M	-	TD	-	-	-
ERICACEAE - HEATH FAMILY												
Arbutus arizonica (A. Gray) Sarg.	-	T	-	-	-	-	M	(L)	-	OK	PN	MX
A. xalapensis Sarg.	-	T	-	-	-	-	M	-	-	-	PN	-
ERYTHROXYLACEAE - COCA FAMILY												
Erythroxylum mexicanum H.B.K.	-	T	-	-	-	S	-	-	TD	-	-	-
EUPHORBIACEAE - SPURGE FAMILY												
Croton cf. niveus Jacq.	-	T	-	-	-	S	-	-	TD	-	-	-
Drypetes gentryi Monach.	-	T	-	-	-	-	-	L	TD	-	-	-
Jatropha cordata (Ort.) Müll. Arg.	-	T	-	-	-	S	-	-	TD	-	-	-
Manihot aesculifolia (H.B.K.) Pohl	-	T	-	-	-	S	-	-	TD	-	-	-
Manihot sp.	-	T	-	-	-	S	-	-	TD	-	-	-
*Ricinus communis L.	G	-	-	-	-	S	-	-	TD	-	-	-
Sapium appendiculatum (Müll. Arg.) Pax & K. Hoffm.	-	T	-	-	-	S	-	-	TD	-	-	-
Sebastiana pavoniana (Müll. Arg.) Müll. Arg.	-	T	-	-	-	-	M	-	TD	-	-	-
FABACEAE (LEGUMINOSAE) - LEGUME OR BEAN FAMILY:												
CAESALPINIOIDEAE - SENNA SUBFAMILY												
Bauhinia pringlei S. Wats.	-	T	-	-	-	S	-	-	TD	-	-	-
Caesalpinia caladenia Standl.	-	T	-	-	-	S	-	-	TD	-	-	-
C. palmeri S. Wats.	-	T	-	-	-	S	-	-	TD	-	-	-
C. platyloba S. Wats.	-	T	-	-	-	S	-	-	TD	-	-	-
Cercidium praecox (Ruiz & Pav.) Harms ssp. praecox	-	T	-	-	-	S	-	-	TD	-	-	-
Conzattia multiflora B.L. Robins.	-	T	-	-	-	-	-	L	TD	-	-	-
Haematoxylum brasiletto Karst.	-	T	-	-	-	S	(M)	-	TD	-	-	-
*Parkinsonia aculeata L.	-	T	-	-	-	-	M	-	TD	-	-	-
Senna atomaria (L.) Irwin & Barneby	-	T	-	-	-	S	-	-	TD	-	-	-
MIMOSOIDEAE - MIMOSA SUBFAMILY												
Acacia pringlei Rose ssp. californica (Brandeg.) Lee, Seigler & Ebinger	-	T	-	-	-	S	-	-	TD	-	-	-
A. cochliacantha Willd.	-	T	-	-	-	S	-	-	TD	-	-	-
A. coulteri Benth.	-	T	-	-	-	S	-	-	TD	-	-	-
A. farnesiana (L.) Willd.	-	T	-	-	-	S	-	-	TD	-	-	-
A. occidentalis Rose	-	T	-	-	-	-	M	-	TD	-	-	-
A. pennatula (Cham. & Schldl.) Benth.	-	T	-	-	-	S	-	-	-	OK	PN	-
Albizia sinaloensis Britt. & Rose	-	T	-	-	-	-	-	L	TD	-	-	-
Leucaena lanceolata S. Wats.	-	T	-	-	-	-	M	-	TD	-	-	-
*L. leucocephala (Lam.) de Wit	-	T	-	-	-	S	-	-	TD	-	-	-
Lysiloma microphyllum Benth.	-	T	-	-	-	-	M	(L)	TD	-	-	-
L. watsonii Rose	-	T	-	-	-	-	M	(L)	TD	OK	-	-
Mimosa palmeri Rose	-	T	-	-	-	S	-	-	TD	-	-	-
*Pithecellobium dulce (Roxb.) Benth.	-	T	-	-	-	-	-	L	TD	-	-	-
P. leucospermum Brandeg.	-	T	-	-	-	S	-	-	TD	-	-	-
P. mexicanum Rose	-	T	-	-	-	-	M	-	TD	-	-	-
Prosopis glandulosa Torr. var. torreyana (L.D. Bens.) M.C. Johnst.	G	-	-	-	-	-	M	-	TD	-	-	-
P. velutina Woot.	-	-	N	-	-	-	M	-	-	OK	-	-

PAPILIONOIDEAE - BEAN SUBFAMILY												
Brongniartia alamosana Rydb.	-	T	-	-	-	S	-	-	TD	-	-	-
Coursetia glandulosa A. Gray	-	T	-	-	-	S	-	-	TD	OK	-	-
Diphysa occidentalis Rose	-	T	-	-	-	S	-	-	TD	-	-	-
D. suberosa S. Wats.	-	T	-	-	-	S	-	-	TD	OK	-	-
Erythrina flabelliformis Kearney	-	T	-	-	-	S	-	-	TD	OK	-	-
Eysenhardtia orthocarpa (A. Gray) S. Wats.	G	-	-	-	-	S	-	-	TD	OK	-	-
Lonchocarpus hermannii Sousa	-	T	-	-	-	S	-	-	TD	-	-	-
Piscidia mollis Rose	-	T	-	-	-	-	M	-	TD	-	-	-
Platymiscium trifoliolata Benth.	-	T	-	-	-	-	M	-	TD	-	-	-
Robinia neomexicana A. Gray var. neomexicana	-	-	N	-	-	S	-	-	-	OK	PN	MX
FAGACEAE - BEECH FAMILY												
Quercus albocincta Trel.	-	T	-	-	-	-	M	-	-	OK	PN	-
Q. arizonica Sarg.	G	-	-	-	-	-	M	-	-	OK	PN	-
Q. chihuahuensis Trel.	-	T	-	-	-	-	M	-	-	OK	PN	-
Q. chrysolepis Liebm.	-	-	N	-	-	S	-	-	-	OK	-	-
Q. coccolobifolia Trel.	-	T	-	-	-	-	M	-	-	OK	PN	-
Q. crassifolia Humb. & Bonpl.	-	T	-	-	-	-	M	-	-	OK	PN	-
Q. durifolia Seemen	-	T	-	-	-	-	-	L	-	OK	PN	-
Q. emoryi Torr.	-	-	-	R	-	-	M	-	-	OK	PN	-
Q. gambelii Nutt.	-	-	N	-	-	-	M	-	-	-	PN	MX
Q. grisea Liebm.	G	-	-	-	-	-	M	-	-	OK	-	-
Q. hypoleucoides A. Camus	-	T	-	-	-	-	M	(L)	-	OK	PN	-
Q. mcvaughii Spellenb.	-	-	-	-	-	-	M	(L)	-	OK	PN	MX
Q. oblongifolia Torr.	-	-	-	R	-	-	M	-	-	OK	-	-
Q. perpallida Trel.	-	T	-	-	-	-	M	-	-	OK	-	-
Q. rugosa Née	G	-	-	-	-	-	M	-	-	OK	PN	-
Q. sideroxyla Humb. & Bonpl.	-	T	-	-	-	-	M	-	-	OK	PN	-
Q. subspathulata Trel.	-	T	-	-	-	-	M	-	-	-	PN	-
Q. tarahumara Spellenb., Bacon & Breedl.	-	T	-	-	-	-	-	L	-	-	PN	-
Q. toumeyi Sarg.	-	-	N	-	-	S	-	-	-	OK	PN	-
Q. tuberculata Liebm.	-	T	-	-	-	-	M	-	(TD)	OK	PN	-
Q. viminea Trel.	-	T	-	-	-	-	M	(L)	-	OK	PN	-
FOUQUIERIACEAE - OCOTILLO FAMILY												
Fouquieria macdougalii Nash	-	T	-	-	-	S	-	-	TD	-	-	-
F. splendens Engelm. ssp. splendens	G	-	-	-	-	S	-	-	-	OK	-	-
JUGLANDACEAE - WALNUT FAMILY												
Juglans major (Torr.) Heller	G	-	-	-	-	-	M	-	-	OK	PN	-
LAURACEAE - LAUREL FAMILY												
Cinnamomum sp.	-	T	-	-	-	-	-	L	TD	OK	-	-
Persea podadenia Blake	-	T	-	-	-	-	-	L	-	OK	PN	-
MAGNOLIACEAE - MAGNOLIA FAMILY												
Magnolia pacifica Vázq. ssp. tarahumara Vázq.	-	T	-	-	-	-	-	L	-	OK	PN	-
MALPIGHIACEAE - MALPIGHIA FAMILY												
Bunchosia sonorensis Rose	-	T	-	-	-	S	-	-	TD	-	-	-
Malpighia umbellata Rose	-	T	-	-	-	S	-	-	TD	-	-	-
MELIACEAE - CHINABERRY FAMILY												
Cedrela odorata L.	-	T	-	-	-	-	-	L	TD	-	-	-
Trichilia americana (Ses. & Moç.) T.D. Penn.	-	T	-	-	-	S	-	-	TD	-	-	-
T. hirta L.	-	T	-	-	-	S	-	-	TD	-	-	-
MORACEAE - MULBERRY FAMILY												
Chlorophora tinctoria (L.) Benth. & Hook. f.	-	T	-	-	-	-	-	L	TD	-	-	-
Ficus cotinifolia H.B.K.	-	T	-	-	-	-	-	L	TD	-	-	-
F. insipida Willd.	-	T	-	-	-	-	-	L	TD	-	-	-
F. maxima Mill.	-	T	-	-	-	-	-	L	TD	-	-	-
F. pertusa L. f.	-	T	-	-	-	-	-	L	TD	-	-	-
F. petiolaris H.B.K.	-	T	-	-	-	-	-	L	TD	(OK)	-	-
F. trigonata L.	-	T	-	-	-	-	-	L	TD	-	-	-
Morus microphylla Buckl.	-	-	N	-	-	S	-	-	-	OK	PN	-
Trophis racemosa (L.) Urban	-	T	-	-	-	-	-	L	TD	-	-	-

MYRSINACEAE - MYRSINE FAMILY												
Ardisia revoluta H.B.K.	-	T	-	-	-	-	M	-	TD	-	-	-
Myrsine coriacea (Sw.) Roem. & Schult.	-	T	-	-	-	-	M	-	-	OK	PN	-
MYRTACEAE - MYRTLE FAMILY												
*Psidium guajava L.	-	T	-	-	-	S	-	-	TD	OK	-	-
P. sartorianum (O. Berg) Ndzu.	-	T	-	-	-	-	M	-	TD	-	-	-
NYCTAGINACEAE - FOUR-O'CLOCK FAMILY												
Pisonia capitata (S. Wats.) Standl.	-	T	-	-	-	S	(M)	(L)	TD	-	-	-
OLACACEAE - OLAX FAMILY												
Schoepfia schreberi J.F. Gmelin	-	T	-	-	-	S	-	-	TD	-	-	-
OLEACEAE - OLIVE FAMILY												
Fraxinus gooddingii Little	-	-	-	-	E	S	-	-	-	OK	-	-
F. papillosa Lingelsh.	-	-	-	R	-	-	M	-	-	OK	PN	MX
F. velutina Torr.	G	-	-	-	-	-	-	L	-	OK	PN	-
OPILIACEAE - OPILIA FAMILY												
Agonandra racemosa (DC.) Standl.	-	T	-	-	-	S	-	-	TD	-	-	-
PLATANACEAE - PLANE-TREE FAMILY												
Platanus wrightii S. Wats.	G	-	-	-	-	-	-	L	TD	OK	PN	-
POLYGONACEAE - BUCKWHEAT FAMILY												
Coccoloba goldmanii Standl.	-	T	-	-	-	S	-	-	TD	-	-	-
RHAMNACEAE - BUCKTHORN FAMILY												
Colubrina triflora Brongn.	-	T	-	-	-	-	M	-	TD	-	-	-
Karwinskia humboldtiana (Zucc.) Roem. & Schult.	-	T	-	-	-	S	-	-	TD	-	-	-
Rhamnus crocea Nutt.	-	-	N	-	-	S	-	-	-	OK	-	-
R. cf. mucronata Schldl.	-	T	-	-	-	S	-	-	-	OK	PN	-
Ziziphus amole (Ses. & Moç.) M.C. Johnst.	-	T	-	-	-	S	-	-	TD	-	-	-
ROSACEAE - ROSE FAMILY												
Prunus emarginata (Dougl.) D. Dietr.	-	-	N	-	-	S	(M)	-	-	-	PN	MX
P. gentryi Standl.	-	-	-	-	E	S	-	-	-	-	PN	-
P. serotina Ehrh. ssp. capuli (Cav.) McVaugh	-	T	-	-	-	-	M	-	-	OK	PN	MX
P. serotina ssp. virens (Woot. & Standl.) McVaugh	-	-	N	-	-	-	M	-	-	OK	PN	-
P. zinggii Standl.	-	-	-	-	E	-	-	L	TD	OK	-	-
Vauquelinia californica (Torr.) Sarg. ssp. pauciflora (Standl.) Hess & Henricks.	-	T	-	-	-	S	-	-	-	OK	-	-
V. californica spp. californica	-	-	N		-	S	-	-	-	OK	-	-
RUBIACEAE - MADDER FAMILY												
Cephalanthus salicifolius Humb. & Bonpl.	G	-	-	-	-	S	-	-	TD	OK	-	-
Hamelia xorullensis H.B.K.	-	T	-	-	-	S	-	-	TD	-	-	-
Hintonia latiflora (Ses. & Moç.) Bullock	-	T	-	-	-	S	-	-	TD	-	-	-
Randia echinocarpa Ses. & Moç.	-	T	-	-	-	S	(M)	-	TD	-	-	-
RUTACEAE - RUE FAMILY												
*Casimiroa edulis Llave & Lex.	-	T	-	-	-	-	M	-	TD	-	-	-
Esenbeckia hartmanii Robins. & Fern.	-	-	-	R	-	S	-	-	TD	-	-	-
Ptelea augustifolia Benth.	G	-	-	-	-	S	-	-	-	OK	-	-
SALICACEAE - WILLOW FAMILY												
Populus angustifolia James	-	-	N	-	-	-	-	L	-	-	PN	-
P. brandegeei Schneid.	-	-	-	R	-	-	-	L	TD	OK	-	-
P. fremontii S. Wats. ssp. fremontii	-	-	N	-	-	-	-	L	-	OK	-	-
P. tremuloides Michx.	-	-	N	-	-	-	M	-	-	-	PN	MX
Salix bondplandiana H.B.K.	-	-	-	-	-	-	-	L	TD	OK	-	-
S. gooddingii Ball	-	-	N	-	-	-	M	(L)	TD	OK	PN	-
S. taxifolia H.B.K.	-	T	-	-	-	S	-	-	-	OK	-	-
SAPINDACEAE - SOAPBERRY FAMILY												
Dodonaea viscosa Jacq.	G	-	-	-	-	S	-	-	TD	OK	-	-
Sapindus drummondii Hook. & Arn.	-	-	N	-	-	S	(M)	-	-	OK	-	-
S. saponaria L.	-	T	-	-	-	-	M	-	TD	-	-	-
Thouinia acuminata S. Wats.	-	T	-	-	-	S	-	-	TD	-	-	-
T. villosa DC.	-	T	-	-	-	S	-	-	TD	-	-	-

SAPOTACEAE - SAPOTE FAMILY												
Sideroxylon capiri (DC.) Pitt. ssp. tempisque (Pitt.) T.D. Penn.	-	T	-	-	-	-	-	L	TD	-	-	-
S. lanuginosum Michx. ssp. rigidum (A. Gray) T.D. Penn.	-	-	N	-	-	S	-	-	-	OK	-	-
S. persimile (Hemsl.) T.D. Penn. ssp. subsessiliflorum (Hemsl.) T.D. Penn.	-	T	-	-	-	-	-	L	TD	OK	-	-
S. tepicense (Standl.) T.D. Penn.	-	T	-	-	-	-	-	L	TD	-	-	-
SIMAROUBACEAE - SIMAROUBA FAMILY												
Alvaradoa amorphoides Liebm.	-	T	-	-	-	S	-	-	TD	OK	-	-
SOLANACEAE - NIGHTSHADE FAMILY												
Cestrum lanatum Mart. & Gal.	-	T	-	-	-	S	-	-	TD	OK	-	-
*Nicotiana glauca Graham	G	-	-	-	-	S	-	-	TD	OK	PN	-
Solanum erianthum D. Don	-	T	-	-	-	S	-	-	TD	-	-	-
STERCULIACEAE - STERCULIA FAMILY												
Guazuma ulmifolia Lam.	-	T	-	-	-	-	M	-	TD	-	-	-
TAMARICACEAE - TAMARISK FAMILY												
*Tamarix ramosissima Ladeb	G	-	-	-	-	S	-	-	TD	-	-	-
TILIACEAE - LINDEN FAMILY												
Heliocarpus attenuatus S. Wats.	-	T	-	-	-	S	-	-	TD	OK	-	-
H. palmeri S. Wats.	-	T	-	-	-	S	-	-	TD	OK	-	-
Tilia floridana Small	G	-	-	-	-	-	M	-	-	-	PN	-
THEOPHRASTACEAE - THEOPHRASTA FAMILY												
Jacquinia macrocarpa Cav. ssp. pungens (A. Gray) Stahl	-	T	-	-	-	S	-	-	TD	-	-	-
ULMACEAE - ELM FAMILY												
Aphananthe monoica (Hemsl.) Leroy	-	T	-	-	-	-	-	L	TD	-	-	-
Celtis iguanea (Jacq.) Sarg.	-	T	-	-	-	S	(M)	-	TD	-	-	-
C. reticulata Torr.	-	-	N	-	-	-	M	-	TD	OK	-	-
*Ulmus pumila L.	-	-	N	-	-	S	-	-	-	OK	-	-
URTICACEAE - NETTLE FAMILY												
Urera caracasana (Jacq.) Griseb.	-	T	-	-	-	S	(M)	-	TD	OK	-	-
VERBENACEAE - VERVAIN FAMILY												
Lippia umbellata Cav.	-	T	-	-	-	S	-	-	TD	OK	-	-
Vitex mollis H.B.K.	-	T	-	-	-	S	(M)	(L)	TD	-	-	-
V. pyramidata Robins.	-	T	-	-	-	S	-	-	TD	OK	-	-
ZYGOPHYLLACEAE - CALTROP FAMILY												
Guaiacum coulteri A. Gray	-	T	-	-	-	S	-	-	TD	-	-	-
	22	166	32	5	8	120	60	54	140	98	75	26

Geographic Variation in Plant Species Richness: Lessons from the Sonoran Desert, U.S.A. and Mexico, and Northern Territory, Australia

Tony L. Burgess[1], Julio L. Betancourt[2], and John R. Busby[3]

Abstract..—Proposed plans for computerized networks of ecological data will involve costly digitizing of existing biological inventories, such as herbaria and museum collections. A potential use of such data is to evaluate and monitor regional biodiversity. We examined variation in the number of vascular plant species per 1° latitude x 1° longitude in digitized inventories for the Sonoran Desert, U.S.A. and Mexico, and Northern Territory, Australia. In both data bases, sampling intensity, rather than environmental or biological factors, explains most of the geographic variation in species richness. The peril to management is that an apparent stability or even an increase in perceived species richness can be created by manipulating the effort given to sampling. Attempts to monitor species richness at landscape to subregional scales will be affected by the quality of the appropriate data bases, and the ability to remedy or correct for sampling bias.

INTRODUCTION

Temporal and spatial variation in diversity are central themes in theoretical and applied ecology. For example, forecasts for future extinctions may be based on the mathematical relation between numbers of species and geographic area, with habitat loss used as a predictor for species loss. Unfortunately, precise estimates of geographic variation in species richness (the simplest measure of diversity), much less the relative abundances of species, are unavailable for most organisms, except for well-known guilds that contain a limited number of species (e.g., oaks in northern Mexico). Even in areas such as the southwestern United States, long considered a haven for naturalists, biological inventories are woefully inadequate for evaluating species-area relations; for relating geographic differences in species richness to historical or physical factors (e.g. climate, soils, or topographic heterogeneity); or for monitoring and predicting how regional diversity might be affected by land use and management.

A common concern about even the best of biological inventories is the degree to which geographic variation in species richness results from unevenness of effort across a region (Connor and Simberloff 1976; Miller and Wiegert 1989) or sampling intensity—i.e., the accumulation of new species as the time spent collecting increases (Soberon and Llorente 1993). Issues such as sample size and sampling effort are dealt with routinely at the plot scale (e.g., Magurran 1988). However, these biases are seldom considered in analyses of species richness at landscape to continental scales, except by paleobiologists sensitive to the fragmentary nature of the fossil record (Raup 1976; Koch 1987). Ecologists working at these larger scales often rely on multiple sources of information collected for various purposes and subject to different biases.

Here, we evaluate the effect of sampling effort on plant species richness at the one degree scale in the Sonoran Desert, USA and Mexico, and Northern Territory, Australia. These are two of the better digitized inventories of plant distribution in the subtropics. We use this simple exercise to

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illustrate how uneven sampling efforts contaminate available data bases and bias our perceptions of regional diversity. These sampling problems should be considered in plans to develop regional and national networks for ecological data.

METHODS

We chose to examine species richness for vascular plants in two relatively well-known semi-arid regions, the Sonoran Desert, U.S. and Mexico, and Northern Territory, Australia. Both areas offered large digitized data bases, each consisting of 80,000-100,000 observations for 3,000-4,000 species distributed across 100-130 one degree cells. Observations consist of either a voucher specimen in a herbarium (Northern Territory), or both voucher specimens and field sightings by a select group of botanists (Sonoran Desert). We compiled the number of species (species richness) and the number of observations (sampling intensity) in each 1° latitude x 1° longitude cell. This is a convenient sampling scale to study the influence of climate, landscape attributes and historical processes on regional diversity (Rickelefs 1987).

The Sonoran Desert analysis is based on an electronic data base of vascular plant distribution (95,000 observations) compiled from 30 years of field logs and supplemented by voucher specimens deposited in regional herbaria (Hastings et al. 1972; Turner et al. in press). We limited our analysis to the 100 grid cells that had more than 15 observations in and around the Sonoran Desert (fig. 1).

The goal of the Sonoran Desert inventory was to extend the earlier biogeographic work of Shreve and Wiggins (1964) in studying the relationships between climate and plant distributions. J.R. Hastings, R.M. Turner, R. Warren and others who compiled this Atlas traveled along roads in Baja California and Sonora, Mexico, making lists of perennial plants at 5-mile intervals, with supplementary observations as needed. The distributional data were augmented by searching collections in regional herbaria (Desert Botanical Garden, San Diego Museum of Natural History, Arizona State University, University of California-Berkeley, University of Texas, and University of Arizona) and copying specimen label data for particular species of interest, so that their total ranges could be represented. Additional data for California and Arizona were taken from site lists gathered from a variety of sources, including the Bureau of Land Management, The Nature Conservancy, doctoral dissertations, and helpful field ecologists.

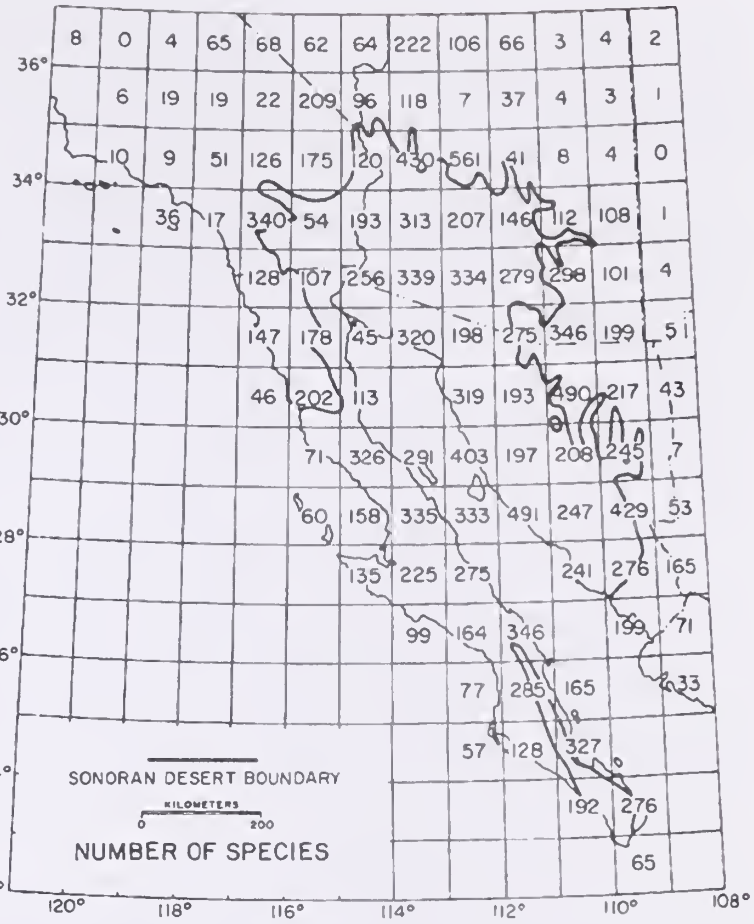

Figure 1.—Map of Sonoran Desert, with number of species per one degree cell.

Various biases have influenced the Sonoran Desert data. The focus was on perennial plants and there are few observations of annuals and short-lived perennials. A general lack of interest in grass identification led to significant underrepresentation of grasses. Observations were concentrated near roads, and many disjunct populations in rugged terrains probably were overlooked. This bias has made it especially difficult to accurately represent the upper elevational limits for most species. More importantly, the Atlas focused on desert elevations and ignores plant distributions in the so-called "sky islands" of southern Arizona and northern Mexico.

The central Australian data consist of an electronic data base for 78,000 voucher specimens in the Northern Territory Herbarium, Darwin, which has been digitized into the Environmental Resources Information Network (ERIN), Australian National Parks and Wildlife Service. ERIN was established in 1989 to provide geographically-related environmental information of an extent, quality and availability required for planning and decision making (Slater 1992;

Tindale-Biscoe 1992). We selected Northern Territory because it is subtropical region of comparable size (129 one degree cells) to the Sonoran Desert with an available digitized inventory of vascular plants.

To assess geographic sampling bias, we constructed one degree gridded maps of the Sonoran Desert and Northern Territory showing variations in the number of species and number of observations (figs. 1-4). In addition, we composed scatter plots of number of species versus number of observations per one degree cell in each of the two regions (figs. 5-6). Because most of the statistical assumptions would have been violated, we did not attempt to fit curves to these data to predict the sample size needed to sample species richness in the "average" grid cell. Although we do not present them here, species accumulation curves for individual cells might have been used to predict the total number of species expected in a given cell (Soberon and Llorente 1993).

RESULTS

Figure 2 shows that sampling was clearly not consistent throughout the Sonoran Desert region. The Sonora coast and the Vizcaino region of Baja California are better represented than the Lower Colorado Valley of southeastern California and the northeastern edge of the Sonoran Desert in Central Arizona. The maps of the number of plant species (fig. 1) and observations in each grid cell (fig. 2) indicate that the pattern of species richness is strongly associated with the number of observations and with latitude. A plot of the number of species versus the number of observations showed that up to a certain threshold (ca. 1900 observations), the number of species observed in the Sonoran Desert is closely related to the number of observations (fig. 5). The large scatter in number of species in grid cells on the higher end of the curve suggests that, in the Sonoran Desert, 2000 observations may be an appropriate sample size to estimate species richness. At this sample size, there may be real rather than perceived differences in the number of species between grid cells.

The maps of the Northern Territory (fig. 3 and 4) reflect relatively heavy sampling in the vicinities of Darwin and Alice Springs, with low numbers of observations thoughout the remainder of the Territory. This confirms spatial analysis of the Census of Australian Vascular Plants, which showed a strong tendency for plant species richness to reflect the population density of plant collectors (Bullen 1991). Figure 6 shows an even closer relationship between number of species and number of observations in Northern Territory than in the Sonoran Desert, even in grid cells with more than 2000 observations. There are at least two explanations: (1) sampling intensity affects inventories from voucher specimens in herbaria more than databases that include additional sources of information; (2) because of less topographic heterogeneity, there are a few abundant species and many rare ones in Northern Territory, requiring greater sampling than in the Sonoran Desert, where many species occur in common abundance.

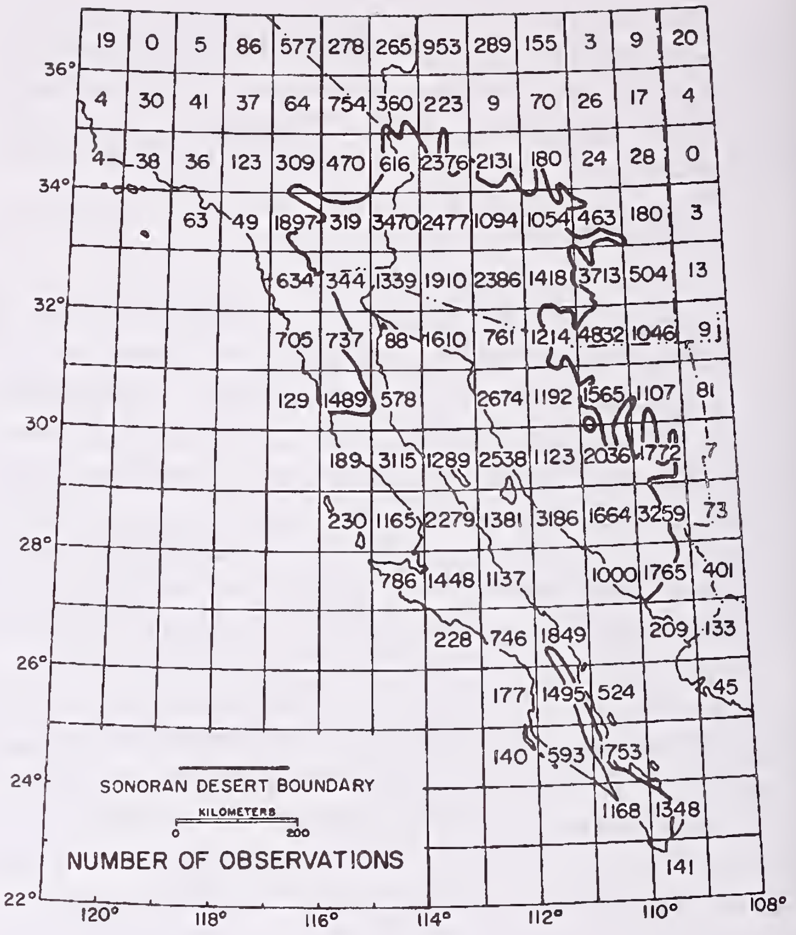

Figure 2.—Map of Sonoran Desert, with number of observations per one degree cell.

DISCUSSION

Most ecologists have an intuitive grasp of diversity patterns that is actually supported by gross comparison of comprehensive regional inventories. For instance, few of us would object to Rzedowski's (1993) rough sketch of floristic richness in Mexico, which contrasts the impoverished Yucatan Platform with the rich band across the Sierra Madre del Sur (Oaxaca) and Sierra Madre de Chiapas. But geographic variations in floristic richness may not always be this apparent, even at this gross scale. For example, one might assume that strong Mexican influence on both the Sonoran Desert and sky islands would contribute to greater species richness in Arizona than in New Mexico. In reality, there is very little difference between the two floras. Arizona has 3,370 species spread across 294,000 km^2 (0.0115 species/km^2) (Kearney and Peebles 1951); New Mexico has 3,728 species spread across 314,260 km^2 (0.0119 species/km^2) (Martin and Huizona, high floên the Sonoran òands is offset by low species richness on the Colorado Plateau. New Mexico includes three relatively rich floristic provinces with a number of endemics: the northern Chihuahuan Desert, the Southern Rockies, and the southern High Plains.

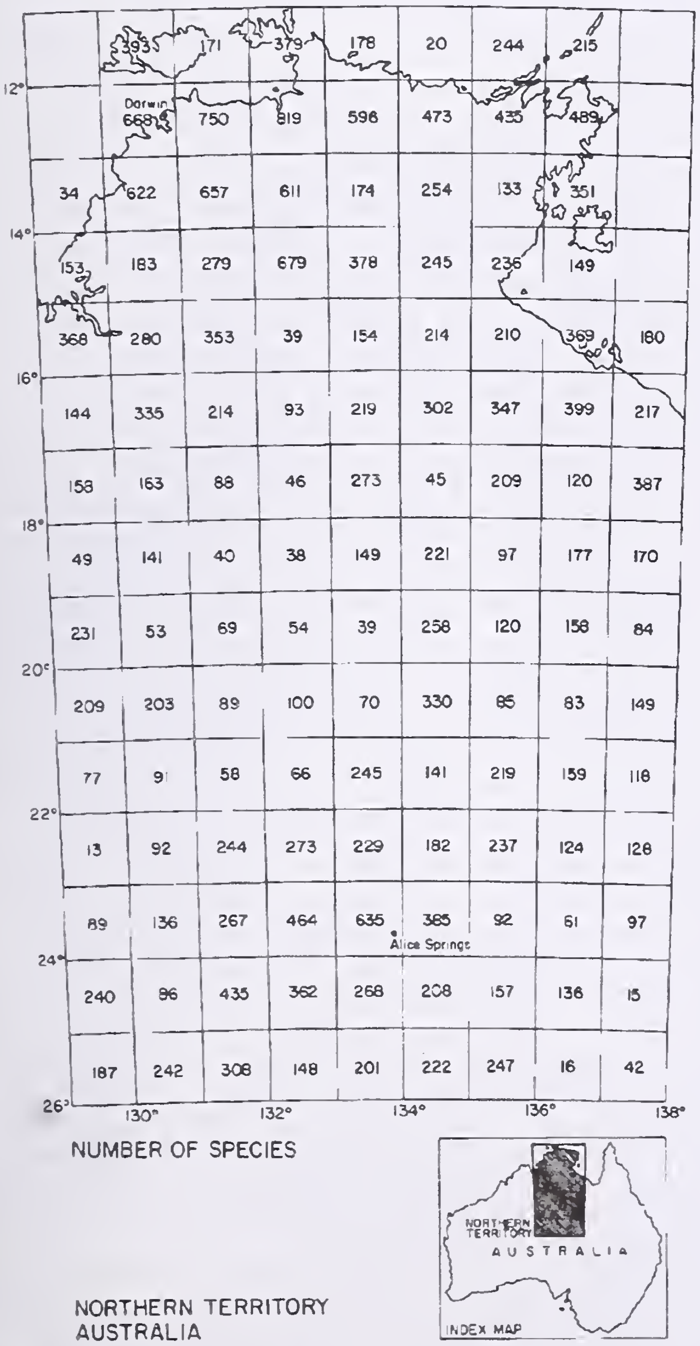

Figure 3.—Map of Northern Territory, Australia, with number of plant species per one degree cell.

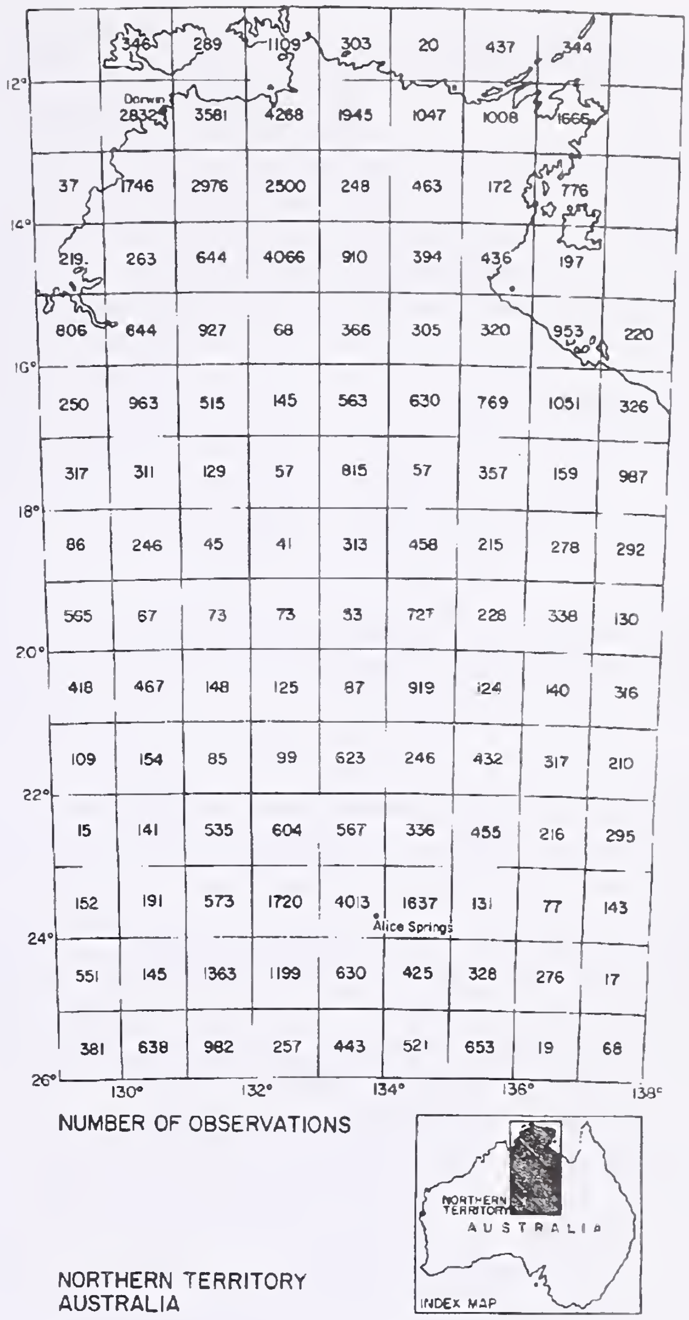

Figure 4.—Map of Northern Territory, Australia, with number of observations per one degree cell.

As the scale of analysis is narrowed to a one degree cell, or approximately 1/30 of either Arizona or New Mexico, there is an overlap in size with natural landscapes (e.g., one of the sky islands), as well as typical land management units (e.g., a district within a particular National Forest or a BLM management area). At this scale, we can no longer rely on comprehensive floras, but must depend on inventories that, if available, are of variable quality. One degree is also a geographical scale where local and regional processes interact to determine species richness (Ricklefs, 1987). The analysis of patterns in these kinds of data bases promises many insights into the relative importance of historical and environmental factors in producing biodiversity, but the validity of conclusions will depend on how well the effects of

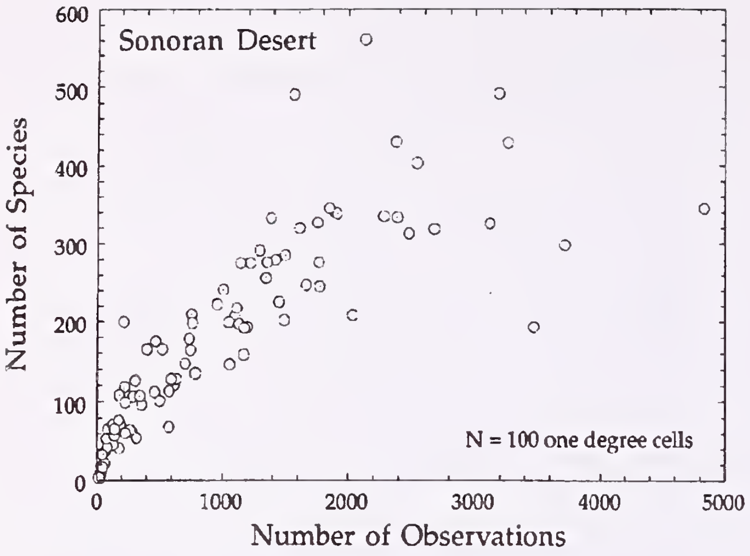

Figure 5.—Scatter plot showing the number of species as an increasing functions of the number of observations in the Sonoran Desert data base ($y = 66.397 + 0.109x$, $r^2 = 0.70$).

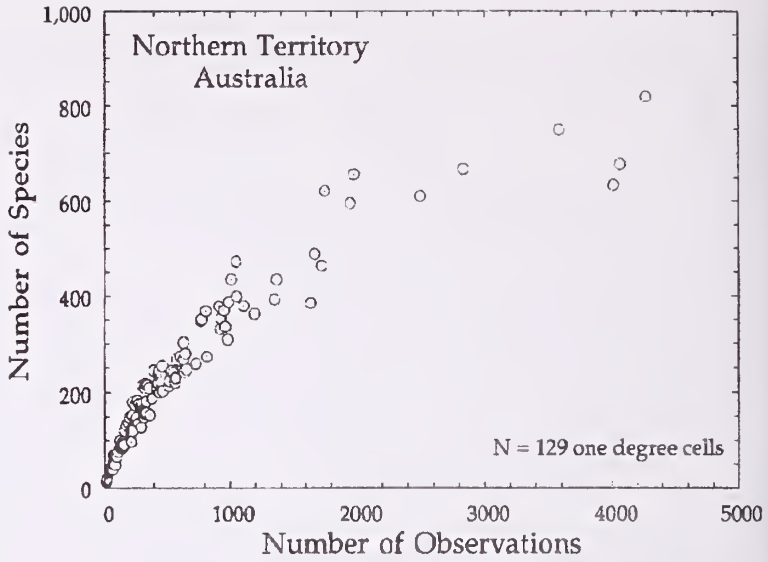

Figure 6.—Scatter plot showing the number of species as an increasing functions of the number of observations in the Northern Territory data base ($y = 105.21 + 0.195x$, $r^2 = 0.85$).

sampling bias can be estimated. Obviously, any attempt to monitor species richness at the landscape scale will be affected by both the availability and quality of the appropriate data bases.

There appear to be four important corollaries from our findings:

1. Our understanding of biotic diversity is obscured by inadequate sampling. This hinders the prediction of consequences deriving from proposed management actions.
2. Not only does inadequate sampling underestimate biodiversity, but an apparent stability or even an increase in perceived species richness also can be created by manipulating the effort given to sampling.
3. Monitoring and evaluating diversity in species-rich, complex landscapes such exist in the southwestern U.S. and northern Mexico will require heroic efforts that will be hard to fund on a long-term basis. Add to this the political complexity of an international boundary and several federal and state agencies, and the task at hand seems even more daunting. Even so, assembling and maintaining such data sets will be critical to the success of biodiversity and global change research as well as to effective management.
4. As with many good investments, the payback from thorough inventories will be slow at first, and the full profit can only be realized with a sustained commitment to providing fundamental information.

It is unconventional to offer methodological hindsight in a scientific paper, but in the context of this conference we believe that sharing our experience in the assembling a data base for the Sonoran Desert may help others avoid similar pitfalls. To effectively manage and maintain biodiversity, we need a much better understanding of how the existing pattern of diversity emerges from the behaviors of populations. With an understanding of dynamics in patterned landscapes, the possible consequences of proposed management actions will become clearer. Learning how to collect and analyze information most effectively is a critical skill for organizations charged with management responsibilities.

Inventories for Baja California and Sonora were started before reliable maps were available. Our location data for these areas were necessarily limited to a precision of 0.1 degree of latitude and longitude. Locality data on herbarium specimens was often imprecise, hence much time was spent resolving uncertain location descriptions, and trying to estimate elevation for geographic locations. This level of resolution and uncertainty has constrained the utility of the Sonoran Desert database for future research. The production of detailed topographic maps for Mexico and the decreasing cost of global position systems promise much greater precision in location coordinates at a reduced cost per location. There is no longer any excuse for professional collectors in the region to have sloppy locality data.

Our understanding of basic autecology would have been greatly expanded had we developed and used a consistent, digitizable system to describe the landscape context where observations were made. An early example is the British Ecological Survey habitat system designed for punch-cards (Elton 1966). Descriptive coding systems for the following information would greatly augment the utility of field observations:

1. Radiant loading, as estimated by slope and aspect.
2. Rainfall runoff or run-on, estimated by topographic position.
3. Vegetation structure. The strictly structural categories used by Mueller-Dombois & Ellenberg (1974) would be adequate.
4. Associated plant species. If listing immediate neighbors is too time-consuming, at least include a biogeographic context, perhaps using the biotic provinces system of Brown and Lowe (1980; see also Brown 1982).
5. Geomorphic context. The categories developed by Peterson (1981) for the Basin and Range physiographic province are appropriate for the southwestern U.S. and Mexico.
6. Lithological and pedological context. These need not be excessively detailed. Simple categories of limestone, granitic, etc. for rock types and alluvium, calcrete, aeolian sand, etc. for soil origin would serve.
7. Substrate surface characteristics, estimated by texture categories that extends from boulder to clay size classes. Most of the critical properties of soil for vegetation dynamics in arid and semiarid systems can be discerned from the top 40 cm of the profile.
8. For species of interest, estimates of the population status in terms of local abundance would be an important addition to a biodiversity database. This could take the form of size distributions within a site, which would be time-consuming to record, or simple densities estimated to the nearest power of two (McAuliffe 1990). The presence and abundance of seedlings should be estimated to evaluate whether or not populations are self-sustaining across the species' range.

Finally, proposed plans to create clearinghouses for ecological data (Raven and Wilson 1992; Craft 1994; National Research Council 1993; Stone 1994) will be compromised by several disturbing trends. Funding for museum, herbaria and other "collecting" institutions is on the downswing, as is expertise in systematics and identification (Systematics Agenda 2000, 1994). Historically, federal agencies have not pooled resources to archive and digitize ecological data, and they now face the formidable task of building data bases and information systems at a time of dwindling resources.

Research scientists tend to focus on general phenomena, and hence they are often less concerned with tracking local details and history. Research institutes and laboratories may not be the best nexuses for ecosystem monitoring. Local naturalists tend to focus on details and natural history, and may not perceive trends or patterns at other scales. They may be unwilling or unable to undertake analysis and evaluation of complex data. Managers need resolution of local details and history in a context of general phenomena and large-scale trends. Hence the organizational framework for monitoring and evaluation must connect scientists, local naturalists and ecosystem managers in a way that empowers and inspires each group.

It is important for the credibility of management that managers are not solely responsible for evaluating effects of their management. If an organization is to continue receiving a mandate for ecosystem management, managers and evaluators should be at least partly independent. Present trends for downsizing indicate that our land and resource management agencies will lack sufficient resources for monitoring and analyzing biotic diversity at the levels desired. The mandate for ecosystem management may impose an unsustainable burden on present institutional resources. Of governmental bodies in the United States, the newly created National Biological Survey seems to be an appropriate context to build the appropriate environmental data sets and information systems. However, an example of what could be accomplished in a relatively short time frame is the five-year (1980-1994) effort to develop the Environmental Resource Information Network (ERIN) in Australia.

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Landscape Complexity, Soil Development, and Vegetational Diversity Within a Sky Island Piedmont:

A Field Trip Guide to Mt. Lemmon and San Pedro Valley

Joseph R. McAuliffe[1] and Tony L. Burgess[2]

Abstract.—This paper focuses on the broad, gently sloping piedmonts between elevations of approximately 950-1450 m which flank the mountains of southeastern Arizona and adjacent regions. The first part briefly reviews general patterns of complexity in geomorphology and soils, how soil characteristics affect water dynamics, and the responses of plants to various soil water conditions. The second part is a detailed road log for a 72 km (45 mile) field trip in the piedmont of the Santa Catalina Mountains near the towns of Oracle and San Manual in Pima and Pinal Counties, Arizona. This road log includes eleven interpretive stops where a variety of complex landscape, soil, and vegetation relationships are presented. This field guide provides a detailed overview of the types of landscape and ecological complexity that are found throughout many piedmonts of the American Southwest.

INTRODUCTION

The "Sky Islands" of the American Southwest are rich reservoirs of biological diversity. The sharp climatic gradients along these abrupt mountain slopes lead to the juxtaposition of floral and faunal elements from more than a dozen degrees latitude to the north and south. Some of the first ecologists to work in the American Southwest focused on the climatic factors responsible for the striking zonation of biotic communities ranging from low elevation desertscrub to the woodlands and coniferous forests of higher elevations (Merriam 1890, Shreve 1915).

Microclimate differences of different slope exposures often produce abrupt vegetation contrasts within small areas, contributing to the diversity of the biota found at any single elevation. Drought-adapted but cold intolerant species extend their upper elevation ranges on warm southern exposures and more mesophytic species extend downward into the arid elevations on cooler, moister northern exposures. Additional ecological variability is often encountered at a single elevation that cannot be explained by such microclimate differences. Such variability is common in the semiarid piedmonts that flank the Sky Island mountains. In these semiarid environments, moisture is typically the most important factor limiting plant growth. Subtle differences in soil conditions greatly affect quantity, timing, and vertical distribution of available soil moisture. Differences in soil moisture regimes within this zone translate into predominance by different life forms of plants. The considerable edaphic variation within the semiarid piedmonts produces complex mosaics of several different kinds of vegetation including woody scrub, grassland, savanna, chaparral, and woodland. In addition, many of these communities are unstable mixes of different species that can undergo rapid shifts in relative dominance in response to disturbances caused by weather events, fire, or grazing (Martin 1975). What results is a virtual 'Ecological Confusion Zone' that is widespread across the semiarid American Southwest. Our goal in this paper is to present a basic framework of knowledge regarding landscape evolution, soil development, and water dynamics that can explain some of these ecological complexities.

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Geologic History of Basin and Range Landscapes

Within the American Southwest, the repeating pattern of isolated mountains separated by broad basins is due to crustal stretching, faulting, and the downdrop of basins relative to uplift of ranges. This process began 12-15 million years ago. Since that time, erosion of upland ranges has contributed vast amounts of sediment that fill adjacent basins. The surface landscape features of most piedmonts are typically of Quaternary age (formed within the last 2 million years) or of late Tertiary age (e.g., see Pearthree et al. 1988). These surface features may consist of either constructional landforms (such as alluvial fans) or degradational landforms, such as pediments produced through erosion of pre-existing landscapes. Piedmonts often consist of distinct alluvial fan deposits that vary widely in age and erosional dissection. Deposition of alluvium within these landscapes has been spatially and temporally discontinuous, producing mosaics of different-aged constructional surfaces (Gile 1975, Peterson 1981, Bull 1991). The morphology and areal extent of different-aged alluvial fan surfaces varies from piedmont to piedmont due to a variety of factors. Where basin floors are in the process of being dissected by erosion due to regional base-level fall, piedmonts are typically deeply incised and contain stair-stepped sequences of alluvial fan remnants of various ages (fig. 1). Base-level lowering of the valley floor has given rise to such stair-stepped sequences of piedmont landforms in a number of areas in Arizona including the San Pedro, Upper Gila, and Upper Verde River valleys. Topographic differences among alluvial fan surfaces of various ages are considerably more subtle in valleys lacking such marked base level change, for example, the Sulfur Springs Valley in southeastern Arizona which lacks an external drainage. Nevertheless, spatially discontinuous burial of older surfaces by younger alluvium and the erosion of older surfaces contributes to complex landscape patterns even in piedmonts that contain relatively smooth, unbroken slopes (Peterson 1981). In addition to alluvial deposits, erosional surfaces cut into bedrock or older alluvial deposits (pediment landforms) may exhibit considerable variability in surface stability and the length of time that has elapsed since past episodes of erosion.

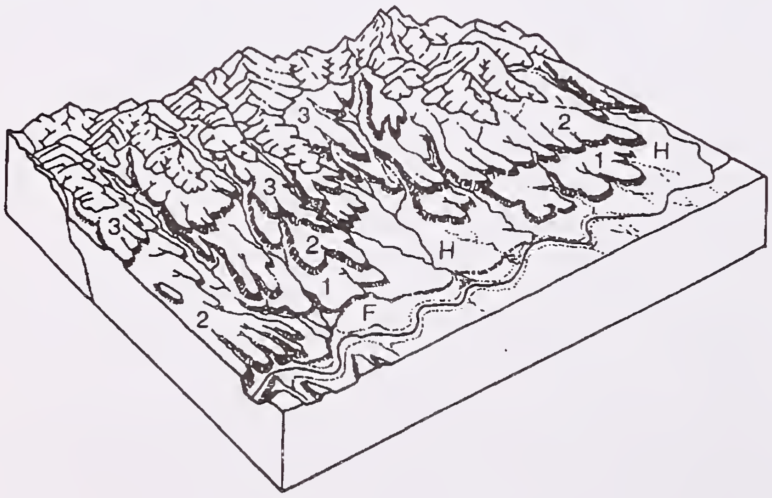

Figure 1.—Block diagram of a highly dissected piedmont in a basin that has experienced substantial lowering of base-level due to incision of the basin floor by an exterior drainage. The piedmont consists of a stair-stepped sequence of alluvial fan remnants with progressively younger surfaces inset within the topographic confines of dissected, older surfaces. Surfaces 1-3 represent Pleistocene surfaces (3=oldest, 1= youngest), H is a Holocene surface and F indicates floodplain deposits associated with the stream of the basin floor. (Adapted from Peterson 1981).

Soil development is in part dependent on the passage of time, therefore, knowledge of the ages and spatial distribution of various parts of the landscape is a prerequisite to understanding soil variability. Two soil horizons typically form and become increasingly strongly developed in noncalcic, gravelly to stony parent materials of fan deposits in arid and semi-regions of the southwest: a clay-enriched argillic horizon and a calcic horizon enriched with calcium carbonate (Gile et al. 1965, Gile and Grossman 1968, Gile 1975, Gile et al 1981, McAuliffe 1994, McAuliffe 1995)(fig. 2). Argillic horizons are extremely important in these semi-arid environments because the considerable water-holding capacity of clay greatly affects infiltration of precipitation, the soil depth at which water is stored, and the seasonal duration of water availability (Walter 1973, Noy-Mier 1973, McAuliffe 1994, 1995, Burgess 1995).

Different spatial and temporal distributions of soil water contribute to the predominance of different plant life forms. Various plant life forms are above-ground expressions of different modes of water use that are generally correlated with different spatial and temporal patterns of below-ground water acquisition. Shallow-rooted plants including most perennial grasses, succulents, and some small, drought-deciduous shrubs are subjected to highly variable water supplies in the uppermost soil horizons. The persistence of these plants is dependent on the intensive exploitation of a highly seasonal pulses of shallow soil moisture coupled with a capacity for either drought-induced dormancy or the storage of water in succulent tissues that enables continued photosynthetic activity into the dry season (fig. 3)(Sala et al. 1982; McAuliffe 1994, 1995). On the other hand, the deeper root systems of most large woody plants occupy a soil environment that exhibits less seasonal variation in water availability (Noy-Mier 1973, Schlesinger et al. 1987, Burgess 1995). The extensive, deeper root systems of these plants are capable of extracting the more widely distributed but more constant supplies of water stored at greater soil depths.

The following field trip guide examines a variety of these relationships between landform development, soils, and vegetation responses within a 200 km2 area of the piedmont flanking the northeast side of the Santa Catalina Mountains (fig. 4).

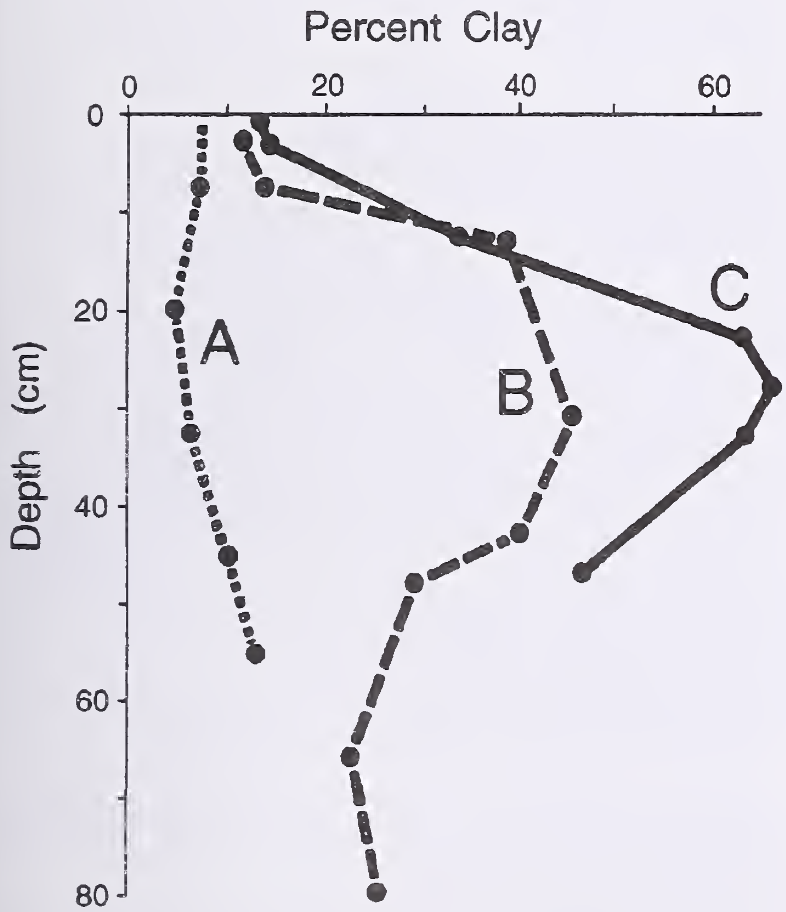

Figure 2.—Accumulation of clay as a function of soil age in coarse gravelly-stony, non-calcic alluvium in a semiarid zone (700-730 m elevation) on the east-facing piedmont of the Tucson Mountains. A - late- to mid-Holocene surface, B - Middle Pleistocene surface, C - Early-Middle Pleistocene surface. Soil data from soil profiles "A", "C", and "D" of McAuliffe (1994), Appendix C.

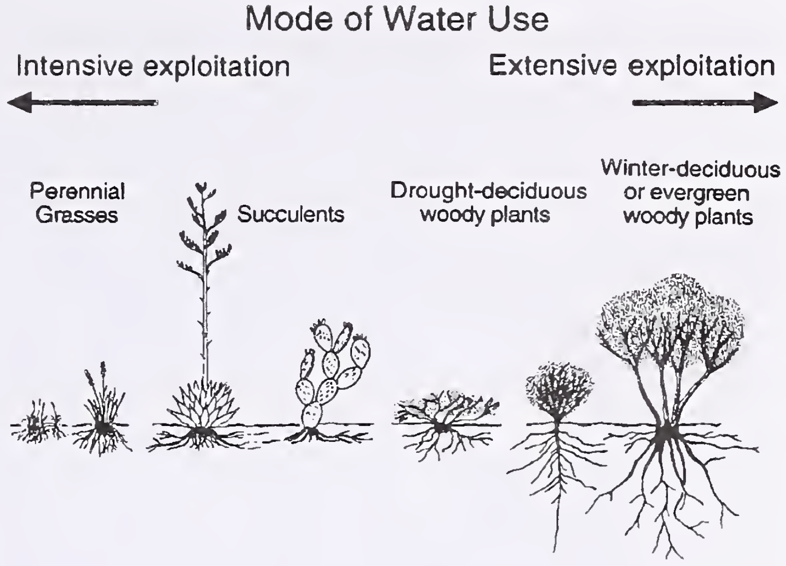

Figure 3.—Mode of water use as a function of above-ground plant life form and associated rooting patterns of plants of semiarid environments.

PART 2: FIELD TRIP GUIDE

Plan two days to complete the entire set of 11 interpretive stops. Stop 5B at the mid-way point of the trip is an area suitable for overnight camping and is far removed from the main road. Developed campground facilities are also present at the Coronado National Forest Peppersauce campground (mile 5.6). A detailed mileage log is for the trip is listed below, followed by a discussion of each of the interpretive stops. Plant species are referred to by scientific names but Appendix 1 also provides a list of common names.

Fieldtrip Mileage Log

mile (km)

0.0 (0.0) - Stop 1 at Ray Spring Hill [on Mt. Lemmon Rd. 2.6 miles (4.2 km) southeast of junction with Oracle business loop of Rte. 77]. General overview of vegetation variability within a small area and of the field trip area to the east and south.

0.5 (0.8) - Junction with Webb Road, turn right (south), remaining on Mt. Lemmon Rd.

1.5 (2.4) - Cross streambed at American Flag Ranch

1.8 (2.9) - Stop 2 at base of grassy hillslope. Example of soil with strong argillic horizon formed on an ancient pediment remnant. Contrast between soils of grass-dominated sites and microphyllous scrub.

2.5 (4.0) - Madrugada Ranch road, continue south on Mt. Lemmon Rd.

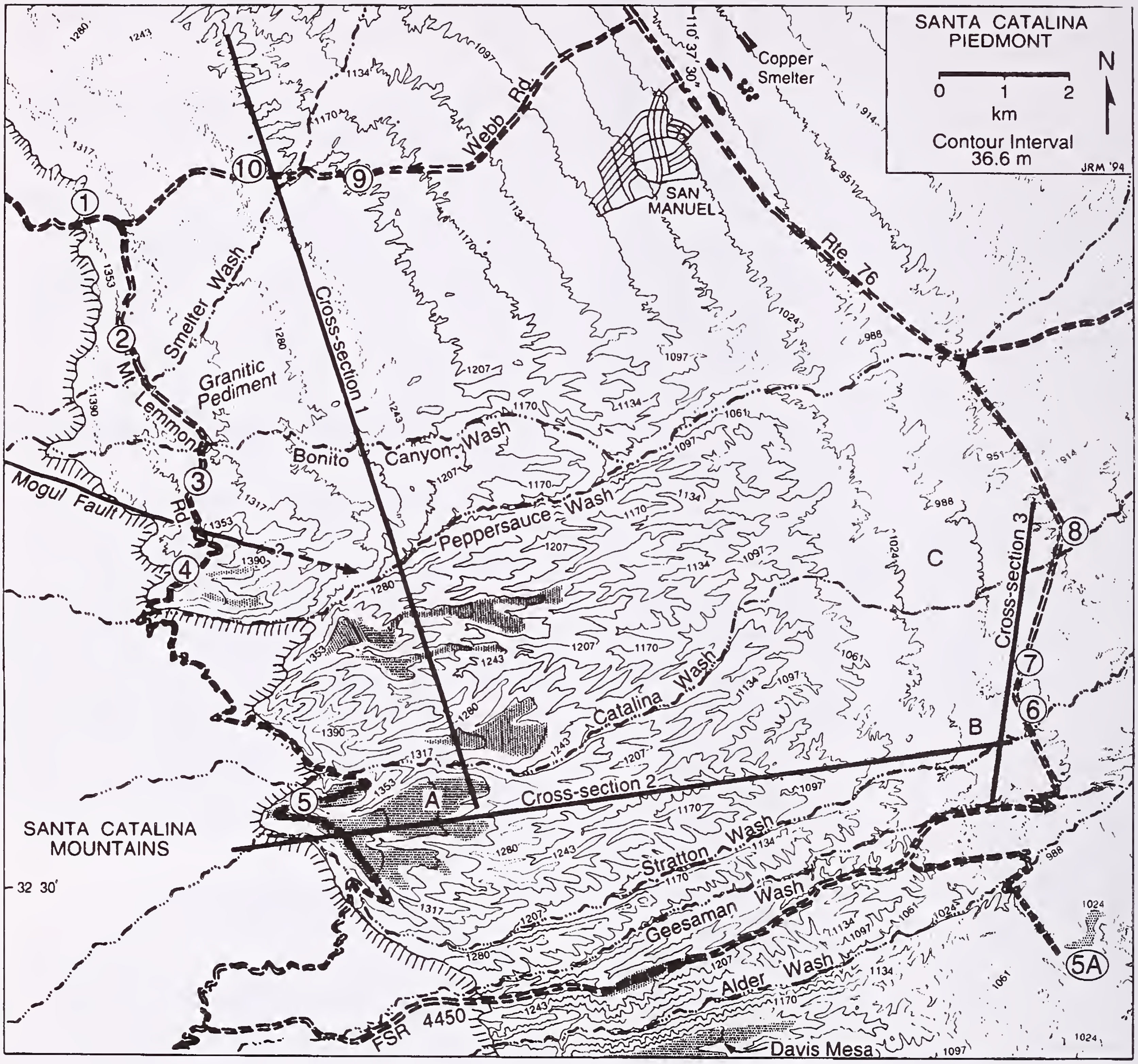

Figure 4.—Map showing route to the 11 field trip stops. Cross-sections 1, 2, and 3 are detailed in Figure 8. Shaded areas "A", "B", and "C" indicate early, middle, and late Pleistocene alluvial fan remnants, respectively, as discussed in text.

2.7 (4.3) - Stop 3 at road cut through granitic pediment surface showing soil structure and root distributions. Proceed south on Mt. Lemmon Rd. Climb up ridgeline across the Mogul fault, from Precambrian granitic rocks (quartz monzonite, commonly called "Oracle granite" to mixed bedrock terrain.

4.4 (7.1) - Summit of ridgeline mantled by early Pleistocene alluvium

5.0 (8.0) - Stop 4 at borrow pit on east side of road. Examination of species-rich vegetation on limestone slopes and how shallow, cemented calcic horizons of soils at foot of slopes affect vegetation. Proceed southwest on Mt. Lemmon Rd.

5.6 (9.0) - Coronado National Forest Peppersauce Campground. Proceed generally south toward Mt. Lemmon. Traverse area of diverse slope exposures and lithologies with juxtaposed grassland, savanna, scrub, and woodland. Rocks are mostly massive, highly fractured shales with some hard, argillaceous sandstones and conglomerates. Occasional highly eroded remnants of late Tertiary and earliest Pleistocene alluvium.

9.2 (14.8) - Cross Catalina Wash. Climb up slope onto earliest Pleistocene alluvial fan remnant covered by savanna with *Hilaria belangeri* and *Prosopis velutina*.

10.0 (16.1) - Stop 5 on planar surface of earliest Pleistocene alluvial fan remnant. Contrast soils and vegetation of remnant surface with those of adjacent, south-facing erosional slopes. Proceed in southerly direction toward Mt. Lemmon.

16.1 (25.9) - Turn left (east) onto Forest Service Road 4450. **CAUTION—DANGEROUS INTERSECTION DUE TO HEAVY TRUCK TRAFFIC FROM MINE.** Proceed east and downhill toward San Pedro River Valley, from warm temperate woodland, savanna, and grassland into subtropical (Sonoran) desertscrub.

23.8 (38.3)- Optional turnoff to the south on unimproved road to stop 5A. This 2.5 mile (4 km) spur leads to a mesa-like landform mantled by earliest Pleistocene alluvium and well-developed, clayey soils supporting savanna. The relative isolation of this site has led to little use by livestock. A comparison of this site with Stop 6 indicates the degree to which use of landscapes by livestock has altered vegetation compositions. The road to stop 5A requires a high-clearance vehicle, but a 4-wheel drive vehicle is unnecessary. To reach the site, travel eastward on the unimproved road, cross the gas pipeline corridor at 0.8 mi (1.3 km) and continue east. At 1.2 mi (1.9 km) from the exit from the main road, the road loops to the south, crosses Alder Wash, climbs the hills south of the wash, eventually linking with the gas pipeline corridor. Follow the pipeline road to a saddle 2.5 mi (4.0 km) from FSR 4450. Stop 5A is located atop topographic high located to the immediate east. Retrace route to return to FSR 4450.

23.8 (38.3) - Return to FSR 4450 from road to Stop 5A (5 miles to Stop 5A not included in mileage total)

24.5 (39.4) - Cross natural gas pipeline corridor

25.3 (40.7) - Turn north on abrupt switchback to enter canyon of Geesaman Wash

25.6 (41.2) - cross Geesaman Wash

25.8 (41.5) - road curves to the north and climbs onto a middle-Pleistocene alluvial fan remnant

26.6 (42.8) - Stop 6 at road cut immediately north of Stratton Wash exposing soil profile in middle Pleistocene alluvial fan remnant. Desertscrub with *Acacia constricta, Zinnia acerosa, Isocoma tenuisecta, Cercidium microphyllum, and Opuntia* spp. on soil with well developed argillic horizon. Example of grazing-induced conversion of savanna to desertscrub accompanied by erosion of surface soil horizons.

26.9(43.3) - Road cut at north margin of middle Pleistocene fan remnant exposing mantle of stony Pleistocene alluvium capping fine-grained Tertiary basin deposits.

27.2 (43.8) - Stop 7 at road cut on highly dissected, fine-grained alluvium of latest Pleistocene to earliest Holocene age. Desertscrub dominated by Larrea tridentata.

28.1(45.2) - Stop 8 on late Pleistocene alluvial fan deposit dominated by Cercidium microphyllum and *Carnegiea gigantea*.

28.5 (45.9) - entrance on east to Black Hills limestone quarry; continue north.

30.3(48.8) - Junction with State Route 76, turn left (northwest) toward San Manuel. **CAUTION—DANGEROUS INTERSECTION.**

34.2 (55.0) - McNab Parkway junction and Chevron store in San Manuel; continue north on Route 76.

34.9 (56.2) - Turn left (southwest) onto Webb Road. Proceed uphill on mixture of gravelly fan deposits and young pediment surfaces cut into Tertiary deposits. Vegetation is a mosaic of desertscrub and savanna with widespread invasion by *Eragrostis lehmanniana*.

38.2 (61.5) - Stop 9 at south-facing hillslope beneath ridge with microwave antennae dishes. Site of burn in August 1993. Contrasting vegetation responses on different soils. Proceed west and upslope across ridgelike landforms capped with earliest Pleistocene quartzite alluvium.

39.0 (62.8) - Cross Smelter Wash

39.2 (63.1) - Turn right (northwest) onto pipeline road. Proceed past gate. **REMEMBER TO CLOSE GATE.**

39.5(63.6) - Stop 10 at excavated cut along base of ridge to west of road. Dissected piedmont with savanna and scrub. Influence of weathering-resistant diabase dikes on development of landforms and soils. Sequences of pedogenesis and erosion have created a context for complex, fine-scaled vegetation patterns. Turn around and retrace route along pipeline road toward Webb Road.

39.9 (64.2) - Turn right (west) on Webb Road toward Oracle.

41.5(66.8) - Turn right (northwest) onto Mt. Lemmon Rd. toward Oracle.

44.6(71.8) - Junction with business loop 77 at Hildreth's Market in Oracle, turn left (west) toward Tucson.

Stop 1: Ray Spring Hill, Elev. 1380 m

From the top of the hill about 100 m north of the road we can view the Santa Catalina Mountains to the southwest, the granitic landscapes of the Oracle pluton to the west, and the piedmont sloping eastward to the San Pedro River. Within view is an elevational gradient from a subhumid temperate climate supporting a "sky island" forest on the mountain peaks to a semi-arid subtropical climate on the valley bottom. The field trip route traverses landscapes between the lower edge of Madrean woodland at an elevation of about 1450 m and the uppermost Sonoran Desertscrub at 950 m (fig. 4). Complex surface geology and landform development have generated correspondingly complex soil patterns across this piedmont. This edaphic complexity in a semiarid climate has produced a mosaic of scrub, savanna, and woodland vegetation: an 'ecological confusion zone' which is widespread at this elevation in the American Southwest (Burgess 1995).

The ridgetop we are standing on is a diabase mass covered by an open savanna of scattered *Calliandra eriophylla, Yucca baccata* and *Dasylirion wheeleri* in a mosaic of grasses including *Hilaria belangeri, Bouteloua curtipendula, B. eriopoda, Heteropogon contortus,* and *Aristida purpurea* var. *wrightii.* This grass-dominated vegetation contrasts strongly with the sclerophyllous scrub and woodland of *Quercus emoryi, Arctostaphylos pungens,* and *Ceanothus greggii* on the adjacent coarse-grained, light-colored granitic rock called quartz monzonite (often referred to in this locale as "Oracle granite"). This pluton of quartz monzonite contains numerous northwest-trending intrusions of dark-colored diabase and occasionally, light-colored aplite (Wallace 1954, Creasey 1967, Brown 1970). At this stop, the road cuts through dikes of these intrusive rocks. Some parts of the diabase intrusion are deeply weathered whereas other parts are extremely weathering resistant. These differences in weathering have influenced the development of landforms and soils and ultimately greatly affect plant distributions. These relationships are examined in detail at the next stop.

Stop 2: Grassy Hillslope South of American Flag Ranch, Elev. 1355 m

Parts of a northwest-trending diabase intrusion have weathered and eroded more slowly than the surrounding quartz monzonite, forming the hills to the west and northwest. The grass-dominated lower hillslope contrasts sharply with the microphyllous scrub on the weathered quartz monzonite landscape located to the east of the road. Immediately west of the road is a contact between the coarse-grained quartz monzonite and a fine-grained, deeply weathered diabase (fig. 5A). The hillcrest consists of diabase that is considerably more resistant to weathering. Weathering-resistant diabase cobbles derived from upslope have mantled portions of the lower slope, armoring and protecting parts of the underlying, highly weathered diabase and quartz monzonite from erosion. Past episodes of clast accumulation on this hillslope apparently stabilized the surface and enabled formation of strongly developed soils. The hillslope is a mosaic of ancient armored pediment remnants containing these well-developed soils and erosional incisions into

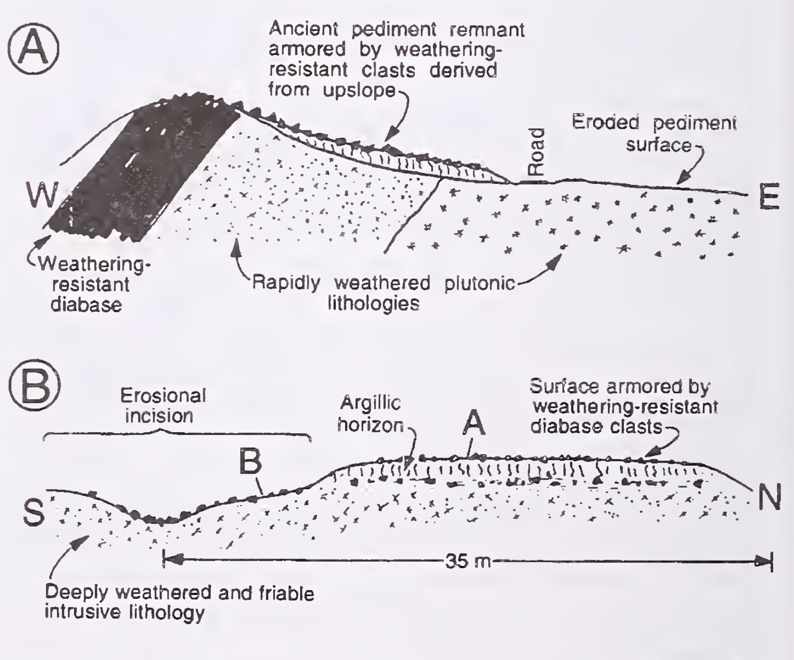

Figure 5.—Landscape cross-sections in vicinity of Stop 2. A. East-west section through hillslope. B. North-south section along foot of hillslope. Area "A" on the armored pediment remnant is dominated by the short, sod-forming grass, Hilaria belangeri and the small drought-deciduous subshrub Calliandra eriophylla. At area "B" along erosional incisions where argillic horizons have been completely truncated, the grass Bouteloua eriopoda is dominant together with patches of B. curtipendula and Calliandra eriophylla on deeply weathered, friable diabase.

the ancient pediment surface. The armored pediment remnants are slightly convex features elevated slightly above adjacent erosional incisions (fig. 5B). Soils of these armored pediment remnants contain very strongly developed, reddened argillic horizons (fig. 6). A long history of surface stability was required for the formation of these argillic horizons. Soils with this degree of development suggest an age of at least late- to mid-Pleistocene. Relatively dense cover by the sod-forming *Hilaria belangeri* protects this soil from erosion much of the time, but when grass cover is markedly reduced by drought or fire, the armoring by surface diabase clasts plays a critical role in stabilizing the surface (see McAuliffe 1995). The diabase clasts found on the surfaces of these ancient pediment remnants are well-rounded due to weathering, and an abundance of rounded pea- to marble-sized weathered diabase fragments indicates that a considerable amount of time has passed since this surface was originally mantled with once larger, more angular clasts derived originally from upslope locations. The weathering and gradual diminution of the surface armoring of diabase cobbles has contributed to erosion of parts of the armored pediment and truncation of the well-developed soils at eroded margins of the remnants. As the older surface erodes, clasts accumulate in the incisions (fig. 5B). The accumulation of a substantial mantle of new diabase cobbles in some of these incisions has led to the diminishment or cessation of channel cutting which may in turn allow new episodes of pedogenesis on these more recently formed, lower surfaces.

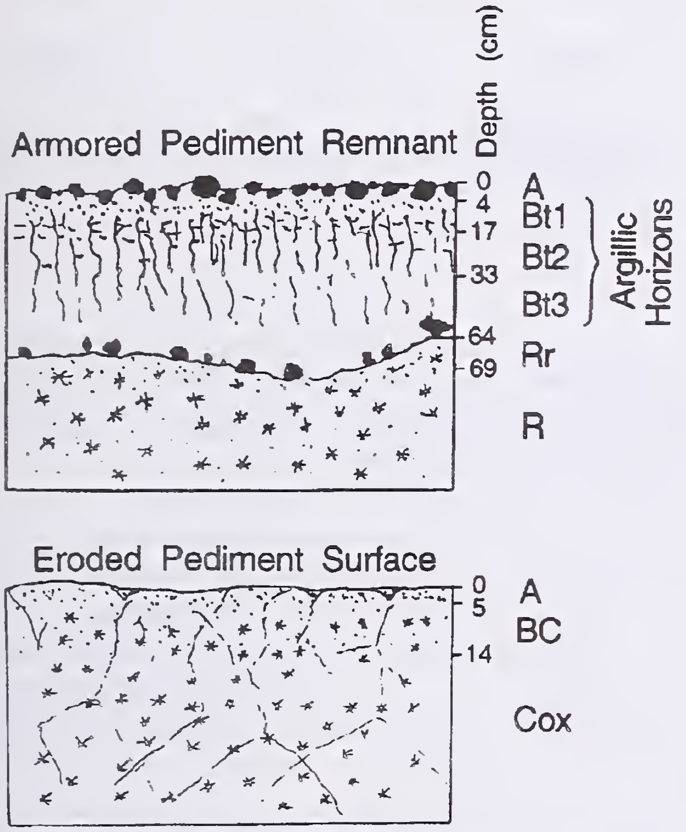

Figure 6.—Soil profiles of the armored pediment remnants at Stop 2 (upper) and the quartz monzonite pediment dominated by woody species at Stop 3. The soil of the armored pediment remnant has a sandy clay loam A horizon. Textures of underlying argillic horizons are clay loam in the Bt1 horizon, grading to clay in the Bt2 and Bt3 horizons. Rr is soft, highly weathered bedrock grading downward to less weathered bedrock (R). The R horizon is apparently not the parent material for the overlying soil, as indicated by the stone line of clasts of a different lithology scattered just above the Bt/Rr boundary. Plant roots (primarily H. belangeri) are common in the A and Bt horizons, but are scarce below the Bt2 horizon.

The young soil of the quartz monzonite pediment has a gravelly sandy loam A horizon. The BC horizon is highly weathered and altered bedrock with a gravelly sandy clay loam texture. The Cox horizon is massive weathered granite with variably spaced joint and shear fractures. Some clay accumulation has occured along these fractures. Plant roots are common in the A horizon, relatively scarce in the BC, and abundant in joints and fractures within the Cox horizon. Soil horizon nomenclature follows Birkeland (1984).

The soils with strong argillic horizons are dominated by *Hilaria belangeri* and *Calliandra eriophylla*. Where the armored pediment remnants have been completely truncated by erosion, friable, coarse textured soils on the deeply weathered, soft diabase favor Bouteloua eriopoda. Soils occupied by B. eriopoda have considerably deeper infiltration and storage of water (fig. 7A) than do those occupied by the shallow-rooted *H. belangeri* (fig. 7B). Quartz monzonite surfaces to the east of the road with poorly formed soils have little stored moisture near the surface but substantial storage along fissures and cleavage planes (fig. 7C). Such soil moisture conditions tend to favor woody plants with extensive root systems.

Stop 3: Granitic pediment surface, Elev. 1340 m

The surface of the quartz monzonite pediment has eroded too fast to allow substantial pedogenesis. The rate of erosion of this pediment surface is indicated by the difference in elevation (about 20-40 m) between the pediment surface and the east-west trending ridges located 1-2 km to the south (Figs. 4, 8A). This abrupt topographic transition marks the east- to west-trending Mogul Fault separating the rapidly weathering, coarse-grained quartz monzonite pluton to the north from a variety of more weathering resistant lithologies to the south. The uppermost crests of the elevated ridges to the south of the Mogul Fault are mantled with coarse, stony alluvium thought to have been deposited approximately 2 million years ago at the time of the Pliocene-Pleistocene transition. A few ridgeline remnants capped with this earliest Pleistocene alluvium are located within the main body of the eroded pediment to the north, indicating an extensive elevated surface mantled by fan deposits once apparently spanned the entire front of the Santa Catalinas within the area of the field trip (fig. 8A). Large areas of these ancient alluvial deposits have been preserved only when they have mantled weathering or erosion-resistant lithologies or have been in topographic positions that have resisted rapid erosional incision (further discussion at Stop 10). Apparently, the area of the quartz monzonite pediment we are presently observing has experienced a net lowering by erosion of approximately 20-40 m during the last two million years.

Soils on this pediment show relatively little pedogenic alteration, often consisting of a thin, gravelly sandy loam A horizon directly over BC and Cox horizons derived from weathered quartz monzonite (fig. 6B). The weathered Cox horizon contains variably spaced joint and shear fractures. Rainfall penetrates along these fractures, creating a deep, uneven distribution of soil moisture (fig. 7C). The extensive root systems of woody shrubs and subshrubs are better suited to exploit moisture from this edaphic environment than are the shallow, diffuse root systems of perennial grasses. Winter-deciduous woody plants, including *Mimosa biuncifera, Prosopis velutina,* and *Acacia greggii* predominate over most of the pediment. These winter-deciduous species flower and are in leaf during the extended pre-summer dry period, indicating that their extensive root systems are tapped into relatively deep, dependable stores of moisture found along the deep bedrock fissures. Another dominant plant, the small, drought-deciduous subshrub *Eriogonum wrightii,* has relatively shallow roots that occupy shallow fractures which are more prone to seasonal drought. At slightly higher elevations this substrate supports sclerophyllous chaparral and evergreen oak woodland.

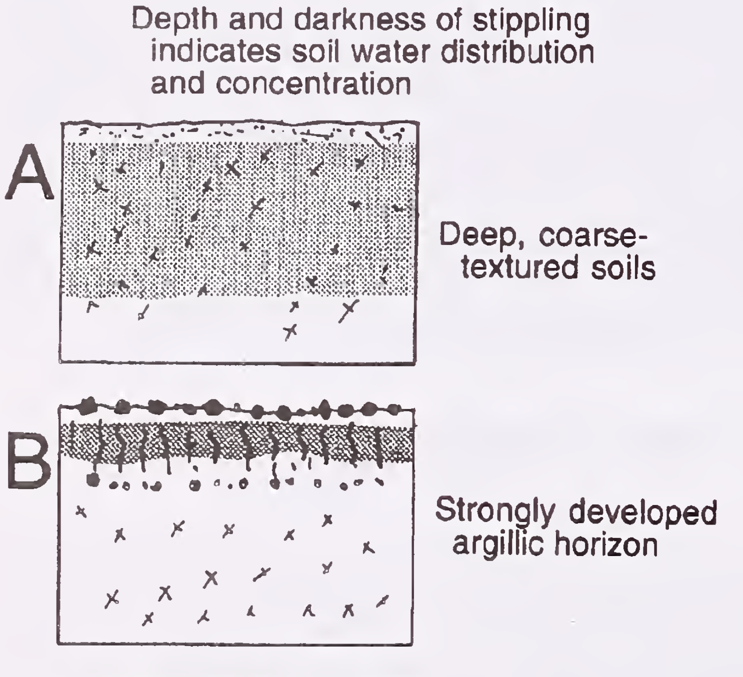

Figure 7.—Vertical distributions of moisture in three different soils following a moderate rain after the onset of a drying cycle. A. Deep, coarse-textured soils such as those occupied by Bouteloua eriopoda at stops 2, 5, and 10 have relatively deep infiltration and storage. B. Due to the high moisture holding capacity of clay, soils with strong argillic horizons retain most water near the surface. C. Weathered and fractured bedrock contains considerable moisture stored at depth within fissures, but little water in thin soil horizons near the surface.

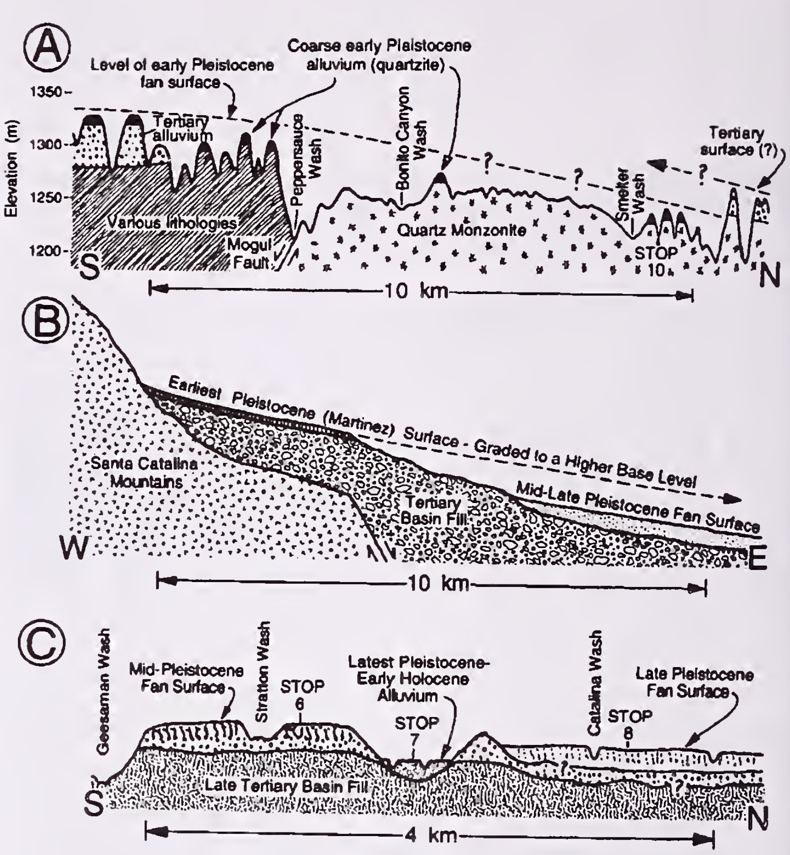

Figure 8.—Landscape cross-sections of field trip area indicated on map of Figure 4. A. Cross-section 1; surface features drawn to scale at a vertical exaggeration of 14.5:1. B. Cross-section 2 (diagrammatic representation, not to scale). C. Cross-section 3 (diagrammatic, not to scale).

Lithological variation within the pediment has contributed to topographic and soil variability. Occurrences of small areas of darker granodiorite and thin intrusive dikes of more weathering-resistant diabase have locally impeded erosion of the pediment surface, producing slight topographic convexities. The road cuts through several of these convexities, revealing the underlying lithological variation. The somewhat greater but highly localized surface stability present on these convexities has contributed to more strongly developed soils. These soils often contain moderately well developed argillic horizons that support a greater abundance of perennial grasses.

Stop 4: Borrow Pit on West Side of Road, Elev. 1460 m

The hillslope of weathered Missisippian Escabrosa limestone west of the road supports a high diversity of plant growth forms and species. This limestone slope contains the greatest number of species and plant life forms of any of the stops along the field trip route. Varied edaphic conditions contribute to this diversity. Mesic edaphic conditions are created by the presence of deep fractures and cleavage planes and large solution pockets filled with loamy soil. Xeric edaphic conditions are present where extremely thin soil layers mantle massive, unfractured bedrock or in very small, soil-filled solution pockets (fig. 9). This mosaic of moisture regimes allows the coexistence of species with very different strategies of soil moisture extraction and use. The vegetation contains many species capable of intensively exploiting shallow, highly seasonal supplies of water, including the many species of perennial warm-season grasses, agaves, cacti, and *Fouquieria splendens*. Conversely, the slope also contains large evergreen woody shrubs such as *Dodonaea viscosa* and *Cercocarpus montanus* which indicate the presence of more seasonally constant, deeper soil moisture sources.

Other factors may also influence the vegetation of limestone landscapes and need further investigation. The basic pH of limestone-derived soils may diminish the availability of phosphates to some plants (McGeorge 1942). The high specific heat of limestone may ameliorate the effects of episodes of extreme cold. This allows some plants and ground-dwelling insects to reach their northern and upper elevation limits on limestone outcrops (Lindroth 1953).

The borrow pit is located at the foot of the limestone slope. The east-facing wall of the pit exposes soils that have developed in carbonate-rich materials that have accumulated on top of bedrock at the foot of the limestone slope. In arid and semi-arid climates, a high carbonate content of parent materials impedes the development of a clay-enriched argillic horizons (Gile et al. 1981), but may accelerate the formation of strong calcic horizons that eventually become cemented and alter the penetration of soil moisture. Toward the center of the exposure along the east-facing wall of the borrow pit, a moderately strongly cemented calcic horizon is located relatively deep (up to 60 cm). Two large woody plants, *Prosopis velutina* and *Acacia constricta* are codominants in this relatively deep soil. However, immediately south of the borrow pit, the rooting environment is considerably shallower with massively cemented calcic horizons present at depths of 15-35 cm. In the more xeric edaphic conditions created by this shallow cemented calcic horizon, *A. constricta* is dominant and *P. velutina* is rare. The capacity for drought deciduousness in *A. constricta* may enable this woody species to predominate in the slightly more xeric soil conditions south of the borrow pit.

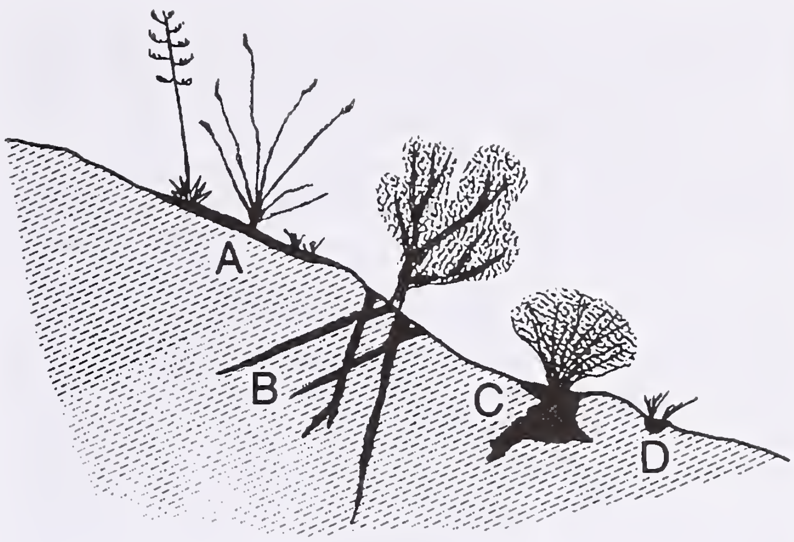

Figure 9.—Varied soil microenvironments in limestone terrains of semiarid landscapes that support a variety of plant life forms. A - shallow, drought-prone soil over bedrock occupied by xerophytic plants capable of intensive, short-duration exploitation of water; B and C - deep fissure planes and solution pockets that store considerable moisture required for large evergreen and winter-deciduous woody plants with extensive root systems; D - shallow, soil-filled solution pockets occupied by intensive water exploiters.

Stop 5: Early Pleistocene Alluvial Fan Remnant, Elev. 1430 m

The elevated, planar surface that we climbed after crossing Catalina Wash is a remnant of an ancient geomorphic surface known as the

Martinez Surface (see Morrison 1985). A geomorphic surface is an area of the land surface that formed during a defined time period and is readily distinguished from adjacent areas by topographic and stratigraphic relationships (see Peterson 1981). Well-preserved planar remnants of the Martinez surface are found throughout southern Arizona, flanking the fronts of many mountain ranges (Menges and McFadden 1981; Morrison 1985). Planar remnants of this surface typically slope away from the mountain front with an inclination of 2-5%. In many cases the upper, planar features of the Martinez surface have been completely removed by erosion, yielding long, subparallel ridges separated by deep ravines (fig. 8A).

In the study area, the Martinez Surface consists of a relatively thin layer of extremely coarse alluvium thought to have been deposited approximately 2 million years ago near the time of the Pliocene-Pleistocene transition. Considerably thicker Tertiary alluvial deposits underlie the thin upper mantle of the earliest Pleistocene alluvium (fig. 8A,B). These underlying Tertiary deposits are exposed along the road south of the Catalina Wash crossing. The coarse, earliest Pleistocene alluvium on the surface includes cobble- to boulder-sized clasts of weathering-resistant quartzite and metamorphosed conglomerate. One of the most distinctive lithologies is the Barnes Conglomerate. These lithologies are exposed in a 3-5 km-wide band located directly south of the Mogul Fault (the Precambrian Apache group and the Cambrian Bolsa and Troy Quartzites)(Ariz. Geol. Soc. 1952, Ariz. Bur. Mines 1959). The presence of remnants of alluvial mantles containing clasts derived from these Cambrian and Precambrian strata in various places across the quartz monzonite pediment to the north indicates that Pleistocene-aged alluvial fans once apparently flanked the entire mountain front within the area of the field trip. However, these fan deposits have been nearly completely removed by erosion in the area of the wide granitic pediment to the north of the Mogul Fault (fig. 8A; see further discussion at Stop 10).

Catalina and Stratton Washes located directly to the north and south of this fan remnant drain large watersheds in the Santa Catalina Mountains (fig. 4). These two drainages provided the runoff and coarse alluvium that contributed to creation of the original fan deposit in earliest Pleistocene times. However, since the deposition of the ancient fan, both washes have incised to a depth of approximately 60 m below the fan's original surface (Figs. 4, 8A). Consequently, the fan remnant has not been hydrologically connected to the substantial watersheds of the mountain slopes for a long time and the only runoff across the surfaces of the planar remnant is derived exclusively from precipitation falling directly on the limited area of the remnant (the shaded area labeled "A" in fig. 4). The preservation of the wide, planar surface of this fan remnant is due, in part, to the physical armoring provided by the large, weathering-resistant metamorphic clasts. The substantially less energetic runoff originating solely from within the planar fan remnant is generally incapable of moving the large cobbles and boulders that were deposited by much larger and powerful stream systems during the fan's original creation. Erosional truncation of this surface proceeds principally by slope retreat at the abrupt margins of remnants overlooking the canyon-like drainages of major streams. The principal erosion occurring on planar surfaces is the selective removal of fines. Large boulders on the surface frequently exhibit a iron oxide-stained collar up to 30 cm above the current soil surface, indicating the erosional removal of some of the fine-textured, reddened soil.

Soils and vegetation. The stability of the planar remnant surface has led to the development of soils with extremely strongly developed, reddened argillic horizons. Color, clay accumulation, and structural development of this soil greatly exceed the clayey soils of the armored pediment remnants of Stop 2, indicating considerable age differences between these two soils. Below the thick argillic horizon is a well developed calcic horizon. The Tertiary deposits beneath the Pleistocene alluvium also contains abundant carbonate, probably of pedogenic origin.

Under the current climate, rainfall seldom penetrates deeply into this clay-rich soil. Consequently, grasses, especially the shallow-rooted *Hilaria belangeri*, are favored at an elevation where woodland might otherwise develop. Shrubby mesquite trees are widespread across the surface and may persist due to their ability to exploit water stored beneath surfaces of large rocks and boulders which is inaccessible to the shallow root systems of grasses.

Soils that mantle the erosional sideslopes differ from those of the upper Martinez surface. Even within a single slope, soils and associated vegetation can vary considerably. For example, directly south of this stop, the moderately steep, south-facing slope (35% inclination), despite continuity in aspect and inclination, contains a sharp transition in soils and dominant grass species (fig. 10). In parts of the slope located below the intact, planar Martinez surface, clay-rich colluvium derived from the argillic horizons of the upper Martinez surface mantles the slope environment (fig. 10A,B). This clay-enriched soil supports a very open savanna vegetation dominated by the grasses Bouteloua curtipendula, Bouteloua filiformis, *Hilaria belangeri, Heteropogon contortus,* abundant *Calliandra eriophylla,* and widely scattered *Prosopis velutina, Acacia constricta,* and *Ferocactus wislizenii.* This slope continues to the west, but as the upper planar remnant of the Martinez surface narrows and is eventually erosionally truncated, soils in downslope locations change markedly. Argillic horizons have been completely lost from this ridgeline remnant and calcic horizons are exposed on the surface of the ridge along the road. In the absence of a source of clay-rich colluvium, soils on the slopes below this ridge are deep, gravelly, calcareous loams (fig. 10). The dominant perennial grasses in this edaphic setting are *Bouteloua eriopoda* and *Tridens muticus* together with *Acacia constricta, Prosopis velutina, Calliandra eriophylla,* and *Fouquieria splendens.*

Profiles of root distributions from the upper Martinez surface, the clay-enriched slope, and the calcareous loam slope indicate considerable differences in the vertical distribution of soil moisture that is related to texture (fig. 11). The clay-rich soil of the intact, planar Martinez surface has an extremely low infiltration capacity. In this soil, the average time required for the infiltration of 1 cm depth of water in dry soil applied in a 15.3 cm diameter ring was 6 minutes, 52 seconds. Additionally, the extremely high water-holding capacity of the clayey soil retains most of the water near the surface, contributing to the dominance of shallow-rooted *H. belangeri* (fig. 11). Infiltration capacities on adjacent erosional slopes are considerably greater, ranging from 21-47 seconds for infiltration of 1 cm depth of water. However, where somewhat finer textures and correspondingly higher moisture-holding capacities are found in subsurface horizons of soils on clayey colluvium (fig. 10B), water would be stored more shallowly than in the loose, calcic loam where a clay-enriched horizon is absent (fig. 10C). These subtle differences in sideslope soils apparently contribute to the predominance of different grass species with differing root distributions (fig. 11B,C).

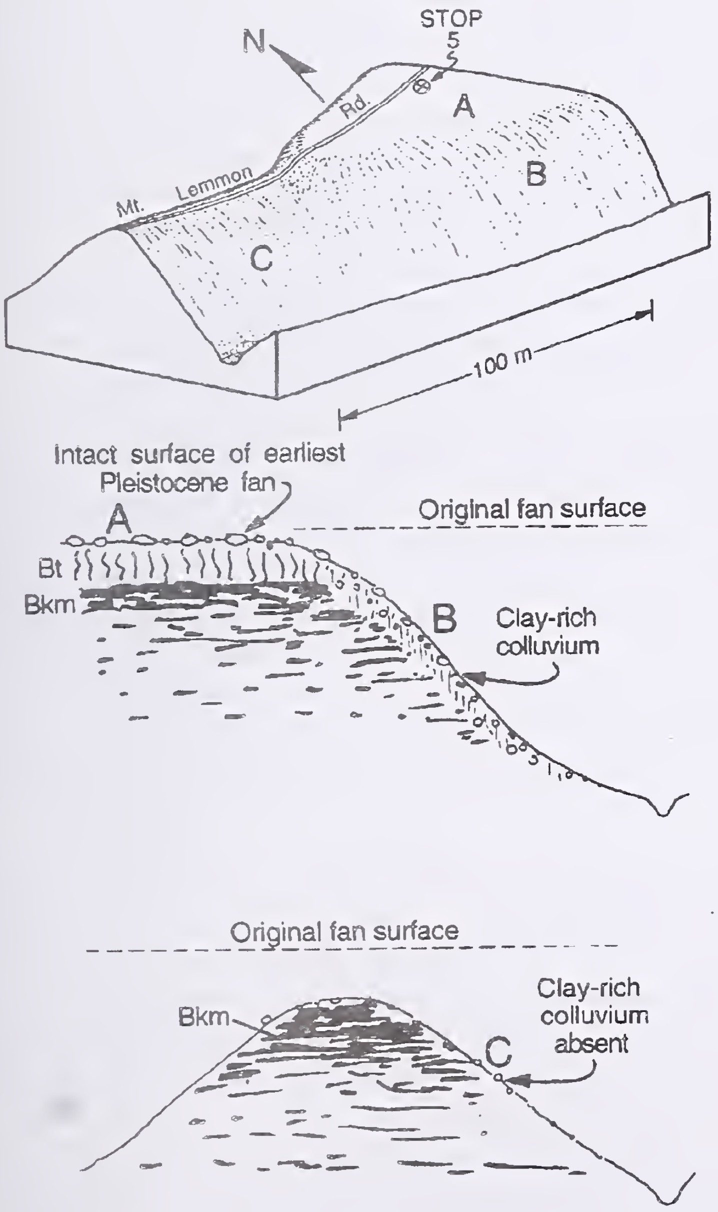

Figure 10.—Block diagram and landscape cross sections showing location and features of the three different soil environments (A, B, C) discussed in the text. The Bt horizon is a clay argillic horizon; Bkm is a massively cemented calcic horizon which is highly weathered and degraded at the surface.

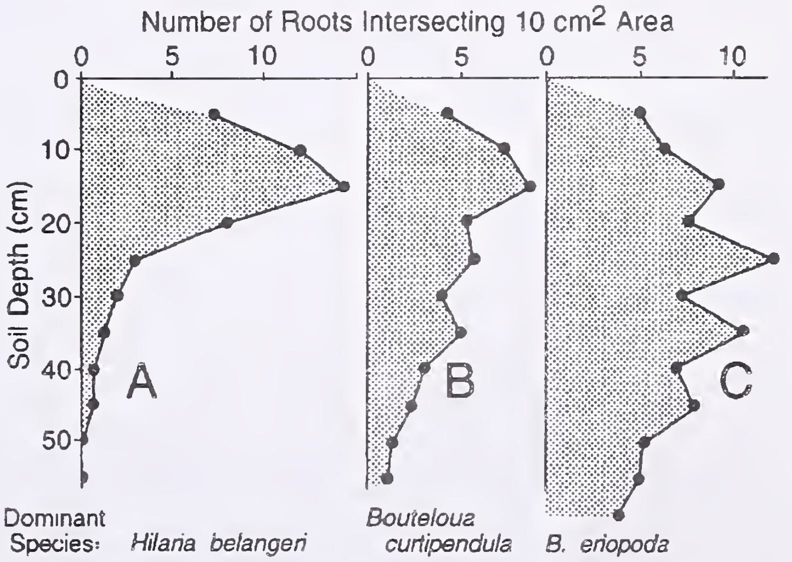

Figure 11.—Root densities of soils from the three different landscape positions (A, B, C) at Stop 5 indicated in Figure 10. Each data point consists of counts of the numbers of roots intersecting three separate 2 cm X 5 cm sample areas in freshly excavated soil pits.

Optional Stop 5A: Lower Elevational Remnant of Martinez Surface, Elev. 1060 mThe top of the mesa-like landform to the east of the saddle where we are parked is an isolated, lower elevational remnant of the Martinez surface. Notice the quartzitic composition of the coarse alluvium capping the remnant is identical to that of the Martinez surface at Stop 5. Finer-grained, calcareous Tertiary deposits underlie the earliest Pleistocene alluvium. Soils with strongly developed argillic horizons mantle the planar surface of the remnant. This surface was once continuous with that of Davis Mesa, located 5 kilometers to the west (fig. 4). Extensive erosion of lower parts of the piedmont have long since removed the once extensive Martinez surface with the exception of this isolated remnant and another narrow ridgeline located 1 km to the northwest.

This isolated remnant is 350 m lower in elevation and 12 km further away from the mountain front than the site at Stop 5. Both factors contribute to increased aridity (lower precipitation and higher temperatures) of the lower site and plant species characteristic of subtropical Sonoran desertscrub are present. *Acacia constricta, Cercidium microphyllum*, and *Prosopis velutina* are the dominant woody species, but these small trees and a diverse array of other woody and succulent plants are inserted in a nearly ubiquitous matrix of perennial grasses. Relatively steep escarpments surround the remnant with the exception of the west end near our parking place. This relative inaccessibility has contributed to little use of the mesa top by domestic stock and considerable cover by perennial grasses has been maintained. This condition contrasts strongly with Stop 6 where a long history of heavy use by livestock apparently has virtually eliminated perennnial grasses from similar, clayey soils. *Hilaria belangeri* is the dominant grass and is abundant in spaces between trees and shrubs, although it does not cover the soil surface as completely as it does in higher elevations. *Bouteloua trifida* is locally dominant in some places where *H. belangeri* is absent. In addition to these two short grass species, the taller grasses *Aristida ternipes, A. purpurea, Setaria macrostachya, Digitaria californica, Bothriochloa barbinodis*, and *Muhlenbergia porteri* are common. The taller, highly palatable grass species are frequently found in the open and are ungrazed, indicating lack of use of the area by livestock. Other grasses present include *Hiliaria mutica, Bouteloua curtipendula, Heteropogon contortus*, and occasionally, the introduced South African *Eragrostis lehmanniana*.

Notice the relatively small sizes of *Cercidium microphyllum, Prosopis velutina,* and *Acacia greggii*. The small stature of these species may be due to limited infiltration of precipitation to substantial depth in the clayey soil. A similar condition exists in the clayey soils at Stop 6, but contrasts strongly with Stop 8 where more permeable soils are present.

Stop 6: Middle Pleistocene Alluvial Fan, Elev. 990 m

North of Geesaman Wash, we began to cross a series of alluvial fan surfaces that are lower in projected elevation and younger than the Martinez surface (fig. 8B). The road cut at this stop shows a fairly old soil containing a well-developed, reddened argillic horizon above a strongly cemented calcic horizon. A soil with this strength of development suggests the fan deposit dates to as old as the mid-Pleistocene. The surface soil horizon has a clay loam texture that impedes rapid infiltration. Presence of soil pedestals beneath some perennial plants and a varnish line on some stones above the present soil surface indicates a history of recent erosion of the A horizon.

A few species of perennial grasses found at Stop 5A are found at Stop 6, but they are exceedingly rare, typically persisting beneath the protective, spiny canopies of acacias or cacti. Before the late nineteenth century, the site probably supported a savanna with considerably greater grass cover, similar to that of Stop 5A. The complete absence of *Hilaria belangeri* from the site is an anomaly, as this grass species and others are present on another Pleistocene fan surface at a lower elevation (927 m), 6 km directly north of Stop 6. Loss of grass cover at Stop 6 may be one factor that has contributed to the accelerated surface erosion, potentially producing a self-enhancing feedback loop of soil degradation that further inhibits recovery of grasses, even if all livestock grazing on the site were to end (see Schlesinger et al. 1990). The abundance of the short-lived, drought-deciduous subshrub *Zinnia acerosa* may be a vegetation response that followed grass decline. This shrub is uncommon in the grass-occupied site at Stop 5A. An independent line of evidence indicating a long history of use by livestock is the great abundance of Opuntia fulgida. The easily detached, spine-covered stem joints are readily spread when they impale the hide of livestock, leading to local increases in areas of livestock concentration. An earthen watering tank, located 0.5 km to the south of our stop and immediately west of the road, encourages the persistent use of this area by stock, despite the general absence of quality forage.

Note the small size of the woody plants *Cercidium microphyllum, Prosopis velutina,* and *Acacia constricta*; we will compare their sizes with those at Stop 8.

Stop 7: Fine-Grained Latest Pleistocene to Earliest Holocene Alluvial Deposit

The gravelly layer that forms the surface of this alluvial terrace is probably a latest Pleistocene or earliest Holocene deposit (fig. 8B). The small drainage basin that supplied these fine-grained, calcareous sediments extends only 2 km to the west of the road in an area of highly dissected, calcareous Tertiary deposits. The absence of an argillic horizon is due to two factors: (1) insufficient time has passed for considerable pedogenic change and (2) abundant carbonates in the original parent material inhibit clay translocation and accumulation within an argillic horizon (Gile et al. 1981). Examination of the soil reveals some structural development of the B horizon (cambic B horizon). *Larrea tridentata* is clearly dominant here, in marked contrast to its virtual absence on the clayey soil at Stop 6. The exclusion of this shrub from soils with strongly developed argillic horizons is a widespread phenomenon in the more moist parts of the Sonoran Desert (McAuliffe 1994) and is apparently related in some way to the control of water infiltration by the argillic horizon. Some of the individuals of *L. tridentata* on this terrace have basal diameters exceeding one meter, indicating these shrubs may have ages of at least several centuries (see Vasek 1980, McAuliffe 1991, 1994). The sizes and probable ages of some of these shrubs indicates that creosotebush probably was a dominant plant in this location before the area began to be heavily used by livestock.

Stop 8: Late Pleistocene Alluvial Fan, Elev. 960 m

The stratigraphic relationship of this alluvial fan and soil characteristics indicates it is younger than the mid-Pleistocene fan of Stop 6 (fig. 8C). An argillic horizon is present, but is less strongly developed than in the soil of Stop 6, indicating a late Pleistocene age for the deposit. An additional contrast between this site and Stop 6 is the presence of a far more permeable, loamy A horizon that facilitates infiltration of precipitation. Perennial grasses are more abundant here than at Stop 6 and *Cercidium microphyllum, Prosopis velutina,* and *Acacia constricta* achieve canopy heights and diameters approximately 25% greater and canopy volumes more than twice as great as they do on the mid-Pleistocene surface. The greater size of these woody species at Stop 8 is probably related to the enhanced infiltration and deeper storage of precipitation in soils at this stop. The vegetation shows a mixture of growth forms and an abundance of stem succulents that is typical of the Arizona Upland Subdivision of the Sonoran Desert (Turner and Brown 1982). Vegetation includes woody plants (*C. microphyllum, Lycium berlandieri, L. fremontii, Ephedra fasciculata, Fouquieria splendens,* and *Janusia gracilis*) and abundant *Carnegiea gigantea*. However, the relatively high number of grass species, the presence of *Zinnia acerosa, Isocoma tenuisecta,* and *Gutierrezia sarothrae,* and the absence of the subshrub *Ambrosia deltoidea* indicate that this site is close to the mesic and frigid upper limit of Sonoran Desertscrub.

Stop 9: Southern Hillslope Exposure Below Microwave Antennae Dishes, Elev. 1210 m

The slope immediately north of the road was almost completely burned in the summer of 1993. Widespread fires occurred in this area as a result of high vegetative production that was stimulated by an unusually wet winter and spring in conjunction with an El Nino event in the Pacific. The crest of the slope is capped by a remnant of a Pleistocene-aged alluvial deposit containing weathering-resistant quartzite clasts. The slope contains a variety of soils and associated dominant grasses. Calcareous loams derived from degraded calcic horizons of the remnant Pleistocene surface are present near the ridgecrest and are dominated by *Bouteloua eriopoda*. Sideslope soils containing weakly developed argillic horizons support stands of *Heteropogon contortus, Hilaria belangeri, Bouteloua filiformis, B. curtipendula, B. rothrockii,* and *Bothriochloa barbinodis*. Small Holocene alluvial fan deposits are located at the foot of the slope, directly below fluves cut into the hillslope (fig. 12). The young, deep, sandy loam soils of these fans supported *Aristida purpurea, Muhlenbergia porteri,* and some *Bouteloua eriopoda* before the fire. The shrub Acacia constricta is present across the entire hillslope.

The various grass species that predominated in different parts of the slope exhibited various responses to the fire of 1993. On the small alluvial fans, most perennial grass clumps did not resprout. By late fall, 1993, these fans were covered by a dense cover of *Bouteloua rothrockii* and *Panicum hirticaule* that germinated after the burn. Most of the *Acacia constricta* rapidly and vigorously resprouted. On the calcareous soils near the ridgetop there are patches of *Bouteloua eriopoda* that escaped the burn. In adjacent burned sites, few *B. eriopoda* survived, and in late August 1993, many burned, dead clumps of *B. eriopoda* were already on small pedestals created by the rapid erosion of soil by summer rains. In midslope positions, *Heteropogon contortus, Bouteloua curtipendula,* and the other grass species rapidly resprouted and exhibited vigorous regrowth. The different responses of various grass species to fire is related to the location of carbohydrate storage within the grasses. The culms serve as principal organs for storage of reserve carbohydrate in both *Bouteloua eriopoda* and *Muhlenbergia porteri*; both of these species are typically damaged or killed by fire. Conversely, grasses that store reserve carbohydrates in a crown located below ground generally respond favorably to fire.

Those who advocate widespread use of fire to maintain grass dominance in these landscapes should pay close attention to soils and the identity of the grasses. Grass species growing on clayey soils will probably respond favorably to burning. However, on coarser-textured soils dominated by *B. eriopoda* and *Acacia constricta,* shrubs may actually show better recovery than perennial grasses after an intense burn. Cable (1965) and Martin (1983) document the damaging effect that fire can have on *B. eriopoda.*

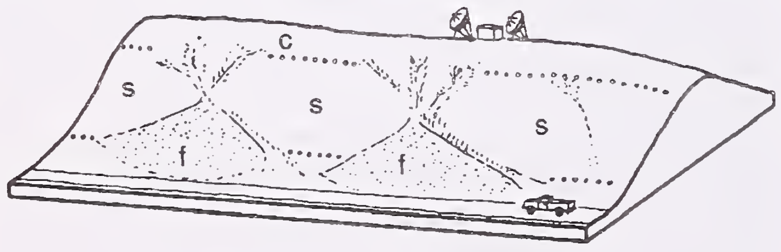

Figure 12.—Block diagram of south-facing hillslope along Webb Road below microwave antennae. Area "c" represents the hillcrest containing calcic, loamy soils, "s" represents sideslopes with moderate argillic horizons and "f" indicates small Holocene-aged fan deposits.

Stop 10: Pipeline Road 0.3 Miles Northwest of Webb Rd., Elev. 1240 m

The ridges directly east of us are quartz monzonite capped by remnants of an older, early Pleistocene alluvial fan surface (fig. 13). Large stream-rounded boulders of quartzite and occasional Barnes conglomerate are found along the ridge crests. In this area, no transversely level surfaces remain of this early Pleistocene fan. Geomorphologists refer to these highly eroded, somewhat humpbacked remnants of ancient fan deposits as "ballenas" (Spanish for "whales") (Peterson 1981). Soils of these ridgeline remnants have been considerably truncated and argillic horizons are absent. Surface soils are highly calcareous due to the exposure and degradation of calcic horizons that originally would have been positioned beneath argillic horizons. Crests of these ridges are elevated approximately 25-30 m above adjacent drainages. The advanced degree of spalling, splitting, and weathering of large stream-rounded quartzite boulders along the ridge suggest considerable age of the remnants of the alluvial deposits. The alluvium capping these separated ridges is all that remains in this area of a middle- or early- Pleistocene alluvial fan, possibly eqivalent to the Martinez surface (fig. 8A). Between 1.5 and 2.5 miles north of this stop, notice a set of four additional, even more elevated ballenas. The crests of these ballenas are approximately 30 m higher in elevation than the ballenas

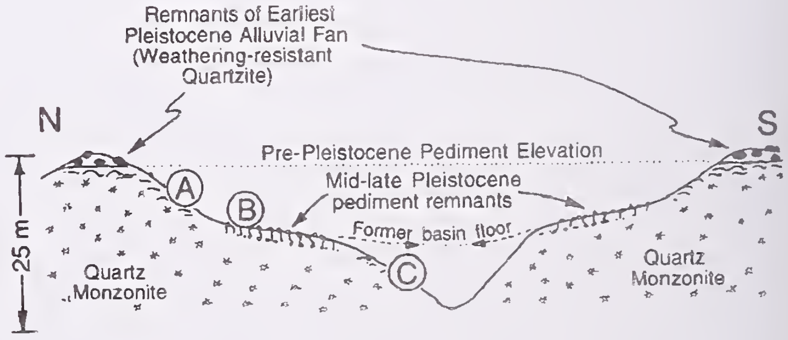

Figure 13.—North-south cross-section through landscape east of pipeline road at stop 10. The south-facing slope (A) has a very open grass-dominated vegetation dominated by Bouteloua eriopoda and Calliandra eriophylla with lesser amounts of Opuntia engelmannii, Erioneuron pulchellum, and Tridens muticus. The clayey soil of the armored pediment remnant (B) supports dense Hilaria belangeri with Calliandra eriophylla and scattered Acacia constricta. The lowest slope (C) contains young, poorly formed soils dominated by A. constricta and B. eriopoda.

immediately east of us. The more elevated set is also capped with coarse quartzitic alluvium and may represent remnants of either an earliest Pleistocene or an even older Tertiary deposit (fig. 8A). However, the ages of the various landforms in this vicinity have yet to be satisfactorily deciphered.

The persistence of these ballenas of quartz monzonite capped with remnants of ancient alluvial deposits within the area of the broad quartz monzonite pediment (figs. 4,8A) is apparently due to the location of a weathering- and erosion-resistant diabase dike directly west of these landforms. This dike forms the prominent north- to south-trending ridge immediately west of the pipeline road. The crest of this ridge lacks any quartzite clasts or other indications of a former alluvial mantle (such as exposed, degraded calcic horizons), indicating that at the time of deposition of the early Pleistocene alluvium which now caps the ballenas to the east, the dike apparently formed a topographic high above the fan surface. This intrusive dike and hills associated with it extend approximately one kilometer to both the north and south of Webb Rd. The presence of this erosion-resistant landscape feature apparently impeded the subsequent ability of fluvial systems shaping the pediment surface to completely remove early Pleistocene alluvial landscape features to the immediate east, whereas to the south, the quartz monzonite pediment has been more uniformly planed down by erosion.

The slopes of the ballenas to the east show a complex history of periods of landscape stability punctuated by erosion (fig. 13). These landscape-shaping processes have given rise to considerable variation in soils and associated vegetation within single hillslopes. Directly to the east, the middle portion of the adjacent north- and south-facing slopes possess small, more gently inclined shoulders dominated by *Hilaria belangeri* and *Calliandra eriophylla*. These landscape features are remnants of a local pediment surface cut into underlying quartz monzonite and graded to the former level of the adjacent drainage (fig. 13). These pediment remnants are armored with cobble-sized quartzite colluvium derived from the early Pleistocene alluvium that caps the ridges. This armor of extremely weathering-resistant cobbles provided substantial protection from erosion of the underlying, highly weathered quartz monzonite. Soils of small pediment remnants are virtually identical to those of the armored pediment remnants examined at Stop 2 and contain strongly developed, clayey argillic horizons above highly weathered quartz monzonite. Quartzite cobbles found at the interface of the lowermost argillic horizon and underlying highly weathered bedrock indicate that initial accumulation of quartzite cobbles on otherwise highly erodable quartz monzonite may have initially contributed to the surface stability required for lengthy pedogenesis. Loamy soils lacking argillic horizons located above, below, and to the sides of the armored pediment remnants lack *H. belangeri* and instead typically contain more deeply rooted *Bouteloua eriopoda* and *Acacia constricta*.

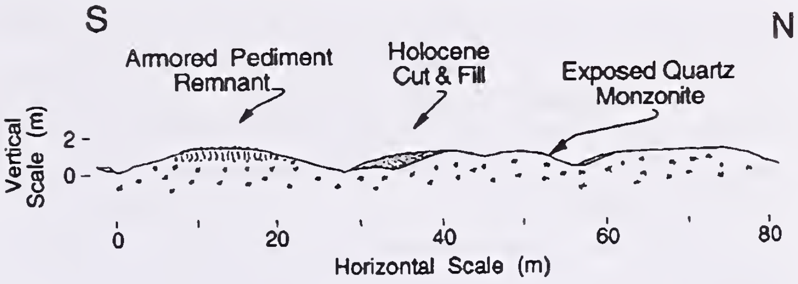

Figure 14.—North-south cross-section of east-facing exposure showing contrasting soils along the pipeline road at Stop 10. Vertical scale is exaggerated as shown. Dominant species on soils with strong argillic horizons of the armored pediment remnant are Hilaria belangeri and Calliandra eriophylla. The young soil on the Holocene alluvium is clearly dominated by Bouteloua eriopoda, with lesser amounts of B. rothrockii, Eriogonum wrightii and C. eriophylla. The weakly formed soils on recently exposed and weathered quartz monzonite are dominated by E. wrightii, and scattered Acacia greggii, Krameria parvifolia, and Mimosa biuncifera with a minor grass component that includes Bouteloua hirsuta, B. eriopoda, and B. curtipendula. A diagrammatic comparison of typical soil moisture distributions in soils from these three microenvironments is shown in Figure 7.

Similar small-scale landform complexity is present on the slope of the diabase ridge immediately west of the pipeline. A cross-section of landscape features and soils along the foot of the slope is clearly visible in the lengthy vertical exposure on the west side of the pipeline (fig. 14). Weathering-resistant clasts derived from upslope locations have contributed to the formation and preservation of an armored pediment remnant at the same elevational level as the pediment remnants on the slopes of the ballenas to the immediate east. This armored pediment has been incised, yielding a slightly convex remnant approximately 15 m across which is dominated by *Hilaria belangeri* and *Calliandra eriophylla*. Adjacent parts of the hillslope with weakly formed soils over highly weathered quartz monzonite are dominated by various deeper-rooted shrubs, including *Eriogonum wrightii, Acacia greggii* and *Mimosa biuncifera*. Bordering the north side of the armored pediment remnant is a Holocene-aged cut-and-fill feature containing a dark sandy loam alluvium (fig. 14) similar to the soils of the small fan deposits discussed at Stop 9. *Bouteloua* *eriopoda* is the dominant species on this deep, young, coarse-textured soil.

This hillslope and exposure at our final stop encapsulate many of the themes of the trip. The temporal and spatial distribution of soil moisture varies considerably from one soil to another. In this semiarid climate the soil moisture regime determines which species and growth forms are most likely to predominate. A knowledge of geomorphology provides a predictive capacity regarding the spatial and topographic positioning of different kinds of soils that otherwise are easily overlooked. If we are to interpret the ecology of these extremely complex landscapes, we must understand the formation and patterning of its landforms and soils, and how they ultimately influence the distribution and availability of water.

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We sincerely thank Mr. Joe Goff, owner and operator of the U-Circle Ranch for the hospitality he extended while we worked on his land and grazing allotments. We also thank Dr. R. B. Scarborough for visiting the stops with us and providing valuable information on local geology. Dr. P. Pearthree reviewed the manuscript.

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APPENDIX 1. SCIENTIFIC AND COMMON NAMES OF PLANTS

GRASSES

Aristida purpurea	Purple three-awn	*Digitaria californica*	Arizona cottontop
Aristida purpurea var. wrightii	Three-awn	*Eragrostis lehmanniana*	Lehmann lovegrass
Aristida ternipes	Spidergrass	*Erioneuron pulchellum*	Fluff grass
Bothriochloa barbinodis	Cane beardgrass	*Heteropogon contortus*	Tanglehead
Bouteloua curtipendula	Sideoats grama	*Hilaria belangeri*	Curly mesquite grass
Bouteloua eriopoda	Black grama	*Hilaria mutica*	Tobosa grass
Bouteloua filiformis	Slender grama	*Muhlenbergia porteri*	Bush muhly
Bouteloua hirsuta	Hairy grama	*Panicum hirticaule*	Annual panic grass
Bouteloua rothrockii	Rothrock grama	*Setaria macrostachya*	Bristlegrass
Bouteloua trifida	Red grama	*Tridens muticus*	Slim tridens

TREES AND LARGE SHRUBS

Acacia constricta	White-thorn acacia	*Fouquieria splendens*	Ocotillo
Acacia greggii	Catclaw acacia	*Larrea tridentata*	Creosotebush
Arctostaphylos pungens	Manzanita	*Lycium berlandieri*	Wolfberry
Ceanothus greggii	Desert ceanothus	*Lycium fremontii*	Wolfberry
Cercidium microphyllum	Foothill paloverde	*Mimosa biuncifera*	Wait-a-minute
Cercocarpus montanus	Mountain mahogany	*Prosopis velutina*	Velvet mesquite
Dodonaea viscosa	Hop bush	*Quercus emoryi*	Emory oak
Ephedra fasciculata	Mormon tea		

SUBSHRUBS

Ambrosia deltoidea	Triangleleaf bursage	*Isocoma tenuisecta*	Burro-weed
Calliandra eriophylla	Fairy duster, False mesquite	*Janusia gracilis*	Slender janusia, samara vine
Eriogonum wrightii	Wright's buckwheat	*Krameria parvifolia*	Range ratany
Gutierrezia sarothrae	Broom snakeweed	*Zinnia acerosa*	Desert zinnia

SUCCULENTS AND ROSETTES

Carnegiea gigantea	Saguaro	*Opuntia engelmannii*	Engelmann's prickly pear
Dasylirion wheeleri	Sotol, Desert spoon	*Opuntia fulgida*	Chain-fruit cholla
Ferocactus wislizenii	Fish-hook barrel cactus	*Yucca baccata*	Banana yucca

A Classification System and Map of the Biotic Communities of North America

David E. Brown, Frank Reichenbacher, and Susan E. Franson[1]

Abstract.—Biotic communities (biomes) are regional plant and animal associations within recognizable zoogeographic and floristic provinces. Using the previous works and modified terminology of biologists, ecologists, and biogeographers, we have developed an hierarchical classification system for the world's biotic communities. In use by the Arid Ecosystems Resource Group of the Environmental Protection Agency's Environmental Monitoring and Assessment Program, the Arizona Game and Fish Department, and other Southwest agencies, this classification system is formulated on the limiting effects of moisture and temperature minima on the structure and composition of vegetation while recognizing specific plant and animal adaptations to regional environments. To illustrate the applicability of the classification system, the Environmental Protection Agency has funded the preparation of a 1:10,000,000 color map depicting the major upland biotic communities of North America using an ecological color scheme that shows gradients in available plant moisture, heat, and cold. Digitized and computer compatible, this hierarchical system facilitates biotic inventory and assessment, the delineation and stratification of habitats, and the identification of natural areas in need of acquisition. Moreover, the various categories of the classification are statistically testable through the use of existing climatic data, and analysis of plant and animal distributions. Both the classification system and map are therefore of potential use to those interested in preserving biotic diversity.

Numerous classifications have been created in an attempt to assess and depict our natural resources. In North America, these efforts have resulted in classification systems and maps of potential natural vegetation (e.g., Shantz and Zon 1924; Küchler 1964, 1967; Flores et al. 1971), forest types (Society of American Foresters 1954, Rowe 1972), wetlands (Ray 1975, Zoltai et al. 1975, Cowardin et al. 1979, Hayden et al. 1984), land use (Anderson et al. 1972, 1976), land cover (Loveland et al. 1991), and vegetation change (Eidenshink 1992). These efforts, including "ecological" maps of states, provinces, regions, and even sub continents, have proven useful to those interested in land use planning and the sampling and stratification of large scale ecological units (see e.g., Holdridge 1959, 1969; Bailey 1976; Garrison et al. 1977; Bailey and Cushwa 1981; Wiken 1986; Wiken et al 1986; Omernik 1987; Wickware and Rubec 1989). Although based primarily on various types of vegetation, these classifications also often incorporate physiographic, climatic, soil, and chemical criteria. Moreover, some of these classifications are hierarchical, thus facilitating land use mapping at various scales. Several recent maps also have the advantage of being derived from high altitude imagery so that they are able to show vegetative and other changes over time. Indeed, the only criticism of these maps and classifications is that their usefulness depends on the designing agency's mission, objectives, and budget. That, and the fact that none of the recent systems is world wide in scope or universal in its application.

Biologists, unfortunately, have also yet to agree on a universal classification system to inventory plant and animal communities. Systems

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and maps currently in use at national scales are either based entirely on potential or dominant vegetation without regard to plant and animal associates, or depend upon one or more land use systems employing anthropogenic and other "non evolutionary" criteria. Furthermore, several recent classifications are non hierarchical or only partially hierarchical. As such, these systems and maps are frequently one dimensional and are not readily subject to user modification when higher or lower levels of assessment are desired. These limitations have caused resource management agencies to combine, create, and adapt a variety of classification systems in their attempts to inventory biotic resources. The result has been a proliferation of large and small scale maps depicting either only limited areas (e.g., Brown and Lowe 1982), or employing classifications that are too broad for detailed biological inquiry (e.g., Bailey and Cushwa 1981). Nonetheless, these efforts, coupled with the accelerated inventory of the world's biota and the development of high quality aerial imagery, now make a biologically universal classification system possible from both a theoretical and practical perspective.

That a national need for a standardized taxonomic system for biotic communities exists is obvious from the requirements of the National Environmental Policy Act of 1969, the National Resource Planning Act of 1974, the Environmental Monitoring and Assessment Program, and numerous other governmental policies and programs. Nor should such a system be confined to the United States and its territories. The present and increasing emphasis on endangered species residing within and outside the U. S. as prescribed in the Endangered Species Act of 1973, the North American Waterfowl Plan and the Neotropical Migratory Bird Inventory now being undertaken by the U. S. Fish and Wildlife Service, and the Biosphere Reserve Program being fostered by the International Union for the Conservation of Nature, dictate a world wide approach to biotic assessment. Clearly, the time has come for a universal classification system for biotic resources.

THE CLASSIFICATION SYSTEM

On two main points every system yet proposed, or that probably can be proposed, is open to objection; they are, — 1stly, that the several regions are not of equal rank; 2ndly, that they are not equally applicable to all classes..." Alfred Russell Wallace, 1878

Modifying the existing works and terminology of other biologists, ecologists, and biogeographers, Brown, Lowe, and Pase(1979, 1980) developed an hierarchical classification system for the biotic communities of North America. This classification system was formulated on natural criteria and recognizes the limiting effects of moisture and temperature minima as well as evolutionary origin on the structure and composition plant and animal communities. The system was originally developed for southwestern North America where its adaptability was demonstrated for both natural and human altered communities (Brown and Lowe 1974a, 1974b, 1980, 1982; Brown 1980. Because the classification system is both parallel and hierarchical (fig. 1), it is adaptable for use at various levels of detail. Mapping can therefore be at any scale or unit of resolution. Moreover, the hierarchical sequence allows for the incorporation of existing vegetation classification taxa in use by federal, state, and private agencies into an appropriate biotic community level within the classification system. The Brown, Lowe, and Pase classification system, however, is not an "ecosystem" classification. Except for their influences on regional climate, evolution, and biota, abiotic factors such as soil, chemistry, and geology are not used as determining criteria. It is intended to be an entirely biological system.

The numerical coding of the hierarchy also makes the classification system computer compatible, thereby readily allowing for the storage and retrieval of information. The Brown, Lowe, Pase system for the North American Southwest is currently in use in the RUN WILD program developed for use on remote terminals by the USDA Forest Service's Southwestern Region and Rocky Mountain Forest and Range Experiment Station (Patton 1978). This classification is similarly incorporated within the files of the Arizona and New Mexico game and fish departments, and is used by industry in environmental analysis procedures as required by the National Environmental Policy Act (e.g., Reichenbacher 1990). Recently this classification has been adopted by the Arid Ecosystems Resource Group of the U. S. Environmental Protection Agency for their environmental monitoring and assessment program (EMAP).

As such, this classification system facilitates biotic inventory and assessment, the delineation and stratification of habitats, resource planning, the interpretation of biological values, and other activities pertaining to natural history inquiry. It has proven especially useful for environmental

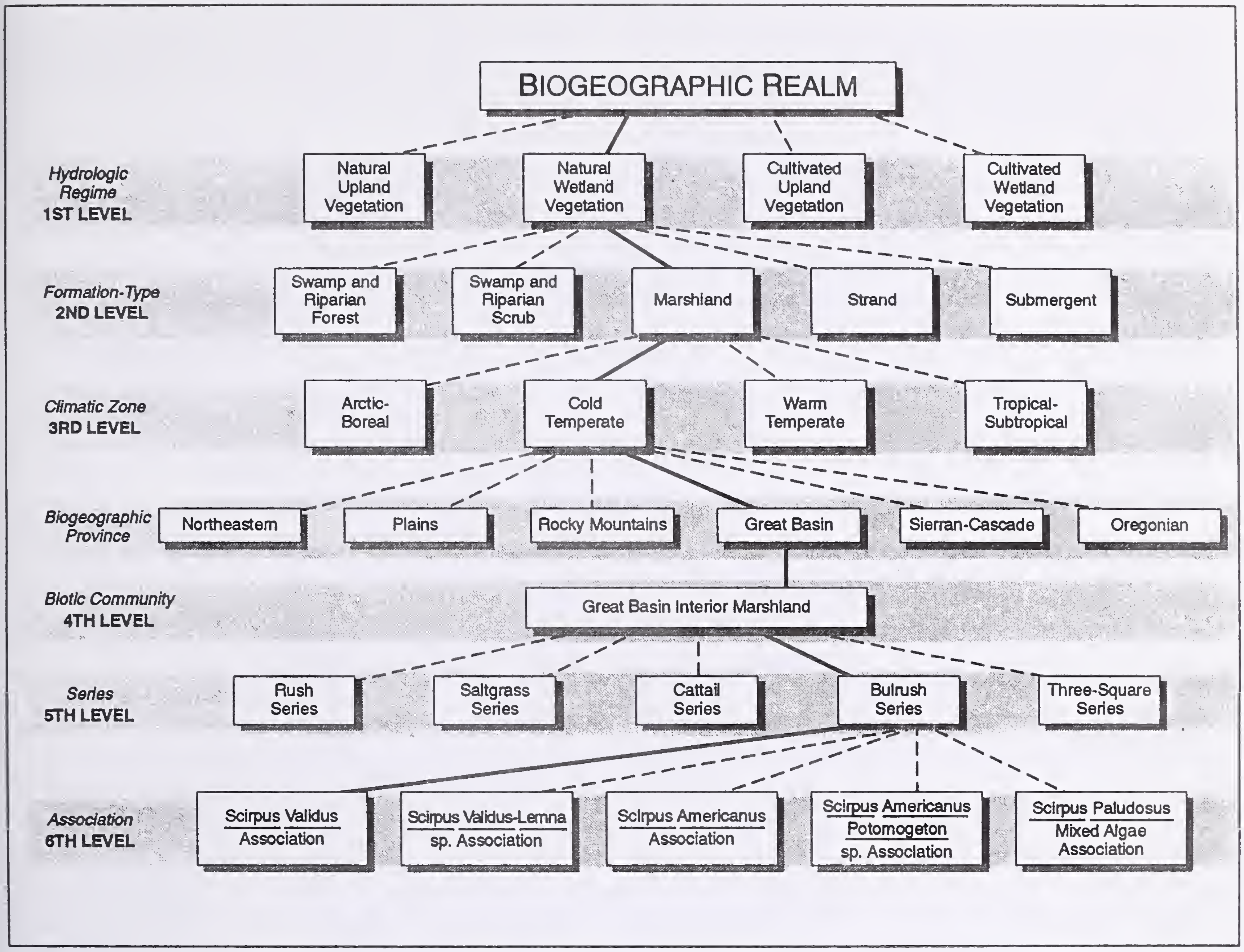

Figure 1.—Hierarchy of a bulrush marsh in Great Salt Lake, Utah, to the association (sixth) level of the classification system.

analysis where the comparison of biological units is desired by governmental, scientific, educational, and other institutions. In short, the classification system is of particular use for those interested in inventorying biotic diversity for resource management, vegetation change, biological study, natural area preservation and habitat acquisition. Moreover, because the system is hierarchical and universal, earlier inventory efforts can usually be accommodated into the system at some level.

The most important value of a natural hierarchical classification system based on biotic criteria is the meaningful assignment of plant and animal habitats. Although most of the classification's categories are determined primarily on the basis of observable vegetation, the inclusion of biotic provinces and biotic communities automatically incorporates the less visible animal components within the hierarchy. The system therefore allows for a meaningful delineation and inventory of specific plant and animal habitats. For example, because biotic provinces are included in the system, a resource manager can determine which marshlands are likely to include nesting black ducks *(Anas rubripes)* as opposed to similar appearing wetlands within other biotic provinces inhabited by Florida ducks (*A. fulvigula fulvigula*), mottled ducks (*A. f. maculosa),* and Mexican ducks (*A. platyrhynchos diazi*). Such separations of plant and animal habitats are important in fulfilling the requirements of the Endangered Species Act, for evaluating the North American Waterfowl Plan, for monitoring warblers and other migratory birds of recent concern, and for following numerous other governmental directives. The inclusion of biogeographic criteria is also of primary importance in the world biosphere reserve program (see e.g. Franklin 1977; McNeely and Miller 1983; Udvardy 1984a, 1984b; IUCN 1974, 1992).

Presented below is a computer compatible hierarchy of the world's biological systems with representative examples of the classification to the series (5th) level for North America. Neither the biotic community (4th) level, nor the series level examples of the classification are complete or final. Similarly, representative examples of the association (6th) level of the system are given only for the Rocky Mountain Montane Conifer Forest biotic community. Unlike previous presentations of the classification system (Brown and Lowe 1974a, 1974b, Brown, Lowe and Pase, 1979, 1980, Brown 1980), in which North America's biotic communities were all contained within the Nearctic biogeographical realm, the classification presented here properly separates the continent into Nearctic and Neotropical realms (fig. 2).

The hierarchy presented below is neither rigorously scientific nor rigidly systematic. Our only intention is to present an hierarchical synthesis of existing biogeographical concepts to aid in the development of a world wide classification system for the world's biota. Neither is it proposed that this system replace existing classifications, or be officially adopted at a national or any other level where workable classification systems have been developed. We also recognize that portions of the classification system are dated or incomplete and require additional work. For example, easily retrievable climatic data from a great variety of stations are now available, and we are currently refining the temperature parameters of the climatic zones to make them more precise and meaningful. Nonetheless, the integrity of the most important levels of the classification are already testable through scientific methodologies. For example, we are now evaluating the reality of the various biotic communities through a statistical analysis of seasonal climatological data. This analysis, and the recent acceleration in floristic and faunistic inventories will help determine the endemic reality of these and possibly other biotic communities.

Table 1.—Summary of world natural vegetation to the first level.

	Biogeographic Realm Natural	1. Upland Natural Vegetation	2. Wetland Vegetation
1,000	Nearctic	1,100	1,200
2,000	Palaearctic	2,100	2,200
3,000	Neotropical Antartican	3,100	3,200
4,000	Indomalayan (Oriental)	4,100	4,200
5,000	African (Ethiopian)	5,100	5,200
6,000	Australian	6,100	6,200
7,000	Oceanic	7,100	7,200

Where:

1,000 = Biogeographic Realm

1,100 = Hydrologic Regime (Upland, Wetland, Cultivated, or Urban)

1,110 = Formation type

1,111 = Climatic Zone

1,111.1 = Biotic Community (= Regional Formation)

1,111.11 = Series (Biociation of Generic Dominants)

1,111.111 = Association (Plant community of specific taxa)

1,111.1111 = Plant and Animal Composition, Age Class, Density,

In previous publications (Brown 1980, 1982; Brown and Lowe 1980; Brown et al. 1979, 1980), we have shown the usefulness of the Series and Association levels of the classification. For the purposes of this publication, discussion will focus on the Biome and above. Here, we present only those North American biomes mapped on the 1:10,000,000 map soon to be released by the Environmental Protection Agency (Reichenbacher and Brown 1994).

The number preceding the comma (e.g., 1,000) differentiates the hierarchy on the basis of the world's biogeographic realms (Table 1). Origin and evolutionary history are thus recognized as being of primary importance in the determination and classification of biotic entities. The mappable reality of the world's biogeographical realms is, as in all natural evolutionary taxonomy, interpretive and dependent on the criteria used. The following seven realms are adapted from Sclater (1858), Wallace (1876), Allen 1878, Sharpe 1893, Hesse et al. (1937), Darlington (1957), Dansereau (1957), Walter (1973), the International Union for Conservation of Nature and Natural Resources (1974), DeLaubenfels (1975), Cox et al. (1976), Udvardy (1975, 1984a).

- 1,000 Nearctic—Continental North America exclusive of the tropics including most of the highland areas of Mexico and parts of Central America (fig. 2).
- 2,000 Palaearctic—Eurasia exclusive of the tropics; Africa north of the Sahel.
- 3,000 Neotropical and Antarctican—South America, most of Central America, and Mexico south of the Tropic of Cancer; Antarctica.

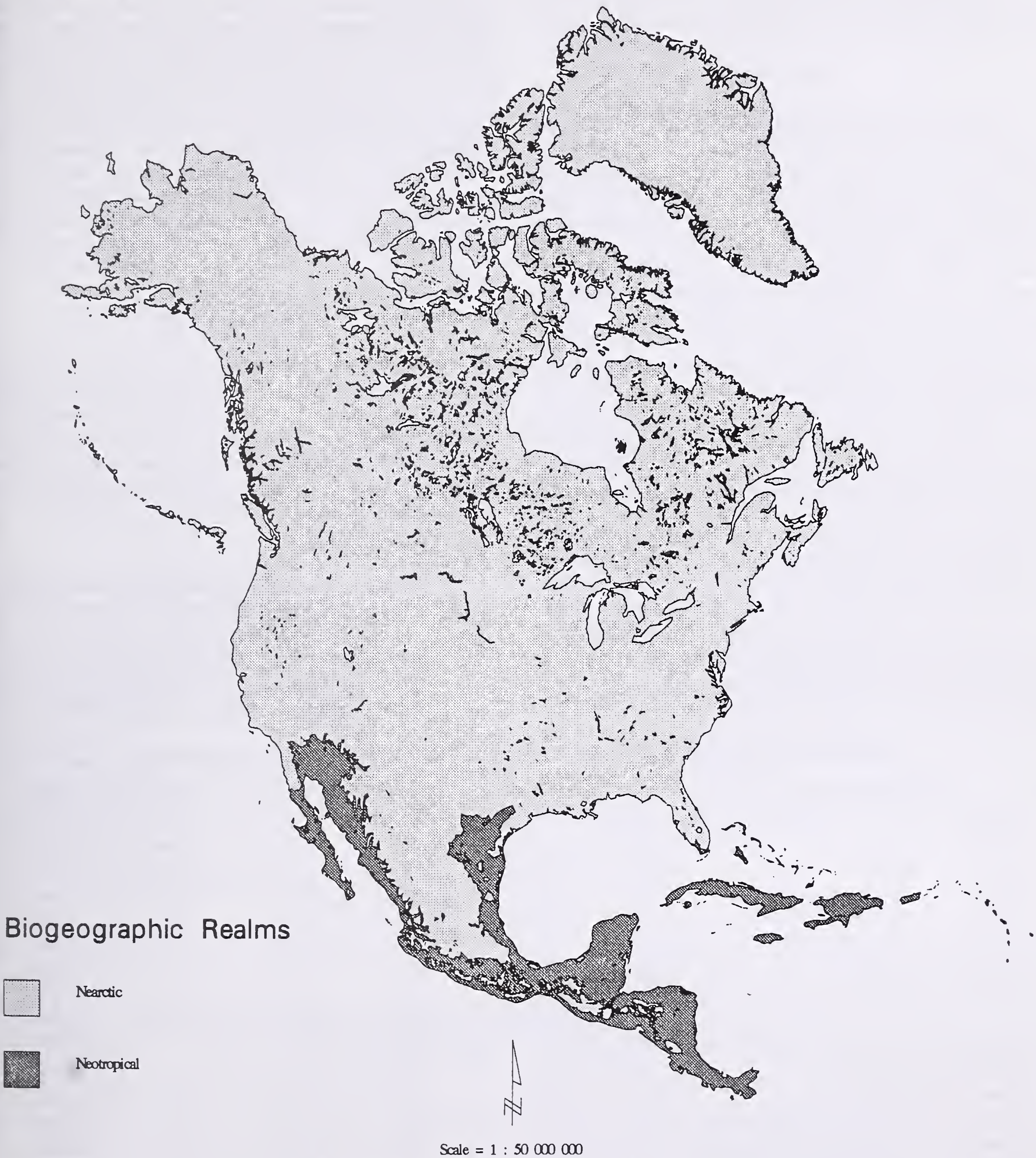

Figure 2.–Biogeographic realms of North America.

- 4,000 Indomalayan (Oriental)—Southeast Asia, the Indian subcontinent, Indonesia, the Phillipines, etc.
- 5,000 African (Ethiopian)—Africa south of the Sahara, Malagasy, and parts of the Arabian peninsula.

- 6,000 Australian—Australia and Tasmania.
- 7,000 Oceanian—Oceanic islands displaying a high degree of endemism.

First Level

The first digit *after* the comma (e.g., 1,100) refers to one of *four hydrologic* regimes including all upland (1,100) and wetland (1,200) communities existing under natural conditions. The important adaptations of plants and animals to terrestrial ecosystems, as opposed to aquatic systems, is thus recognized early in the classification system. The classification of submerged freshwater (e.g. 1,300) and marine (e.g. 1,400) environments is as yet in a tentative stage (see e.g. Ray 1975 and Maxwell et al. (1994). Although accommodated in the system, the classification of these aquatic communities is outside the scope of the present work and will not be elaborated on further. Because almost all "natural communities" are now more or less influenced by human activity, we include all terrestrial and wetland vegetation communities composed of native, naturalized, or adventive plants as belonging to either the natural upland regime or a natural wetland regime (Table 1).

In this classification system, wetlands include all periodically, seasonally, or continually submerged lands populated by species and/or life forms different from the immediately adjacent upland vegetation (see also e.g., Martin et al. 1953, Lowe 1964, and Cowardin et al. 1979). Hence, riparian communities containing both upland and wetland components are included here in the natural wetland regime (1,200, Table 1). Only a few wetland biomes are included because most would not appear on the 1:10,000,000 map (Reichenbacher and Brown 1994) we produced to illustrate the application of the classification. Coastal wetlands, in partiucular, are difficult to map at this scale and are grouped into a 1,200. Undifferentiated Nearctic Wetland and a 3,200. Undifferentiated Neotropical Wetland category.

Second Level

The second digit *after* the comma, e.g.(1,110) refers to one of the following recognized plant formations, or as they are called on a worldwide basis, *formation types* (Table 2). Formation types are vegetative responses to integrated environmental factors, most importantly, available soil and plant moisture.

Upland Formations

- Tundra—Communities existing in an environment so cold that moisture is unavailable during most of the year, precluding the establishment of trees, and in which the maximum development is perennial herbaceous plants, shrubs, lichens, and mosses, with

Table 2.–Summary for the natural upland and wetland vegetation of the world to the second level.

Biogeographic Realm		Formation-type 1. Tundra	2. Forest and Woodland	3. Scrubland	4. Grassland	5. Desert-land	6. Non-Vegetated
UPLAND							
1,100	Nearctic	1,110	1,120	1,130	1,140	1,150	1,160
2,100	Palearctic	2,110	2,120	2,130	2,140	2,150	2,160
3,100	Neotropical-Antarctican	3,110	3,120	3,130	3,140	3,150	3,160
4,100	Indomalayan (Oriental)	4,110	4,120	4,130	4,140	4,150	4,160
5,100	African (Ethiopian)	5,110	5,120	5,130	5,140	5,150	5,160
6,100	Australian	6,110	6,120	6,130	6,140	6,150	6,160
7,100	Oceanic	7,110	7,120	7,130	7,140	7,150	7,160
		1. Wet Tundra	2. Forest*	3. Swamp-Scrub	4. Marshland	5. Strand	6. Non-Vegetated
WETLAND							
1,200	Nearctic	1,210	1,220	1,230	1,240	1,250	1,260
2,220	Palearctic	2,210	2,220	2,230	2,240	2,250	2,260
3,200	Neotropical-Antarctican	3,210	3,220	3,230	3,240	3,250	3,260
4,200	Indomalayan (Oriental)	4,210	4,220	4,230	4,240	4,250	4,260
5,200	African (Ethiopian)	5,210	5,220	5,230	5,240	5,250	5,260
6,200	Australian	6,210	6,220	6,230	6,240	6,250	6,260
7,200	Oceanic	7,210	7,220	7,230	7,240	7,250	7,260

*Swamp-forests, bog forests, and riparian forests.

grasses poorly represented or at least not dominant.

- Forests and Woodlands—Communities dominated principally by trees potentially over 10 meters in height, and characterized by closed and/or multi layered canopies (forests); or, communities comprised principally of trees with a mean potential height usually under 10 meters, the canopy of which is usually open, interrupted, and singularly layered (woodlands).
- Scrubland—Communities dominated by sclerophyll or microphyll shrubs and/or multistemmed trees generally not exceeding 10 meters in height, usually presenting a closed physiognomy, or if open, interspaced with other perennial vegetation.
- Grassland—Communities dominated actually, or potentially by grasses and/or other herbaceous plants.
- Desertland—Communities in an arid environment (usually less than 300 millimeters precipitation per annum) in which plants are separated by significant areas devoid of perennial vegetation.

Wetland Formations

- Wet Tundra—Wetland communities existing in an environment so cold that plant moisture is unavailable during most of the year, precluding the establishment of trees and all but a low herbaceous plant structure in a hydric matrix.
- Swamp and Riparian Forests—Wetland communities possessing an overstory of trees potentially more than 10 meters in height and frequently characterized by closed and/or multi layered canopies.
- Swamp and Riparian Scrub—Wetland communities dominated by short trees and/or woody shrubs, generally under 10 meters in height and usually presenting a closed physiognomy.
- Marshland—Wetland communities in which the principal plants are herbaceous emergents having their basal portions annually, periodically, or continually submerged.
- Strand—Beach and river channel communities subject to regular to infrequent submersion, wind driven waves or spray. Plants are separated by significant areas devoid of perennial vegetation.

Some upland and wetland communities, e.g. dunes, lava flows, salt lakes, etc., are essentially without vegetation and are populated only by one cell organisms. For purposes of classification, these areas can be considered as belonging to a non vegetated or a "non vascular formation" if a desertland or strand formation type is considered inappropriate (Table 2).

Third Level

The third digit beyond the comma (e.g., 1,11<u>1</u> refers to one of the four world *climatic zones* (see e.g. Walter 1973, Ray 1975, Cox et al. 1976) in which minimum temperatures are recognized as a major evolutionary control of and within formation types (Table 3, fig. 3):

- Arctic Boreal (Antarctic–Austral)—Lengthy periods of freezing temperatures with the coldest month isotherm -3 degrees C (Köppen 1931); growing season generally averaging less than 100 days, occasionally interrupted by nights of below freezing temperatures.
- Cold Temperate—Freezing temperatures usually of moderate duration, although of frequent occurrence during winter months. Potential growing season generally from 100 to 200 days and confined to late spring and summer when freezing temperatures are infrequent or absent.
- Warm Temperate—Freezing temperatures of short duration but generally occurring every year during winter months. Potential growing season over 200 days with an average of less than 150 days a year subject to temperatures below 0 degrees C or chilling fogs.
- Tropical Subtropical—Infrequent or no 24 hour periods of freezing temperatures, cold fogs, or chilling winds.

Fourth Level

The fourth level (e.g., 1,111.<u>1</u>) refers to a regional formation or *biotic community* within a biogeographic region or province (Clements and Shelford 1939; Pitelka 1941; Dice 1943; Goldman and Moore 1945; Odum 1945; Blair 1950; Webb 1950; Miller 1951; Kendeigh 1952; Aldrich 1967; Franklin 1977; Udvardy 1975a, 1975b, 1984a, 1984b). Each biogeographic province is characterized by a particular precipitation pattern and other climatic regimen so that the plant and animal species found therein share a more or less distinctive evolutionary history. Hence, each biogeographic province comes with a name that describes its geographic center or an important

Biotic Classification System

Brown, Reichenbacher

Level Descriptions

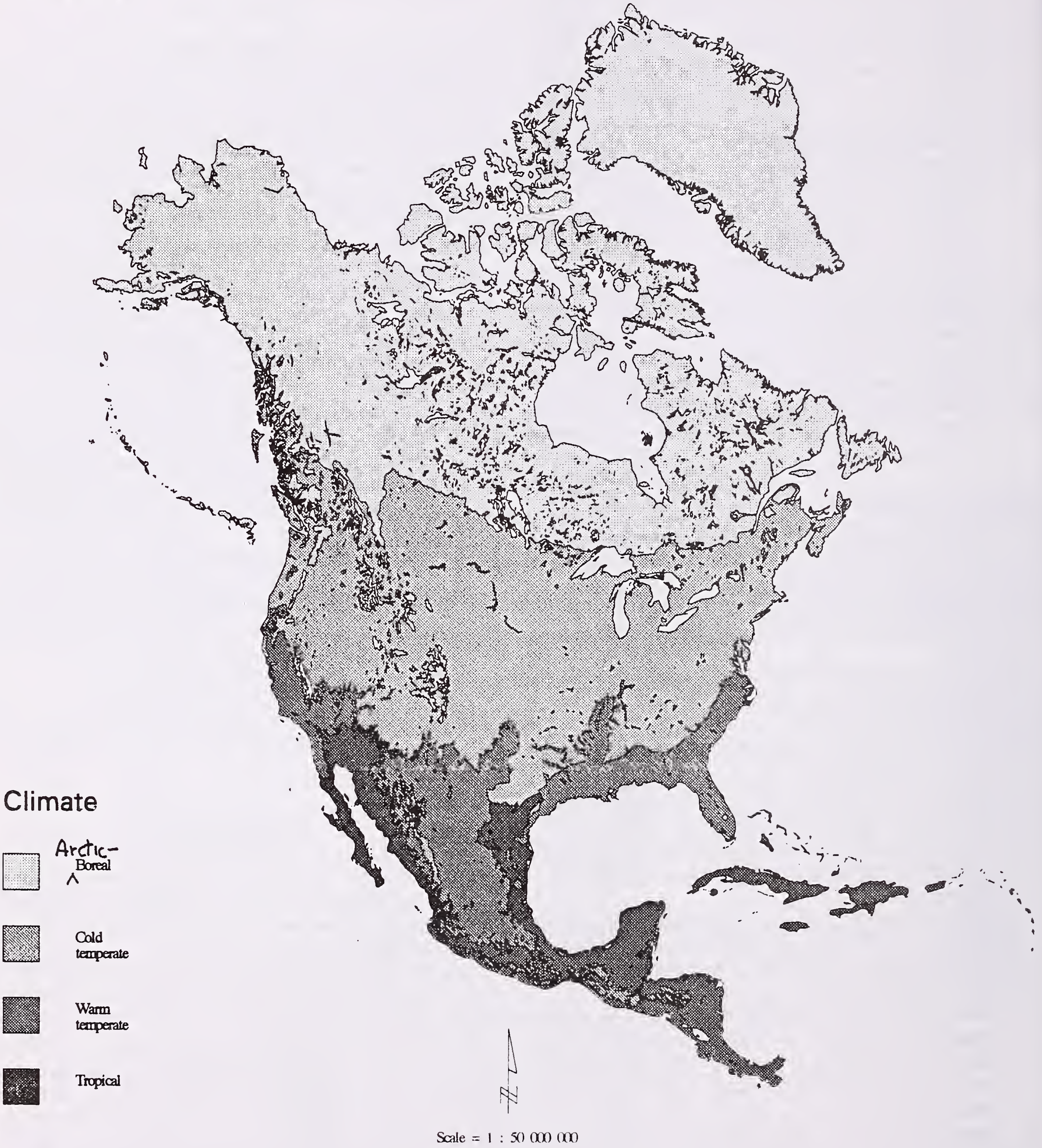

Figure 3.—Climatic zones of North America.

Table 3.—Summary for the natural upland and wetland vegetation of Nearctic and Neotropical North America to the third level.

Formation		Climatic (thermal) Zone			
		1. Arctic Boreal	2. Cold Temperate	3. Warm Temperate	4. Tropical-Subtropical
		NEARCTIC			
UPLAND					
1,110	Tundra	1,111			
1,120	Forests and Woodland	1,121	1,122	1,123	1,124
1,130	Scrubland	1,131	1,132	1,133	1,134
1,140	Grassland	1,141	1,142	1,143	1,144
1,150	Desertland	1,151	1,152	1,153	1,154
1,160	Nonvegetated	1,161	1,162	1,163	1,164
WETLAND					
1,210	Wet Tundra	1,211			
1,220	Swamp and Riparian Forests	1,221	1,222	1,223	1,224
1,230	Swamp and Riparian Scrub	1,231	1,232	1,233	1,234
1,240	Marshland	1,241	1,242	1,243	1,244
1,250	Strand	1,251	1,252	1,253	1,254
1,260	Nonvegetated	1,261	1,262	1,263	1,264
		NEOTROPICAL			
UPLAND					
3,110	Tundra and Paramo	3,111			
3,120	Forest and Woodland	3,121	3,122	3,123	3,124
3,130	Scrubland	3,131	3,132	3,133	3,134
3,140	Grassland	3,141	3,142	3,143	3,144
3,150	Desertland	3,151	3,152	3,153	3,154
3,160	Nonvegetated	3,161	3,162	3,163	3,164
WETLAND					
3,210	Wet Tundra	3,211			
3,220	Swamp and Riparian Forest	3,221	3,222	3,223	3,224
3,230	Swamp and Riparian Scrub	3,231	3,232	3,233	3,234
3,240	Marshland	3,241	3,242	3,243	3,244
3,250	Strand	3,251	3,252	3,253	3,254
3,260	Nonvegetated	3,261	3,262	3,263	3,264

physiographic feature that importantly contributes to its ecological isolation (fig. 4). In the West, as in Mexico and Central America, where topography, altitudinal, and climatic influences are extremely complicated, biotic provinces diminish in size and increase in number, and their boundaries, following certain topographical features, become highly complex (Udvardy 1969). Although the delineation of biogeographic provinces is interpretive in part and often arbitrary, the identification of biotic communities only requires the assignation of recognizable communities of plant dominants (5th level of the classification system) and their known animals to the province in which these species are known to be important constituents.

Biotic communities are characterized by distinctive plants and animals living within a single formation type (third level of the classification system) and commonly called "indicator species" (Merriam 1890, Clements 1920, Shelford 1963). Because each biotic community is a complete ecosystem of plants, animals,and their habitat, this level is the natural unit for studying the interrelations of plant and animal species (Odum 1945, Shelford 1945, Kendeigh (1952). Although the original concept of "ecosystems" involved the exchange of chemical energy within a given community (Odum 1945), this term, as it is often presently used, is equivalent to biotic community. As ecological units of regional isolation, the reality of biotic communities can be tested statistically through the analysis of climatic data and the presence and distributions of endemic species and/or subspecies.

It is this fourth (biotic community) and the fifth (series) levels that have been most often used to map regions, states, and countries (e.g., Bruner 1931; Rasmussen 1941; Hayward 1948; Webb 1950; Allred et al. 1963; Aldrich 1967; Küchler 1964, 1977; Franklin and Dyrness 1973; Brown 1973, Brown and Lowe 1982). Biogeographic provinces and biotic communities are also the bases for biosphere reserve programs in the United States and elsewhere(I.U.C.N. 1974, Franklin 1977, Udvardy 1984b).

Tables 4 and 5 list those biotic communities shown on the 1:10,000,000 color map (Reichenbacher and Brown 1994). Present plans are to describe each of these biotic communities in detail in a publication similar to one for the southwest United States and northwest Mexico (Brown 1982). Neither the classification nor the map is meant to be final. Additional biotic communities will undoubtedly be identified, and others may be deleted, upon further analysis and consideration.

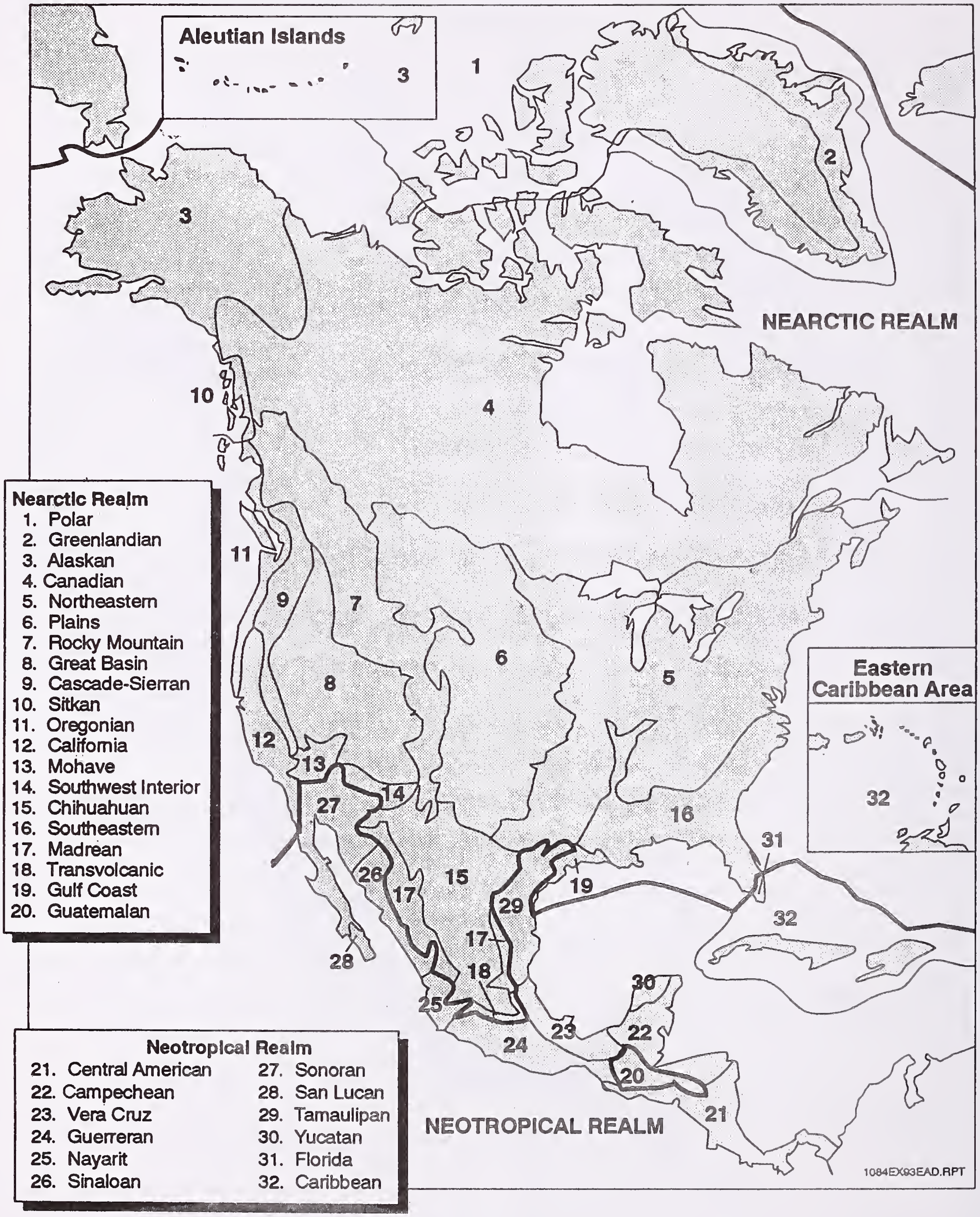

Figure 4.—Biogeographic Provinces of North America.

Fifth Level

The fifth level beyond the comma (e.g., 1,111.11) provides the principal plant animal communities within the biotic communities, each recognized by one or more indicator plants, and called a *series*. These generic series, sometimes referred to as cover types (Society of American Foresters 1954), are in turn composed of one or more plant associations within the same biotic community (Oosting 1956, Lowe 1964, Braun 1967, Franklin and Dyrness 1973, Pfister et al. 1977). For example, a yellow pine series would include all plant associations within a biotic community in which *Pinus ponderosa* was a dominant component (table 4). Because the number of series

Table 4.—Nomenclature of upland biotic communities (fourth level) of Nearctic and Neotropical North America. A more complete list is presented in Brown et al. (1982). The list of biomes presented here includes only those illustrated on the 1:10,000,000 map of the biotic communities of North America (Reichenbacher and Brown 1994).

- 1,000. NEARCTIC REALM
  - 1,100. Natural Upland Vegetation
    - 1,110. Tundra Formation
      - 1,111. Arctic-Boreal Tundras
      - 1,111.1 Polar (High Arctic) Tundra
      - 1,111.2 Alaskan Coastal Tundra
      - 1,111.3 Canadian (Low Arctic) Tundra
      - 1,111.4 Greenlandian Coastal Tundra
      - 1,111.5 Arctic-Alpine Tundra
      - 1,111.6 Rocky Mountain and Great Basin Alpine Tundra**
      - 1,111.7 Cascade-Sierran Alpine Tundra
      - 1,111.8 Adirondack-Appalachian Alpine Tundra
      - 1,111.9 Transvolcanic Tundra
- ***120. Forest and Woodland Formation
    - 121. Boreal and Subalpine Forests and Woodlands
      - 121.1 Alaska-Yukon Subarctic Conifer Forest
      - 121.2 Canadian Taiga
      - 121.3 Rocky Mountain Subalpine Conifer Forest
      - 121.4 Cascade-Sierran Subalpine Conifer Forest
      - 121.5 Adirondack-Appalachian Subalpine Conifer Forest
      - 121.6 Transvolcanic Subalpine Conifer Forest
    - 122. Cold Temperate Forests and Woodlands
      - 122.1 Northeastern Deciduous Forest
      - 122.2 Sitka Coastal Conifer Forest
      - 122.4 Cascade-Sierran Montane Conifer Forest
      - 122.5 Rocky Mountain Montane Conifer Forest
      - 122.6 Great Basin Conifer Woodland
      - 122.7 Madrean Montane Conifer Forest
      - 122.8 Transvolcanic Montane Conifer Forest
    - 123. Warm Temperate Forests and Woodlands
      - 123.1 Southeastern Deciduous and Evergreen Forests
      - 123.2 Oregonian Deciduous and Evergreen Forests
      - 123.3 California Evergreen Forest and Woodland
      - 123.4 Madrean Evergreen Forest and Woodland
      - 123.5 Transvolcanic Evergreen Forest and Woodland
      - 123.7 Guerreran Evergreen Woodland
      - 123.8 Guatemalan Cloud Forest
      - 123.9 Guatemalan Evergreen Forest and Woodland
      - 123.1a Vera Cruz Cloud Forest
      - 123.1b San Lucan Evergreen Forest and Woodland
- 130. Scrubland Formation
    - 131. Arctic-Boreal Scrublands
      - 131.1 Alaskan Coastal Scrub
    - 132. Cold Temperate Scrublands
      - 132.1 Great Basin Montane Scrub
    - 133. Warm Temperate Scrublands
      - 133.1 California Chaparral
      - 133.2 California Coastalscrub
      - 133.3 Southwestern (Arizonan) Interior Chaparral
      - 133.4 Chihuahuan Interior Chaparral
- 140. Grassland Formation
    - 142. Cold Temperate Grasslands
      - 142.1 Plains Grassland
      - 142.2 Great Basin Shrub-Grassland
    - 143. Warm Temperate Grasslands
      - 143.1 Semidesert Grassland
      - 143.2 California Valley Grassland
      - 143.3 Gulf Coastal (Tamaulipan) Grassland
- 150. Desertland Formation
    - 152. Cold Temperate Desertlands
      - 152.1 Great Basin Desertscrub
    - 153. Warm Temperate Desertlands
      - 153.1 Mohave Desertscrub
      - 153.2 Chihuahuan Desertscrub
- 3,000. NEOTROPICAL REALM
  - 3,100. Natural Upland Vegetation
    - 3,110. Tundras and Paramo Formation
      - 3,111. Alpine Paramos
        - 3,111.1 Central American Paramo
- ***120. Forest and Woodland Formation
    - 124. Tropical-Subtropical Forests and Woodlands
      - 124.1 Central American Cloud Forest
      - 124.2 Central American Evergreen Rain Forest
      - 124.3 Central American Semi-evergreen Forest
      - 124.4 Central American (Guanacaste) Dry Forest
      - 124.5 Campechian Evergreen Rain Forest
      - 124.6 Campechian Semi-evergreen Forest
      - 124.7 Yucatan Semi-deciduous Forest
      - 124.8 Yucatan Dry Deciduous Forest
      - 124.9 Guerreran Dry Deciduous Forest
      - 124.1a Vera Cruz Evergreen Rain Forest
      - 124.1b Vera Cruz Semi-evergreen Forest
      - 124.1c Nayarit Semi-evergreen Forest
      - 124.1d Sinaloan Dry Deciduous (Monsoon) Forest
      - 124.1e Tamaulipan Semi-deciduous Forest
      - 124.1f San Lucan Dry Deciduous Forest
      - 124.1g Caribbean Cloud and Montane Forest
      - 124.1h Caribbean Coastal Evergreen and Semi-evergreen Forest
      - 124.1i Caribbean Dry (Monsoon) Forest
      - 124.1j Floridian Evergreen Forest
- 130. Scrubland Formation
    - 134. Tropical-Subtropical Scrublands
      - 134.1 Guerreran Thornscrub
      - 134.2 Sinaloan Thornscrub
      - 134.3 Tamaulipan Thornscrub
      - 134.4 San Lucan Thornscrub
      - 134.5 Caribbean Thornscrub
      - 133.6 Central American Thornscrub
- 140. Grassland Formation
    - 144. Tropical-Subtropical Grasslands
      - 144.1 Central American Savanna Grassland
      - 144.2 Campechian Savanna Grassland
      - 144.3 Vera Cruz Savanna Grassland
      - 144.4 Caribbean Savanna Grassland
      - 144.5 Sonoran Savanna Grassland
      - 144.6 Tamaulipan Savanna Grassland
- 150. Desertland Formation
    - 154. Tropical-Subtropical Desertlands
      - 154.1 Sonoran Desertscrub

*** The first "1" (in front of the comma and representing the Nearctic realm) is understood and dropped for tabular convenience only from this point onward.

*** The first "3" in front of the comma and representing the Neotropical Realm is dropped for tabular convenience from this point onward.

within any given biotic community may be large, and because some biotic communities are as yet little studied and imperfectly known, only illustrative examples of the fifth level are given for the biotic communities listed in Tables 4 and 5. For these same reasons, the numerical prefix given for a particular series is also illustrative only and may be modified at will for regional studies.

It should be noted that tropical and subtropical series are inherently more diverse than those in arctic boreal and temperate biotic communities. Series in tropical and subtropical biotic communities frequently contain dozens, if not hundreds, of competing species of plants and animals per acre; arctic boreal series typically contain only one or two plant dominants. Series in arctic boreal and temperate environments also tend to be larger in extent and fewer in number than those in the tropics. For these reasons the identification and classification of fifth level communities is more easily determined in Canada and the United States than in Mexico or Central America (compare e.g., Halliday 1937, Küchler 1964, Braun 1967 and Franklin and Dyrness 1973 with Tosi 1969 and Rzedowski 1978).

Some plant dominants are highly facultative, and the same species may be dominant in more than one formation type. As an extreme example, mesquite (*Prosopis juliflora*) may be the dominant life form in forest and woodland, scrubland, desertland, and even disclimax grassland formations. The distributions of some plant dominants also span more than one climatic zone, e.g., mesquite, creosote bush (*Larrea tridentata*), and the introduced saltcedar (*Tamarix chinensis*). The plant and animal associates of these sometime dominants differ when passing from one formation type or climatic zone to another, however. These and other generic dominants and some of their associates may also occur in more than one biotic community (e.g., *Larrea*, *Populus*, *Salix*, *Quercus*, etc.). Nonetheless, further investigation should show a significant change in plant and animal species when passing from one biotic community to another. Furthermore, when the same species is present in more than one biotic community, the different populations exhibit genetic and other differences (Yang 1970).

Table 5.—Nomenclature of wetland biotic communities (fourth level) of Nearctic and Neotropical North America. A more complete list is presented in Brown et al. (1982). The list of biomes presented here includes only those illustrated on the 1:10,000,000 map of the biotic communities of North America (Reichenbacher and Brown 1994).

- 1,000. NEARCTIC
  - 1,200. Natural Wetland Vegetation
    - *** 220. Forest Formation
      - 223. Warm Temperate Swamp and Riparian Forests
        - 223.1 Southeastern Swamp and Riparian Forest
    - 230. Swamp-Scrub Formation
      - 231. Arctic Boreal Swamp-Scrubs
        - 231.3 Alaskan Swamp Scrub
    - 240. Marshland Formation
      - 243. Warm Temperate Interior Marshland
        - 243.8 Everglades Interior Marshland
- 3,000. NEOTROPICAL REALM
  - 3,200. Neotropical Natural Wetland Vegetation

*** The first "1" (in front of the comma and representing the Nearctic realm) is understood and dropped for tabular convenience only from this point onward.

Sixth Level

The sixth level after the comma (e.g., 1,111.111) refers to a distinctive *association* which has been defined by the International Botanical Congress as a plant community having a certain floristic composition, uniform habitat conditions, and uniform physiognomy (see also eg., Braun Blanquet 1932). Plant associations are therefore more or less local in distribution, and as used here, generally equivalent to niches (Pitelka 1941) and habitat types as outlined by Daubenmire and Daubenmire (1968), Layser (1974), and Pfister et al. (1977). Although we provide plant association examples for two 5th level series within one 4th level biotic community (Douglas fir and Yellow Pine series within Rocky Mountain Montane Conifer Forest), the enormous numbers of possible sets preclude presentation for the continental treatments in tables 4 and 5.

This level of the classification emphasizes actual vegetation. As a working system, it accommodates, but does not stress, both subclimax and disclimax plant associations (and associes) as well as potential natural vegetation (see e.g., Clements 1916, Weaver and Clements 1938, Clements and Shelford 1939, Oosting 1956, Küchler 1964). Those plant associations judged to be subclimax or seral in nature can be indicated by an "a" in the numerical code, e.g. 111.111a. Similarly, those series and associations considered to be in a disclimax condition can be indicated by a "D" at the series (5th) level or a "d" at the plant association level. Plant associations may therefore be expanded to any length for regional studies.

Seventh Level

The seventh level (e.g., 1,111.1111) accommodates detailed assessment of *composition, structure, density*, or other quantitative determinations for plant and animal species within a plant association. In that implementation of this level in the system is intended for intensive studies of limited areas (e.g., Dick Peddie and Moir 1979), no examples are provided in Tables 4 and 5.

THE BIOTIC COMMUNITIES OF NORTH AMERICA MAP

The 1:10,000,000 color map (Reichenbacher and Brown 1994) depicts the continent's major upland biotic communities (4th level of the classification system) using Gaussen's (1953) ecological color scheme that illustrates gradients in available plant moisture, heat, and cold. The base map was reproduced at scale on an acetate overlay of a 1:8,000,000 Kummerly and Frey stereographic chart, and the biotic communities delineated in 83 vinyl colors using as source data the maps, terminology, and descriptions found in the Literature cited and. Because of the limitations of scale, upland biotic communities such as Relict Conifer Forests and Central American Thornscrub, which occupy areas less than 10 km^2 in extent, are omitted from the map. Their enormous diversity, dynamic nature, and generally limited area, also preclude all but the highest level illustration of the largest wetland communities. Nonetheless, the biogeographic affiliation of a particular wetland can be readily determined by referring to the biotic community in which it occurs. It is expected that further research and peer review will result in improvements in the nomenclature and delineation of the biotic communities depicted, particularly those in Latin America.

The biotic communities shown depict regional formations within recognized biotic or floristic regions as modified from Dice (1943), Goldman and Moore (1945), Shreve (1951), Rzedowski(1978), and other biogeographers. The boundaries and terminology are importantly based on the system developed by the IUCN and UNESCO and proposed for use in the International Biosphere Reserve program (Udvardy 1974, 1984b). Neither the biotic community designations, nor their delineations, however, need to be considered as final. Indeed, it is hoped that the use of high altitude imagery and other recently developed techniques (see e.g., Loveland et al. 1991) will result in an improved understanding and depiction of the continent's biota.

Even a cursory examination of the map shows some portions of the North American continent to be more biotically homogeneous than others. Of particular concern to some users will be the large uniform areas of Northeastern Deciduous Forest, Canadian Taiga, and Plains Grassland as compared to the smaller, more numerous biotic communities in Mexico and the American Southwest. This apparent discrepancy at the biotic community level is real, however, and reflects an increasing biotic diversity as one travels westward and southward across the North American continent—a phenomenon long recognized by biologists (e.g., Simpson 1964, Kiester 1971, and Wilson 1974). Mexico, despite only having 11% of the land area of Canada and the U. S., has more species of mammals, more species of birds, and more reptiles and amphibians than the two northern countries combined. One Mexican state, Chiapas, has 8,250 known species of plants compared to the twice as large (115,719 km^2 vs. 74,000 km2) and botanically rich American state of Ohio's 2700 species (Ramamoorthy et al. 1993). The large number of Mexican species is the result of Mexico's and the American Southwest's great topographic and climatic diversity. Climatic variation and evolutionary isolation are the two primary factors in the determination of biotic communities. Hence, these parts of North America possess a greater degree of endemism at both the species and community levels than areas to the north and east (Klopfer and MacArthur 1960, Wilson 1974).

Nonetheless, further research may show that one or more of the biotic communities depicted are not sufficiently distinct to warrant separation at the biotic community level. Future investigators, for example, may conclude that the Neotropical Realm's Yucatan Dry Deciduous Forest is not sufficiently different from Central American Dry Forest to justify separate biotic community status. Similarly, additional study may support the division of Plains Grassland or other fourth level community into one or more biotic communities as was suggested by Dice (1943). In either event, biotic communities can easily be deleted or added in the classification system. Also, should additional biotic detail be desired within a biotic community, future editions of the map can provide series or fifth level community designations as was done for the Northeastern Deciduous Forest by Braun (1967) and for Sonoran Desertscrub by Brown and Lowe (1980, 1982).

The map has been digitized by the Environmental Protection Agency's Environmental Monitoring Systems Laboratory in Las Vegas, Nevada. Digitization will facilitate modifying the biotic communities based on peer review along with the overlay of land use data. It will also facilitate the division of the larger biotic communities such as the Northeastern Deciduous Forest and Plains Grassland into large general series should such a subdivision be desired. Also, by using the map as a sample frame, EMAP can stratify the various biotic communities for conducting wildlife surveys and other monitoring activities. And finally, the map permits those interested in biological diversity to determine the percentage of each biotic community remaining in a natural state and/or having protected status.

In summation, the purpose of the map is to illustrate the applicability of the classification system for inventorying the continent's biotic resources and to provide a sample frame for those interested in stratifying natural history information. With the recent availability of highly detailed aerial imagery, one could feasibly now also overlay land use, thus evaluating the extent of those biotic communities remaining in a natural state. National park boundaries and other enhancements would also enable resource managers to identify those biotic communities having protected status and determine which ones are in need of additional protection. A biotic communities map also facilitates the evaluation of candidate areas for biosphere reserves and wilderness status. Enhanced with land use information, such a map can also assist in the interpretation of environmental change and the gathering of base data for the environmental monitoring and assessment program (EMAP) currently underway by the U. S. Environmental Protection Agency (Kepner and Fox 1991).

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Another Jewel in the Crown: A Report on the Flora of the Sierra De Los Ajos, Sonora, Mexico

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Abstract. —We report here on the flora of the Sierra de los Ajos, Sonora, Mexico, based on collections made in 1992 and 1993. The known flora of this Sky Island range contains 376 species of vascular plants in 93 families. Based on our collections and the results of floristic studies of other Sky Island ranges, we anticipate that the total flora of the Sierra de los Ajos contains over 1000 species. We have documented the only known occurrences in Mexico of two species that are candidates for listing as threatened or endangered species in the United States, various new distribution records for Mexico and Sonora, and large range extensions of a number of other plants. This work contributes to a projected flora of the Sky Island region.

INTRODUCTION

The flora of the Sierra de los Ajos includes several notable taxa, including some that are considered in danger of extinction, some that are far disjunct from the nearest known populations, and some that show a marked extension of their known range. We have documented several state and national distribution records in the Ajos. We predict that the total flora of the range will exceed 1000 species, and will contain a highly diverse mixture of biogeographic elements, as is typical of regional Sky Island ranges. Because they occur near the center of the Sky Island bioregion, which includes isolated mountain ranges south of the Mogollon Rim and north of the Sierra Madre Occidental, the flora of the Sierra de los Ajos provides an important basis for understanding the flora of the bioregion as a whole.

The Sierra de los Ajos occur in a botanically underexplored region of North America. Despite over 70 years of intensive collecting, the Sky Island bioregion remains one of the least well known floristic areas of temperate North America. The paucity of floristic information about the Sky Islands north of the Mexico-U.S. border is surprising considering that the floras of New Mexico and Arizona were first produced in the early part of this century (Wooton and Standley 1915, Kearney and Peebles 1942). In fact, many of the additions to the flora of Arizona have come from botanical exploration of the Sky Islands (e.g. Lehr and Pinkava 1980, 1982). It is perhaps less surprising that the ranges that lie to the south of the international border have received comparatively less attention, because of their location on the northwestern frontier of Mexico. To date, reasonably complete floras have been published for only three of the aproximately two dozen Sky Island ranges: the Sierra del Tigre in Sonora (White 1948) and the Rincon Mountains (Bowers and McLaughlin 1987) and Pinaleno Mountains (McLaughlin 1993) in Arizona. The flora of the Huachuca Moutains in Arizona is in preparation and will soon be submitted for publication (J. Bowers and S. McLaughlin, *personal communication*).

The Sierra de los Ajos lie just south of the international border, which nearly bisects the region (fig. 1). Like the Sky Island region generally, the Ajos occur at the juncture of four major biogeographic regions: Madrean, Sonoran, Chihuahuan, and Southern Rockies/Mogollon, in approximate order of their contribution to the flora. Streams rising in the Ajos contribute to three major river systems: the northward-flowing Río San Pedro and the southward-flowing Río Sonora

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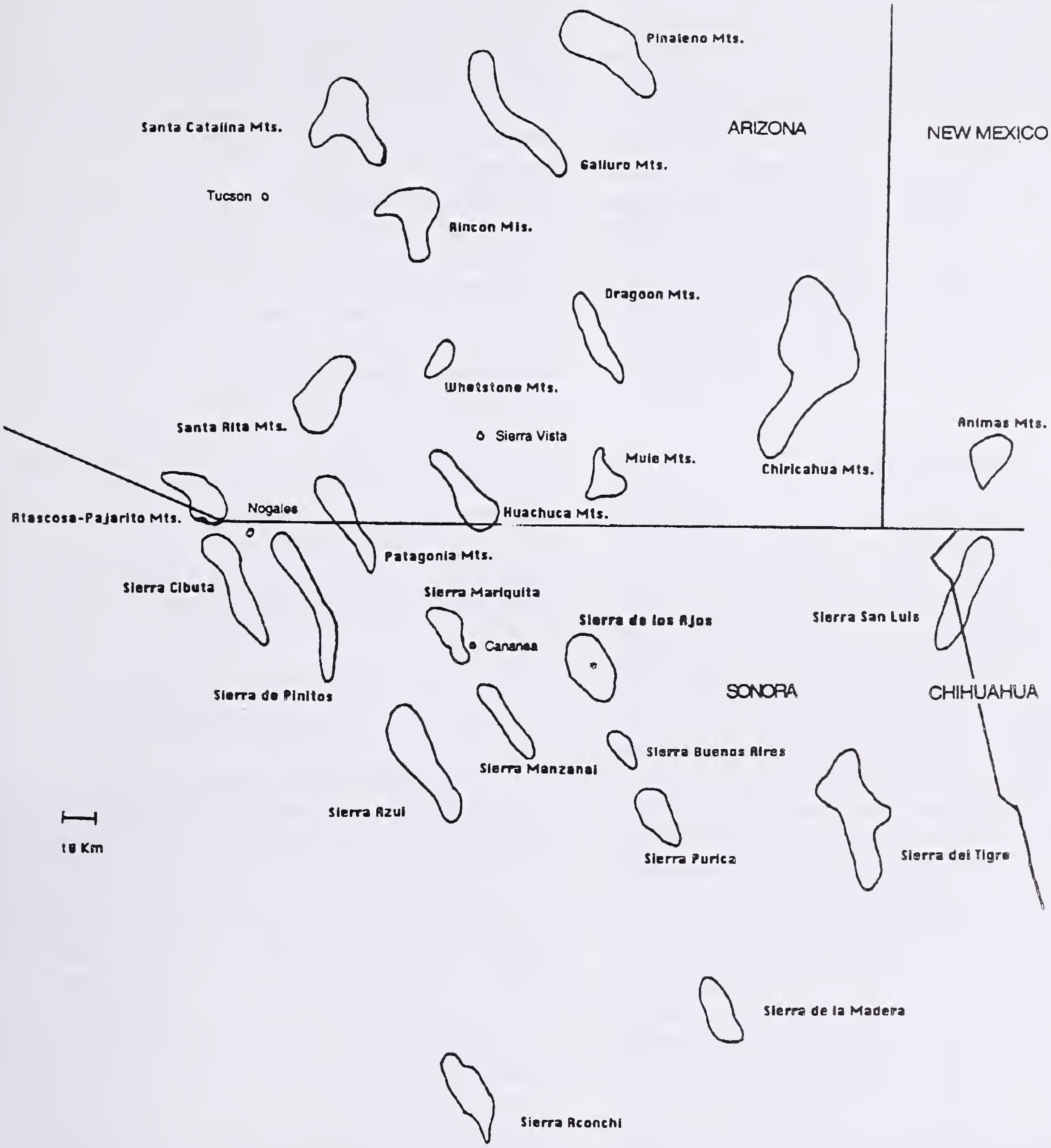

Figure 1.—The Sky island bioregion of northwestern Mexico and southwestern United States. Sierra de los Ajos are indicated by an asterisk (*).

and Río Yaqui. Although several streams have perennial stretches, none have perennial flows beyond the pediment of the range or reach the major rivers of the valleys.

The low point in the valleys surrounding the Ajos occurs at Bacoachi on the Río Sonora (~1050 m). The highest peak, Cerro de las Flores, rises to 2625 m and is the highest point in the state of Sonora. Thus, the overall relief in the Ajos is approximately 1575 m. This elevational range lies between that of the Huachuca Mts. (~1375 m) and the Rincon Mts. (~1725 m) and is an intermediate value for the Sky Islands.

The prevalent geological formations in the Sierra de los Ajos are volcanic and of Tertiary origin. An unusual feature of the range, and one that is presumably important to the flora and vegetation, is the large outcrop of limestone (probably of Cretaceous origin) that forms the three highest peaks of the range. Following the formation of these rocks, basin and range faulting and subsequent erosion created the present-day topography of these mountains.

The climate of the Ajos is typical of the region, with bimodal, nearly equally distibuted summer and winter rainfall, interrupted by a hot arid foresummer (Solis-Garza, et al. 1993). Near desert conditions prevail at the lowest elevations, whereas the highest peaks experience a much cooler and wetter climate due to orthographic processes. Microclimate diversity also contributes to the floristic diversity Southern exposures that are protected from frost can support species with "tropical" affinities, whereas steep north-facing canyons with cold air drainage support species with northern affinities.

VEGETATION

Biotic communities in the Sierra de los Ajos include mixed conifer forest, montane meadows, "montane chaparral", pine-oak forest, oak woodland, oak and mesquite grassland, and riparian forest. Only a brief discussion of these communities, which have been discussed in detail elsewhere (e.g. Marshall 1957, Brown 1982), will be presented here.

Mixed conifer forest is of limited extent in the Ajos and is restricted to north-facing slopes at high elevation. Common trees include *Abies concolor*, *Pinus ponderosa* var. *arizonica*, *Pinus strobiformis*, and *Pseudotsuga menziesii*. Montane meadows occur at sites that would support mixed conifer, pine, or pine-oak forest in the absence of fire. Because of the fire history of the Ajos (see below), these areas now support a diverse assemblage of herbs and grasses including *Blepharoneuron tricholepis*, *Delphinium tenuisectum*, *Glandularia bipinnatifida*, *Koehleria macrantha*, *Salvia lemmoni*, *Silene laciniata*, and *Viguiera multiflora*. "Montane chaparral" occurs at high elevations on exposed limestone ridges, including the tops of the highest peaks. Common species in this association include *Cercocarpus brevifolius*, *Eriogonum jamesii*, *Holodiscus dumosus*, and *Quercus gambelii*.

Pine-oak forest is the most wide spread forest type in the Ajos and is predominant at mid-elevations. Common trees and shrubs include *Arbutus arizonica*, *Arctostaphylos pungens*, *Ceanothus depressus*, *Garrya wrightii*, *Juniperus deppeana*, *Pinus engelmannii*, *P. ponderosa* var. *arizonica*, *Quercus arizonica*, *Q. emoryi*, *Q. hypoleucoides*, and *Rhus trilobata*. Oak woodland and grassland occur on north-facing slopes at the lowest elevations and on south-facing slopes from low- to mid-elevations. The common oaks are *Quercus emoryi*, *Q. oblongifolia*, and *Q. arizonica*. Common grasses include *Bouteloua* spp., *Eragrostis* spp., *Bothriochloa barbinodis*, and *Aristida* spp. Other conspicuous species include *Juniperus deppeana*, and *Agave* cf. *palmeri*. Some level sites in this elevational range are dominated by *Juniperus coahuilensis* and *Yucca arizonica*.

Riparian forests change more gradually with elevation than the corrsponding ridge and slope vegetation. At low elevations xeroriparian areas support a sparse woodland of *Celtis reticulata*, *Chilopsis linearis*, and *Prosopis velutina*. At the foot of the range, *Populus fremontii*, *Platanus wrightii* and *Fraxinus velutina* form streamway forests. At mid-elevations in Cañón Evans, a diverse riparian assemblage includes *Acer grandidentatum*, *Alnus oblongifolia*, *Juglans major*, *Juniperus scopulorum*, and *Populus fremontii*. *Abies concolor*, *Acer grandidentatum*, and *Populus tremuloides* occur at the heads of the major canyons. Riparian communities along one stream in the Ajos are described by Solis-Garza and associates (1993).

FLORA

The earliest botanical collections from the Sierra de los Ajos preserved in herbaria are likely to be those of George Thurber, botanist with the first U.S.-Mexico Boundary Commission. The commission approached the Ajos from the east and skirted the eastern and southern flanks of the range in May and June of 1851 on their way to Bacoachi, on the Río Sonora (Bartlett 1854).

The first collections from this century that we have seen were made by Joe Marshall in 1951. Marshall collected extensively in Cañón Evans, a very large, north and west trending canyon that contains the largest perennial stream in the range. Marshall was the first to document a distinct Madrean pine-oak forest that extends north through the Sky Islands in his classic publication on birds of the pine-oak woodland (Marshall 1957).

We are aware of four collections from the Sierra de los Ajos from the 1980's and early 1990's. In September 1982, Frank Reichenbacher made an extensive collection in Cañón Evans. Paul Martin and associates made small collections in July 1983 and April 1991, also in Cañón Evans. Peter Warren and Esther Saucedo surveyed this canyon for rare plants in 1989. Prior to our efforts, most collecting in the range has occurred in Cañón Evans.

Thus far we have made two extensive collecting trips in the Sierra de los Ajos totaling ten person-days of fieldwork. In October 1992 we surveyed the grassland on the north side of the range, the lower reaches of Cañón Evans, a transect leading up the north side of the range (along an old roadway), the heads of the major east- and west-trending streams (Arroyo Frijolito and Hoya del Packard, respectively), the saddle between the highest peaks of the range, and the north slope and top of the highest peak (Cerro de las Flores). In July 1993 we surveyed in the southern portion of the range, mostly in the vicinity of Arroyo La Cieneguita and the southern crest of the range, as well as the pass between the Ajos and the Sierra Buenos Aires. Our collections are thus biased towards the summer flora and we expect that further additions to the flora will contain many cool-season ephemeral and spring-flowering perennial species.

To date we have documented 376 species of vascular plants in 246 genera and 93 families (Appendix 1). Our records are based primarily on our collections, the first set of which is deposited at the University of Arizona Herbarium (ARIZ); a second set is deposited at the herbarium at the Instituto de Biología, UNAM (MEXU), and additional duplicates are deposited elsewhere. Some records are based on other collections at ARIZ, on our photo vouchers, and on undocumented observations. The five families that contribute the most to the known flora are Asteraceae (62 species), Poaceae (49), Fabaceae (33), Lamiaceae (9), and Scrophulariaceae (9). These families account for 43% of the specific and intraspecific taxa in the known flora. The nine largest genera in the flora are *Muhlenbergia* (Poaceae, 9 species), *Asclepias* (Asclepiadaceae, 8), *Quercus* (Fagaceae, 8), *Aristida* (Poaceae, 5), *Bouteloua* (Poaceae, 5), *Brickellia* (Asteraceae, 5), *Erigeron* (Asteraceae, 5), *Pinus* (Pinaceae, 5), and *Senecio* (Asteraceae, 5).

One of the significant results of our surveys is the documentation of previously unknown populations of species being considered for listing as endangered or threatened in the United States, new records for Mexico and Sonora, and extensions of the known ranges of various species (Table 1). We located new populations of *Lilium parryi* (Liliaceae) and *Rumex orthoneurus* (Polygonaceae), both Category 1 candidates for listing as federally endangered or threatened species by the United States Fish and Wildlife Service, and both previously unknown in Mexico (Felger and Fishbein 1993, Fishbein and Felger 1993). Two of the more surprising collections from the Ajos are the southwest extension of the range of *Arenaria stricta* ssp. texana from west Texas and the northwest extension of Tinantia erecta from southwestern Chihuahua.

Table 1.—Notable Collections in the Sierra de los Ajos.

Species (Family)	Significance
Antennaria marginata (Asteraceae)	New record for Sonora
Arenaria stricta (Caryophyllaceae)	New record for Sonora, new record for Sky Islands, range extension from western Texas
Asclepias nyctaginifolia (Asclepiadaceae)	New record for Sonora
Botrychium virginianum (Ophioglossaceae)	Only extant Sky Island population (see text)
Cheilanthes eatonii (Adiantaceae)	New record for Sonora?
Desmanthus cooleyi (Fabaceae)	New record for Sonora
Euphorbia melanadenia (Euphorbiaceae)	New record for Sonora
Galium pilosum (Rubiaceae)	New record for Mexico, range extension from Pinaleño Mts.
Lilium parryi (Liliaceae)	New record for Mexico
Rumex orthoneurus (Polygonaceae)	New record for Mexico
Smilacina racemosa (Convallariaceae)	New record for Mexico?
Smilacina stellata (Convallariaceae)	New record for Mexico?
Thermopsis montana (Fabaceae)	New record for Mexico?
Tinantia erecta (Commelinaceae)	New record for Sonora, new record for Sky Islands, range extension from southwestern Chihuahua
Trifolium wormskioldii (Fabaceae)	New record for Mexico?

In a sense, the Sierra de los Ajos and Huachuca Mountains can be thought of as "sister ranges" because of their close proximity and similar geology and elevational range. Because the Huachucas have a well-documented flora (J. Bowers and S. McLaughlin, in preparation), it is interesting to note which taxa occur in the Ajos but not in the Huachucas. We have documented 20 such taxa (Table 2). Most of these taxa are Madrean species that reach their northern limit in the Sierra de los Ajos (e.g. Ratibida mexicana, Quercus mcvaughii, Q. viminea, Tinantia erecta). Some, however, are species apparently restricted to very mesic or high elevation habitats (i.e. Alnus oblongifolia, Botrychium virëa maculata, Galérorum, and Thermopsis moning that these pæual populationse Ajos, but not tsidering that the Huachucas occur further north and rise to an elevation 270 m higher than the Ajos. Botrychium virginianum was known elsewhere in the region only from the Santa Rita Mountains, where it has not been seen for about 100 years and is presumed extirpated. Galium pilosum is otherwise known in the region only from two collections from the Pinaleño Mountains. Juniperus scopulorum is unknown elsewhere in the region.

The proportion of non-native species in the flora is remarkly low (14 species, or 3.7% of the total flora). This low figure may reflect sampling bias (e.g. if the spring flora has disproportionately more non-natives) or an actual deficit of introduced species. If this pattern is supported by further collections, it certainly merits future investigations into the cause of the resistance of the Sierra de los Ajos to non-native plant invasions.

McLaughlin's (1993) analysis of the relationship of elevational range and native species richness in the southwestern United States would predict about 600 species for the Sierra de los Ajos, based on elevational range alone. Although the known flora of the Pinaleño Mountains is well-predicted by this relationship, other Sky Islands (i.e. the Rincon Mountains and the Huachuca Mountains) greatly exceed their predicted values, by 50% in the case of the Rincons and 90% in the case of the Huachucas. Based on these values, the flora of the Ajos should contain 900-1100 species.

HUMAN INFLUENCES AND FUTURE PROSPECTS

A major factor influencing the vegetation of the Sierra de los Ajos has been frequent fires. Especially in the last century, fires have dramatically altered the appearance and composition of vegetation (M. Fishbein, personal observation; Swetnam 1988). This is particulary evident in the high country, which is covered by meadows and "chaparral" rather than forest. Compared to similar ranges in the United States, there is a relative lacknce in the formùo los Ajos. The Ajos have been cited as an example of an area that has experienced natural fire regimes in the period since European colonization (Swetnam 1988). The Huachuca Mountains, which have arguably experienced more catastrophic fires in the last two decades because of a history of fire suppression, make an interesting comparison to the Sierra de los Ajos. Such a comparison would be a valuable first step in generating hypotheses about the effects of burn suppression on floras.

Table 2.—Native vascular plant taxa known from the Sierra de los Ajos that are unknown from the Huachuca Mountains.

Species (Family)
Agastache pallida (Lamiaceae)
Alnus oblongifolia (Betulaceae)
Arenaria stricta (Caryophyllaceae)
Botrychium virginianum (Ophioglossaceae)
Chimaphila maculata (Ericaceae)
Conopholis alpina (Orobanchaceae)
Galium pilosum (Rubiaceae)
Gutierrezia alamanii (Asteraceae)
Hoffmanseggia glauca (Fabaceae)
Juniperus scopulorum (Cupressaceae)
Lopezia gracilis (Onagraceae)
Penstemon campanulatus (Scrophulariaceae)
Phlox nana (Polemoniaceae)
Quercus mcvaughii (Fagaceae)
Quercus viminea (Fagaceae)
Ratibida mexicana (Asteraceae)
Seymeria bipinnatisecta (Scrophulariaceae)
Thermopsis montana (Fabaceae)
Tinantia erecta (Commelinaceae)
Yucca arizonica (Agavaceae)

Mining seems to have been of limited scope in the Sierra de los Ajos. Although there are no currently active mines, the geology of the range and the proximity to the large mines at Cananea suggest potential mineral exploitation in the future.

Current human uses of the Sierra de los Ajos center on cattle ranching. The lower elevations are readily accessible to cattle and are utilized as rangelands. The steepest high-elevation canyons and some lower elevation cliffs are inaccessible to livestock. In 1993, some riparian areas on the south side of the range showed evidence of the cumulative impacts of intensive grazing. Overgrazed clumps of grass were very sparse and large stands of weedy native (e.g. *Croton texensis*) and non-native (e.g. *Nicotiana glauca*) species formed dense and extensive patches.

The Sierra de los Ajos has been included in a system of state level ecological preserves in the SANPES program. Although it was formerly managed by the federal forestry agency (SARH), management of many preserves in the SANPES program are administered by the Centro Ecologico de Sonora. The Ajos were originally included among these, but their mangement has now reverted to SARH.

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Appendix 1. Checklist of the Flora of the Sierra de los Ajos, Sonora, Mexico. Records are based primarily on specimens collected by the authors and associates, 1992-1993. A few records are based on other collections, photo vouchers, or observations. Non-native and apparently self-reproducing species are indicated by an asterisk (*).

Acanthaceae
Dyschoriste decumbens (A. Gray) Kuntz

Aceraceae
Acer grandidentatum Nuttall

Adiantaceae
Argyrochosma limitanea (Maxon) Windham var. *mexicana* (Maxon) Windham
Bommeria hispida (Kuhn) Underwood
Cheilanthes bonariensis (Willdenow) Proctor
Cheilanthes eatoni Baker
Cheilanthes wrightii Hooker
Pellaea atropurpurea (L.) Link

Agavaceae
Agave cf. *palmeri* Englemann
Agave parryi Engelmann var. *huachucensis* (Baker) Little *ex* L.D. Benson
Yucca arizonica McKelvey
Yucca schottii Engelmann

Alliaceae
Allium plummerae S. Watson

Amaranthaceae
Alternanthera repens (L.) Kuntze ?
Amaranthus graecizans L.
Amaranthus cf. *palmeri* S. Watson

Anacardiaceae
Rhus trilobata Nuttall
Rhus choriophylla Wooton & Standley
Rhus glabra L.
Toxicodendron radicans Kuntze var. *divaricatum* (Greene) Barkley

Apiaceae
Eryngium heterophyllum Engelmann
Eryngium lemmoni Coulter & Rose
Ligusticum porteri Coulter & Rose
Pseudocymopterus montanus (A. Gray) Coulter & Rose

Apocynaceae
Macrosiphonia brachysiphon (Torrey) A. Gray

Araliaceae
Aralia racemosa L.

Asclepiadaceae
Asclepias asperula (Decaisne) Woodson ssp. *asperula*
Asclepias elata Bentham
Asclepias hypoleuca (A. Gray) Woodson
Asclepias lemmoni A. Gray
Asclepias nummularia Torrey
Asclepias nyctaginifolia A. Gray
Asclepias subverticillata (A. Gray) Vail
Asclepias tuberosa L. ssp. *interior* Woodson

Aspleniaceae
Asplenium resiliens Kunze

Asteraceae
Ageratina herbacea (A. Gray) King & Robinson
Ageratina rothrockii (A. Gray) King & Robinson
Ambrosia psilostachya DC.
Antennaria marginata Greene
Artemesia dracunculus L.
Artemesia ludoviciana Nuttall var. *mexicana* (Willdenow *ex* Sprengel) Fernald
Aster potosinus A. Gray
Baccharis salicifolia (Ruiz & Pavón) Persoon
Baccharis thesioides H.B.K.
Baccharis cf. *pteronioides* DC.
Bahia dissecta (A. Gray) Britton
Bidens aurea (Aiton) Sherff
Bidens bigelovii A. Gray
Brickellia betonicaefolia A. Gray
Brickellia eupatorioides (L.) Shinners var. *chlorolepis* (Wooton & Standley) B. Turner
Brickellia grandiflora (Hooker) Nuttall
Brickellia rusbyi A. Gray
Brickellia simplex A. Gray
Centaurea rothrockii Greenman
Cirsium sp. 1
Cirsium sp. 2
Conyza canadensis (L.) Cronquist
Cosmos parviflorus (Jacquin) H.B.K.
Erigeron arisolius Nesom
Erigeron arizonicus A. Gray
Erigeron cf. *flagellaris* A. Gray
Erigeron neomexicanus A. Gray
Erigeron platyphyllus Greene
Galinsoga parviflora Cavanilles
Gnaphalium macounii Greene
Guardiola platyphylla A. Gray
Gutierrezia alamanii A. Gray var. *megalocephala* (Fernald) M.A. Lane

Gutierrezia wrightii A. Gray
Gymnosperma glutinosum (Sprengel) Lessing
Helianthus petiolaris Nuttall
Heterotheca subaxillaris (Lamarck) Britton & Rusby
Hieracium crepidispermum Fries
Hieracium fendleri Schultz-Bipontinus
Hymenoclea sp.
Hymenothrix wrightii A. Gray
Lactuca graminifolia Michaux
Leibnitzia seemannii (Schultz-Bipontinus) Nesom
Machaeranthera sp. 1
Machaeranthera sp. 2
Melampodium longicorne A. Gray
Psilactis gentryi (Standley) Morgan
Ratibida mexicana (S. Watson) Sharp
Senecio carlomasonii B. Turner & T. Barkley
Senecio flaccidus Lessing var. *douglasii* (DC.) B. Turner & T. Barkley
Senecio neomexicanus A. Gray
Senecio parryi A. Gray
Senecio wootoni Greene
Solidago scabrida DC.
Solidago wrightii A. Gray var. *adenophora* Blake
Stevia serrata Cavanilles var. *serrata*
Tagetes lemmoni A. Gray
Thelesperma megapotamicum (Sprengel) Kuntze
Verbesina longifolia A. Gray
Viguiera annua (Jones) Blake
Viquiera multiflora (Nuttall) Blake var. *multiflora*
Xanthium strumarium L.
Zinnia peruviana L.

Betulaceae
Alnus oblongifolia Torrey

Bignoniaceae
Chilopsis linearis (Cavanilles) Sweet ssp. *arcuata* (Fosberg) Henrickson

Boraginaceae
Lithospermum cobrense Greene
Macromeria viridiflora DC

Brassicaceae
Draba petrophila Greene var. *viridis* (Heller) C.L. Hitchcock
Erysimum capitatum (Douglas) Greene
Lepidium thurberi Wooton
**Rorippa nasturtium-aquaticum* (L.) Hayek
Schoenecrambe linearifolia (A. Gray) Rollins
Thlaspi montanum L. var. *montanum*

Cactaceae
Coryphantha recurvata (Engelmann) Britton & Rose
Echinocereus cf. *coccineus* Engelmann
Echinocereus rigidissimus Rose
Opuntia cf. *engelmannii* Salm-Dyck
Opuntia spinosior (Engelmann & Bigelow) Toumey
Opuntia cf. *versicolor* Engelmann

Campanulaceae
Lobelia anatina Wimmer

Caparaceae
Polanisia dodecandra (L.) DC.

Caprifoliaceae
Lonicera sp.
Sambucus sp.
Symphoricarpos oreophilus A. Gray var. *oreophilus*

Caryophyllaceae
Arenaria lanuginosa (Michaux) Rohrbach ssp. *saxosa* (A. Gray) Maguire
Arenaria stricta Michaux ssp. *texana* (Robinson) Maguire
Drymaria leptophylla (Chamisso & Schlechtendal) Rohrb. var. *nodosa* (Engelmann) J. Duke
Silene laciniata Cavanilles var. *greggii* A. Gray

Chenopodiaceae
Chenopodium incisum Poiret
**Salsola kali* L.

Cochlospermaceae
Amoreuxia palmatifida Moçino & Sessé

Commelinaceae
Commelina dianthifolia Delile
Tinantia erecta (Jacquin) Schlechtendal

Convallariaceae
Smilacina racemosa (L.) Desfontaines
Smilacina stellata (L.) Desfontaines

Convolvulaceae
Convolvulus equitans Bentham
Evolvulus arizonicus A. Gray
Ipomoea longifolia Bentham
Ipomoea thurberi A. Gray

Crassulaceae
Sedum stelliforme S. Watson

Cucurbitaceae
Apodanthera undulata A. Gray
Cucurbita foetidissima H.B.K.

Cupressaceae
Juniperus deppeana Steudel
Juniperus coahuilensis (Martinez) Gaussen *ex* R.P. Adams
Juniperus scopulorum Sargent

Cyperaceae
Cyperus cf. *hermaphroditis* (Jacquin) Standley
Cyperus cf. *pringlei* Britton
Cyperus rusbyi Britton
Eleocharis montevidensis Kunth

Dennstaedtiaceae
Pteridium aquilinum (L.) Kuhn var. *pubescens* Underwood

Dryopteridaceae
Cystopteris fragilis (L.) Bernh.
Woodsia cochisensis Windham

Equisetaceae
Equisetum sp.

Ericaceae
Arbutus arizonica (A. Gray) Sargent
Arctostaphylos pungens H.B.K.
Chimaphila maculata (L.) Pursh
Monotropa hypopitys L.

Euphorbiaceae
Acalypha lindheimeri Müller-Argoviensis
Cnidoscolus angustidens Torrey
Croton texensis (Klotsch) Müller-Argoviensis
Euphorbia alta Norton
Euphorbia melanadenia Torrey
Euphorbia pediculifera Engelmann var. *pediculifera*
Jatropha macrorhiza Bentham
Tragia laciniata (Torrey) Müller-Argoviensis

Fabaceae
Acacia angustissima (Mill.) Kuntze
Amorpha fruticosa L.
Astragalus nothoxys A. Gray
Calliandra eriophylla Bentham
Chamaecrista serpens (L.) Greene var. *wrightii* (A. Gray) Irwin & Barneby
Cologania angustifolia H.B.K.
Cologania obovata Schlechtendahl
Coursetia caribea (Jacquin) Lavin var. *sericea* (A. Gray) Lavin
Dalea cf. *candida* (Michaux) Willdenow
Dalea filiformis A. Gray
Dalea versicolor Zuccarini var. *sessilis* (A. Gray) Barneby
Desmanthus cooleyi (Eaton) Trelease
Desmodium grahami A. Gray
Erythrina flabelliformis Kearney
Eysenhardtia orthocarpa (A. Gray) S. Watson var. *orthocarpa*
Galactia wrightii A. Gray
Hoffmanseggia glauca (Ortega) Eifert
Lathyrus lanzwertii Kellog var. *leucanthus* (Rydberg) Dorn
Lotus oroboides (H.B.K.) Ottley
Lupinus huachucanus Jones
Lupinus sp.
**Medicago sativa* L.
Mimosa cf. *aculeaticarpa* Ortega
Mimosa dysocarpa Bentham
Mimosa grahamii A. Gray var. *grahamii*
Phaseolus sp.
Prosopis cf. *velutina* Wooton
Rhyncosia senna Gilles *ex* Hooker var. *texana* (Torrey & Gray) M.C. Johnston
Robinia neomexicana A. Gray var. *neomexicana*
Tephrosia thurberi (Rydberg) C.E. Wood
Thermopsis montana Nuttall var. *montana*
Trifolium wormskioldii Lehm. var. *longicaule* (Wooton & Standley) L. Benson
Vicia pulchella H.B.K.

Fagaceae
Quercus arizonica Sargent
Quercus emoryi Torrey
Quercus gambelii Nuttall
Quercus hypoleucoides Camus
Quercus mcvaughii Spellenberg
Quercus oblongifolia Torrey
Quercus rugosa Née
Quercus viminea Trelease

Fouquieriaceae
Fouquieria splendens Engelmann ssp. *splendens*

Garryaceae
Garrya wrightii Torrey

Gentianaceae
Gentianella microcalyx (Lemmon) J.M. Gillett

Geraniaceae
Geranium caespitosum James
Geranium richardsonii Fischer & Trautvetter

Hydrangeaceae
Philadelphus microphyllus A. Gray

Hydrophyllaceae
Phacelia heterophylla Pursh

Iridaceae
Iris missouriensis Nuttall
Nemastylis tenuis (Herbert) Baker
Sisyrinchium scabrum Schlechtendahl & Chamisso

Juglandaceae
Juglans major (Torrey) Heller

Juncaceae
Juncus ensifolius Wikström var. *brunnescens* (Rydberg) Cronquist
Juncus tenuis Willdenow

Lamiaceae
Agastache pallida (Lindley) Cory var. *pallida*
Hedeoma sp.
**Marrubium vulgare* L.
Monarda citriodora Cervantes *ex* Lagasca ssp. *austromontana* (Epling) Scora
Salvia cf. *arizonica* A. Gray
Salvia lemmoni A. Gray
Salvia reflexa Hornemann
Stachys coccinea Jacquin
Trichostema arizonicum A. Gray

Liliaceae
Lilium parryi S. Watson

Linaceae
Linum lewisii Pursh
Linum puberulum (Engelmann) Heller

Loasaceae
Mentzelia sp.

Lythraceae
Lythrum californicum Torrey & Gray

Malpighiaceae
Aspicarpa hirtella L.C. Richard

Malvaceae
Gossypium thurberi Todaro
Sphaeralcea angustifolia (Cavanilles) G. Don

Melanthiaceae
Zigadenus virescens (H.B.K.) Macbride

Nolinaceae
Dasylirion wheeleri S. Watson
Nolina microcarpa S. Watson

Nyctaginaceae
Allionia incarnata L.

Oleaceae
Fraxinus gooddingii Little
Fraxinus pappilosa Lingelsheim
Fraxinus velutina Torrey

Onagraceae
Epilobium canum (Greene) Raven
Epilobium ciliatum Rafinesque ssp. *ciliatum*
Gaura sp.
Lopezia gracilis S. Watson
Oenothera elata H.B.K. ssp. *hirsutissima* (A. Gray) Dietrich
Oenothera laciniata Hill var. *pubescens* (Willdenow) Munz

Orchidaceae
Hexalectris sp.
Malaxis corymbosa (S. Watson) Kuntze
Malaxis ehrenbergii (Reichenbach) Kuntze
Malaxis macrostachya (Lexarza) Kuntze
Platanthera limosa Lindley

Ophioglossaceae
Botrychium virginianum (L.) Swartz

Orobanchaceae
Conopholis alpina Liebmann var. *mexicana* (A. Gray *ex* S. Watson) Haynes

Oxalidaceae
Oxalis cf. *albicans* Kunth ssp. *pilosa* (Nuttall) Eiten
Oxalis alpina (Rose) Kunth

Papaveraceae
Argemone pleiacantha Greene

Passifloraceae
Passiflora mexicana Jussieu

Phytolaccaceae
Rivina humilis L.

Pinaceae
Abies concolor (Gordon & Glendinning) Hoopes
Pinus cembroides Zuccarini
Pinus engelmannii Carrière
Pinus leiophylla Schiede & Deppe var. *chihuahuana* (Engelmann) Shaw
Pinus ponderosa Lawson var. *arizonicus* (Engelmann) Shaw
Pinus strobiformis Engelm.
**Pinus sylvestris* L.
Pseudotsuga menziesii (Mirbel) Franco

Plantaginaceae
**Plantago major* L.
Plantago patagonica Jacquin

Platanaceae
Platanus wrightii S. Watson

Poaceae
Aegopogon tenellus (Cavavilles) Trinius
Aristida adscensionis L.
Aristida arizonica Vasey
Aristida divaricata Humboldt & Bonpland
Aristida ternipes Cavanilles var. *hamulosa* (Henrard) Trent
Aristida ternipes Cavanilles var. *ternipes*
**Avena* cf. *fatua* L.
Blepharoneuron tricholepis (Nash) Torrey
Bothriochloa barbinodis (Lagasca) Herter
Bouteloua aristidoides (H.B.K.) Grisebach
Bouteloua curtipendula (Michaux) Torrey
Bouteloua gracilis (H.B.K.) Lagasca *ex* Steudel
Bouteloua hirsuta Lagasca
Bouteloua radicosa (Fournier) Griffths
Bromus anomalus Rupr. *ex* Fournier
Bromus ciliatus L.
Chloris virgata Swartz
**Cynodon dactylon* (L.) Persoon
**Digitaria sanguinalis* (L.) Scopoli
Echinochloa crusgalli (L.) Beauvois
Elymus arizonicus (Scribner & Smith) Gould
Elymus elymoides (Rafinesque) Swezey
Eragrostis intermedia A.S. Hitchcock
Eragrostis mexicana (Hornemann) Link var. *mexicana*
Eragrostis pectinacea (Michaux) Nees var. *miserrima* (Fournier) J. Reeder
Eragrostis pectinacea (Michaux) Nees var. *pectinacea*
Eriochloa acuminata (Presl) Kunth var. *minor* R.B. Shaw
Heteropogon contortus (L.) Beauvois
Koehleria macrantha (Ledeb.) Schultes
Leptochloa viscida (Scribner) Beal
Lycurus setosus (Nuttall) C. Reeder
Muhlenbergia longiligula A.S. Hitchcock
Muhlenbergia minutissima (Steudel) Swallen
Muhlenbergia montana (Nuttall) A.S. Hitchcock
Muhlenbergia pauciflora Buckley
Muhlenbergia repens (Presl) A.S. Hitchcock
Muhlenbergia rigida (H.B.K.) Trinius
Muhlenbergia sinuosa Swallen
Muhlenbergia trifida Hackel
Muhlenbergia wolfii (Vasey) Rydberg
Panicum bulbosum H.B.K.
Paspalum distichum L.
Piptochaetium fimbriatum (H.B.K.) A.S. Hitchcock
Piptochaetium pringlei (Beal) L. Parodi
**Polypogon viridis* (Gouan) Breistroffer
**Rhynchelytrum repens* (Willdenow) C.E. Hubbard
Setaria grisebachii Fournier
**Sorghum halapense* (L.) Persoon
Sporobolus cf. *airoides* Torrey

Polemoniaceae
Ipomopsis macombii (Torrey) V. Grant
Phlox nana Nutall var. *glabella* (A. Gray) Brand

Polygalaceae
Polygala obscura Bentham

Polygonaceae
Eriogonum jamesii Bentham var. *undulutam* (Bentham) Stokes
Eriogonum wrightii Torrey
Polygonum sp.
**Rumex crispus* L.
Rumex orthoneurus Rechinger

Portulacaceae
Talinum marginatum Greene

Potamogetonaceae
Potamogeton sp.

Primulaceae
Samolus vagans Greene

Ranunculaceae
Aquilegia chrysantha A. Gray
Clematis sp.
Delphinium andesicola Ewan
Delphinium tenuisecta Greene
Thalictrum fendleri A. Gray

Rhamnaceae
Ceanothus depressus Bentham
Condalia correlii M.C. Johnston
Rhamnus betulaefolia Greene

Rosaceae
Agrimonia striata Michaux
Cercocarpus brevifolius A. Gray var. *brevifolius*
Holodiscus dumosus (Nuttall) Heller var. *australis* (Heller) Ley
Potentilla thurberi A. Gray var. *atrorubens* (Rydberg) Kearney & Peebles
Prunus serotina Ehrhart ssp. *virens* (Wooton & Standley) McVaugh var. *rufula* (Wooton & Standley) McVaugh
Prunus serotina Ehrhart ssp. *virens* (Wooton & Standley) McVaugh var. *virens*

Rubiaceae
Bouvardia ternifolia (Cavanilles) Schlechtendal
Galium mexicanum Kunth ssp. *asperrimum* (A. Gray) Dempster
Galium pilosum Aiton
Galium wrightii A. Gray
Houstonia wrightii A. Gray

Rutaceae
Ptelea angustifolia Bentham

Salicaceae
Populus fremontii S. Watson ssp. *fremontii*
Populus tremuloides Michaux
Salix bonplandiana H.B.K.

Sapindaceae
Dodonea viscosa L.

Saxifragaceae
Heuchera sanguinea Engelmann

Scrophulariaceae
Castilleja austromontana Standley & Blumer
Castilleja patriotica Fernald
Castilleja tenuiflora Bentham
Mimulus cf. *cardinalis* Douglas
Mimulus guttatus DC.
Penstemon barbatus (Cavanilles) Roth ssp. *torreyi* (Bentham) Keck
Penstemon campanulatus (Cavanilles) Willdenow ssp. *chihuahuensis* Straw
Penstemon stenophyllus A. Gray
Seymeria bipinnatisecta Seemann

Solanaceae
Datura wrightii Regel
**Nicotiana glauca* Graham
Physalis sp.
Solanum eleagnifolium Cavanilles
Solanum cf. *rostratum*
Solanum sp.

Ulmaceae
Celtis reticulata Torrey
Valerianaceae
Valeriana arizonica A. Gray
Valeriana edulis Nuttall
Valeriana sorbifolia H.B.K.

Verbenaceae
Glandularia bipinnatifida (Nuttall) Nuttall var. *bipinnatifida*
Verbena carolina L.

Violaceae
Viola canadensis L.
Viscaceae
Phoradendron coryae Trelease
Vitaceae
Vitis arizonica Engelmann

Zygophyllaceae
Kalstroemia grandiflora Torrey

Flora of the Huachuca Mountains, Cochise County, Arizona

Janice E. Bowers and Steven P. McLaughlin[1]

Abstract.—The Huachuca Mountains, Cochise County, Arizona, are one of about two dozen "sky islands" in southeastern Arizona. A herbarium search revealed that, prior to 1990, 849 species had been documented from the Huachuca Mountains. Field work conducted between 1990 and 1994 added another 144 species to the flora. Altogether, 993 species in 467 genera and 101 families are now known from the range. Of these, 65 are introduced. Madrean floristic elements dominate the flora, accounting for 69.9% of all native species. Sonoran elements (5.0% of all native species) are relatively poorly represented in the Huachuca Mountains compared to more arid mountain ranges in southeastern Arizona. The flora of the Huachuca Mountains is comparatively rich for an Arizona local flora, with 29-39% more species than expected based on its elevational range and collecting history. Substrate complexity and the presence of many well-watered canyon habitats and springs contribute to the high species diversity.

INTRODUCTION

The Huachuca Mountains (fig. 1), located in southwestern Cochise County on the United States-Mexico border, are one of two dozen mountain ranges in southeastern Arizona. Often referred to as "sky islands" (Heald 1951), these ranges form a floristically diverse archipelago that has been of keen interest to botanists for more than a century. The Huachuca Mountains in particular have a long and illustrious botanical history. Plant collection dates back to the botanical explorations of John Gill Lemmon and Sara Plummer Lemmon in 1882 (Crosswhite 1979) and has continued until the present day (fig. 2). Floristic work includes an enumeration of Timothy E. Wilcox and Marcus E. Jones collections (Britton and Kearney 1894, Jones 1930) and checklists for Fort Huachuca, Ramsey Canyon, Garden Canyon and Coronado National Memorial (Goodding 1950a, 1950b; Pratt 1963; Toolin 1980; Yatskievych 1980-81; Ruffner and Johnson 1991; Parfitt and Christy 1992). Altogether, 84 collectors have taken more than 4000 specimens from the range.

Our initial objective was, based on the work of these many collectors, to assemble a plant checklist for the entire range so that we could detemine if the flora was indeed, as Wallmo (1955) characterized it, "quite well known." Eventually, we also became interested in how plant checklists grow and shrink. In this paper, we compare the flora of the Huachuca Mountains with floras of other sky islands in southeastern Arizona, and demonstrate that species composition of local floras is dynamic, subject to historical changes in climate, land use, and other factors. The checklist will be published at a later date.

STUDY AREA

The north-south trending Huachuca Mountains belong to the Basin and Range Province (Hunt 1967). Maximum elevations are 9,466 feet (2885 m) on Miller Peak, 9220 feet (2810 m) on Carr Peak, 8725 feet (2659 m) on Ramsey Peak, and 8410 feet (2563 m) on Huachuca Peak. Several major canyons with perennial reaches drain the precipitous eastern slope and eventually flow into the San Pedro River. The western slope, part of the Santa Cruz River watershed, has only a few streams with perennial reaches. Overall, the

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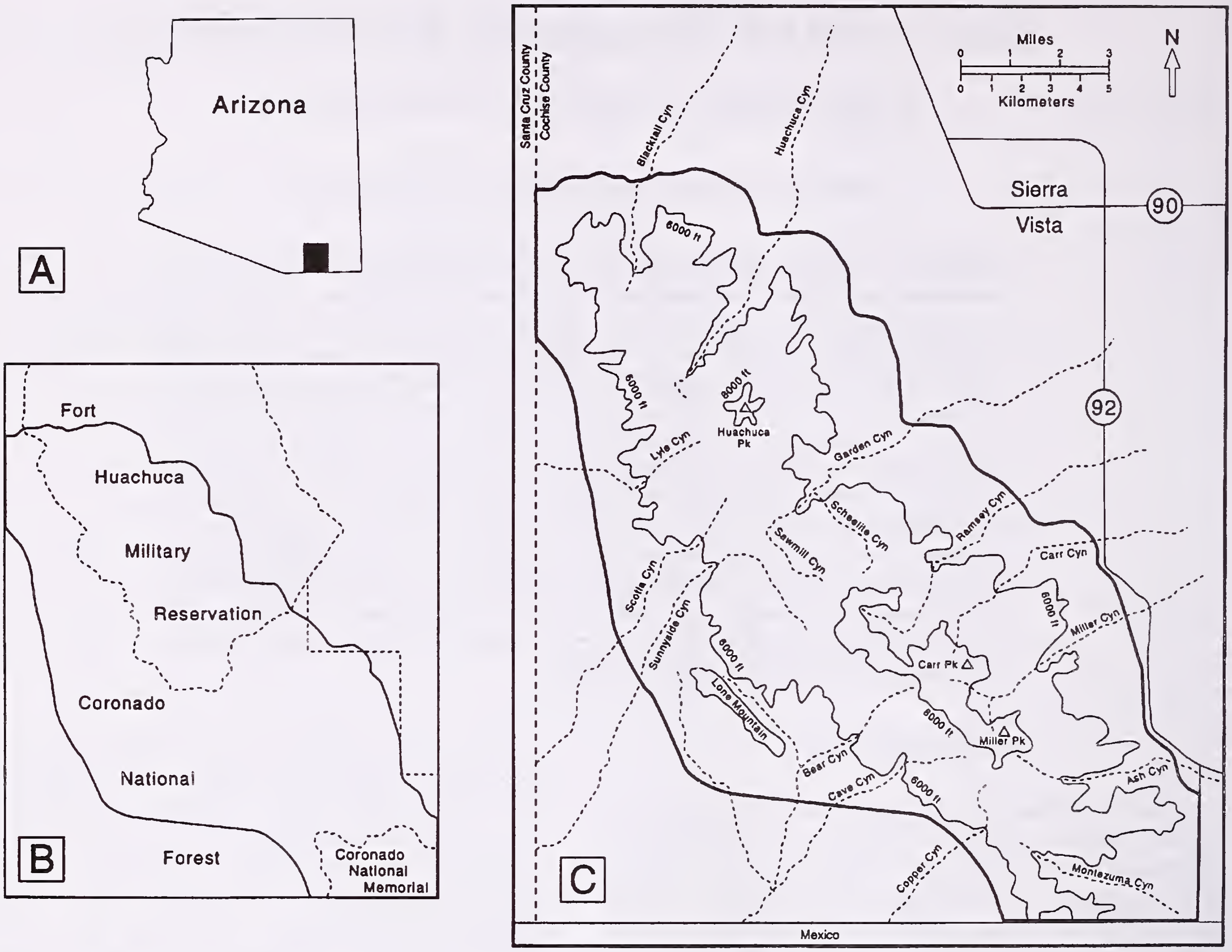

Figure 1.—Huachuca Mountains and vicinity. The heavy black line shows the study area boundary. A, Location of the Huachuca Mountains in Arizona; B, administrative units in and near the Huachuca Mountains; C, major drainages and peaks of the Huachuca Mountains.

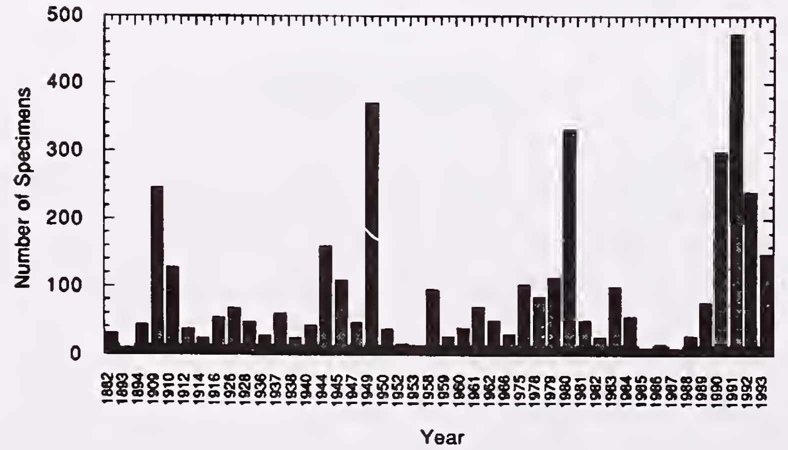

Figure 2.—Plant collection by year, Huachuca Mountains (omitting all years in which fewer than 10 specimens were collected). Based on specimens deposited at the University of Arizona herbarium

Huachuca Mountains appear highly dissected, with a large ratio of canyon to ridge habitat.

Our study area had an elevational range of 4466 feet (1361 m) and covered about 122 square miles (31,600 ha). The northern and eastern boundaries roughly followed the base of the range, which varies from 5000-5200 feet (1524-1585 m) above sea level. The southern edge coincided with the International Boundary. The 5500-foot (1676 m) contour approximated the western boundary. We excluded most private lands at the base of the range, with the exception of the Ramsey Canyon Nature Preserve, Peterson Ranch in Scotia Canyon, and aquatic habitats at Beatty's Miller Canyon Orchard in Miller Canyon. The lower elevations of Fort Huachuca Military Reservation were also excluded from our study area.

Topography and Geology

The range is geologically diverse. Bolsa Quartzite, the basal sedimentary unit, rests unconformably on Precambrian granite. On the eastern slope, Paleozoic sedimentary rocks, mainly limestone but also some shales and siltstones, top the Bolsa quartzite. On the western slope, sedimentary rocks of Cretaceous age, including conglomerates and shales, interfinger with Triassic-Jurassic volcanic and sedimentary rocks (Keith and Wilt 1978).

Climate

Weather stations are maintained at Fort Huachuca at the northern end of the range and at Coronado National Memorial at the southern end. Annual precipitation at Fort Huachuca (4664 feet, 1422 m) is 14.6 inches (37.1 cm). About half falls in July and August as high-intensity "monsoonal" rains that originate as scattered convectional thunderstorms triggered and enhanced by surface heating and orographic effects. Winters at Fort Huachuca are rather dry. December and January, the wettest winter months, average 1.78 inches (4.5 cm) of precipitation. About 10% of winter precipitation falls as snow, which seldom stays on the ground more than a day or two. At higher elevations, annual rainfall exceeds 25 inches (63.5 cm), and snow can remain on the ground all winter. Winter storms result from cyclonic storms and frontal systems associated with large-scale low pressure systems that typically originate off the coast of California and Baja California. They are less variable spatially and more variable temporally than summer storms (Sellers and Hill 1974).

Summers and winters at Fort Huachuca are mild. The average January temperature is 46.3°F (7.9°C), with average daily maximum and minimum temperatures of 58.4 and 34.2°F (14.7 and 1.2°C). Summer temperatures are moderated by afternoon cloud cover. The average July temperature is 77.5°F (25.3°C), with daily maximum and minimum temperatures of 88.6 and 66.4°F (31.4 and 19.1°C). At higher elevations, the average January temperature is 40°F (4.4°C), and the average July temperature is 65°F (18.3°C) (Sellers and Hill 1974).

THE FLORA

Plant Checklist

In winter 1990 and spring 1991, we searched the University of Arizona herbarium (ARIZ) and the herbarium at Fort Huachuca for specimens from the Huachuca Mountains. We critically evaluated all collections, and, if necessary, redetermined them. Starting in August 1990 and continuing through June 1994, we made 41 trips into the range, mostly during the April-October growing season, and also in November and January. We attempted to sample every habitat throughout the growing season with special emphasis on discontinuous habitats such as cattle tanks, springs, peaks, and cliffs. Most of our effort was concentrated along trails and roads.

Between 1882 and 1989, collectors documented a total of 849 species in the Huachuca Mountains. During the course of our project, we found 137 species that were new to the flora. Another 7 species were added by other collectors between 1990 and 1993. The total flora comprises 993 species and infraspecific taxa in 467 genera and 101 families. Of these, 65 species are introduced. The native flora comprises 906 species and 27 infraspecific taxa.

How Plant Checklists Grow

It is common for plant checklists to expand over several decades of collecting. The Mount Shasta, California, flora grew from 425 species and infraspecific taxa in 1940 to 525 in 1963 (Cooke 1940, 1941, 1949, 1963), an increase of about 1 percent per year. The flora of Tumamoc Hill, Tucson Mountains, Arizona, increased 0.6 percent per year between 1909 and 1985, from 238 to 346 species (Thornber 1909, Bowers and Turner 1985). The flora of Organ Pipe Cactus National Monument grew from 522 species in 1980 (Bowers 1980) to 571 in 1992 (Pinkava et al. 1992), an increase of 0.8 percent per year. The flora of the White Mountains, California, increased 3 percent per year between 1973 and 1987, from 761 to 1078 species (Lloyd and Mitchell 1973, Morefield 1992). The small yearly increment in each case suggests that the initial floras were fairly complete. Linear regression of percent increase against final size of the flora suggests that, not surprisingly, the larger the flora, the more difficult it is to collect completely ($R^2 = 0.95$).

Most additions to local floras are probably plants that have been previously overlooked. On occasion, however, movement of species onto a site increases the size of a local flora. New arrivals may be natives or exotics. In either case, careful observation is needed to distinguish newly arrived species from those that were simply overlooked. Especially in recent years, introduction of exotics, either deliberately or accidentally, has expanded the size of many local floras. At Glacier National Park, Montana, exotics increased at an accelerating rate between 1920 and 1993 (Lesica et al. 1993). Over 76 years, the number of introduced species in the Tumamoc Hill flora increased by an order of magnitude, from 2 to 52 (Bowers and Turner 1985, Burgess et al. 1991). Such examples could be multiplied many times. In the Huachuca Mountains flora, the 65 exotics include species seeded by the Forest Service to prevent erosion after fire (*Dactylis glomerata, Sanguisorba minor, Melilotus* spp.); escapes from cultivation (*Pyracantha koidzumii, Hedera helix, Vinca major, Rubus procera*); and naturalized exotics (*Erodium cicutarium, Bromus rubens, Polypogon interruptus*). About half of the exotic flora was first documented after 1962. The rapid vegetative growth and smothering habit of *Rubus procera* and *Vinca major* represent serious threats to the biodiversity of lower mesic canyons in the Huachuca Mountains.

The concentrated effort of compiling a plant checklist is another reason local floras increase in size. After 98 years of casual and infrequent collecting in the Rincon Mountains, the documented flora was 517 species (Bowers, unpublished data). The final checklist of 986 species (Bowers and McLaughlin 1987) represented an increase of 18 percent per year. McLaughlin (1993) doubled the known size of the Pinaleño Mountains flora, from 406 in 1988 (Johnson 1988) to 824 in 1993. In the Huachuca Mountains, collectors documented a total of 849 species between 1882 and 1989. Between 1990 and 1994, 144 species were added to the flora, an increase of about 5 percent per year. This modest increment suggests that the flora was indeed comparatively well known at the start of our project.

How Local Floras Shrink

Loss of species from local floras has been noted infrequently in southeastern Arizona. Bowers and McLaughlin (1987) were unable to relocate 41 species in the Rincon Mountains; of these, 22 had originally been collected before 1909. Rondeau (1991) did not find 55 species that had been collected in the Tucson Mountains between 1903 and 1988. In the Huachuca Mountains, 31 species may no longer belong to the flora, despite concerted efforts to locate many of them. Inevitably, collectors of local floras seldom if ever relocate all the plant species documented from an area. Some are simply overlooked. Mislabeled vouchers might not have belonged to the flora in the first place. This is a particular problem for collectors in southeastern Arizona, where Lemmon's labels are notoriously unreliable (Kearney and Peebles 1960). *Matelea balbisii, Spirodela polyrhiza, Woodsia scopulina* and several other species reported from the Huachuca Mountains might well have been mislabeled as to location. Some species are "lost" as a result of taxonomic recombination; in our study area, *Aquilegia longisissima, Polygala piliophora* and a few others might not prove to be good species.

Of greater biological interest are species that apparently no longer occur in an area. Some plants lost from the Huachuca Mountains flora are exotics that apparently failed to become established, including *Coriandrum sativum, Pastinaca sativa, Lonicera japonica,* and several others. A few native species may have been eliminated by development of the lower reaches of Carr, Miller, and Ramsey canyons. *Odontrichum decompositum,* for example, was last seen at "James's resort" near the mouth of Ramsey Canyon (Jones 1930), now an area of houses, gardens, and pastures. *Melica porteri* "cannot exist in the presence of a cow" (Goodding 1950a) and may have been eliminated by grazing. Eventually, proliferation of exotic grasses such as *Eragrostis lehmanniana* and *E. curvula* might have deleterious effects on the native flora. Both species dramatically decrease the diversity and productivity of native grasses (Cable 1971, Bock et al. 1986). *Eragrostis lehmanniana* was introduced into Cochise County in the late 1940s; by 1951 it had spread onto Fort Huachuca, apparently from nearby highways (Goodding 1950a). *Eragrostis curvula* was introduced into the United States in 1928 (Crider 1945). These two exotics are now among the most common plants at low to moderate elevations in the Huachuca Mountains.

The fossil record demonstrates dramatic alteration of floras as a result of climatic change (Betancourt et al. 1990). Historical climatic change repeats this process on a briefer time-scale, especially among small, local populations. Extirpation of 6 native perennials formerly found at high elevations in the Rincon Mountains might have resulted from severe winter drought during 1920-1930 or 1942-1958 (Bowers and McLaughlin 1987). During the seasonally dry months of April, May and June, such species depend on soil moisture left by the winter snowpack. Severe winter drought could have eliminated their presumably small populations. A similar set of circumstances might have claimed some species in the Huachuca Mountains. High-elevation mesophytes not collected there since 1913 include *Adiantum pedatum, Achillea millefolium, Dugaldia hoopesii, Macromeria viridiflora, Sidalcea neomexicana,* and *Veronica serpyllifolia.* Currently, *Vaccinium myrtillus, Pyrola chlorantha, Mertensia franciscana, Pedicularis grayi, Actaea rubra, Hypericum formosum, Senecio huachucanus* and several others are known in the Huachuca Mountains only from small populations at high elevations and may be similarly vulnerable.

Natural disasters, particular fire and flood, may also have eliminated species from the flora. The Huachuca Mountains have experienced frequent severe fires in recent years (Taylor 1991, Wohl and Pearthree 1991). The southern end of the range has been particularly hard-hit, notably in 1977, 1988, and 1991 (Taylor 1991). The disappearance or retreat of several species can perhaps be ascribed to these or earlier fires. *Rosa woodsii,* collected in "moist draws" on Carr Peak in 1909, is now known only from upper Bear Canyon; *Hypericum formosum,* collected on "moist slopes" of Carr Peak in 1909, is now known only from Bond and Sawmill springs. *Valeriana edulis,* which is no longer known from the flora, may have been eliminated by fire.

The most destructive fires may be followed by floods and debris flows, especially in steep drainages (Wohl and Pearthree 1991), with dire consequences for riparian herbs (Gori 1992). The small, scattered populations of *Lilium parryi* have experienced catastrophic declines in recent years as a result of flooding (Warren and Reichenbacher 1991, Wood 1992). Riparian plants that might have been eliminated from the Huachuca Mountains flora by floods or debris flows are *Dryopteris filix-mas, Aster coerulescens, Monarda fistulosa, Oenothera kunthiana, Rubus arizonensis* and *Glyceria borealis.* Small populations of riparian plants might have been eliminated during drought years, as well.

Clearly, a variety of natural and man-made disasters can eliminate species from local floras, particularly when populations are small and local. Although our failure to relocate 31 species provides only negative evidence, we find it suggestive that distinct patterns such as fire, flood, drought and development can be identified. Some apparently extirpated species might well still occur in less accessible parts of the mountain range.

FLORISTIC ANALYSIS

All native species occurring in the Huachuca Mountains flora were classified into floristic elements based on the system of floristic areas for the western United States developed by McLaughlin (1992). Methods for assigning species to floristic elements are given in McLaughlin and Bowers (1990) and McLaughlin (1994). For comparison, the floristic analysis of the Huachuca Mountains flora is presented along with those from the Rincon and Pinaleño mountains (Bowers and McLaughlin 1987, McLaughlin 1993) (Table 1).

The system of floristic elements of McLaughlin (1992) is hierarchical. Five floristic provinces are recognized for the western United States: Cordilleran, Intermountain, Sonoran, Californian and Madrean. These provinces are subdivided into subprovinces, which are in turn subdivided into districts. Table 1 provides a breakdown of floristic elements for the Madrean Floristic Province. "Widespread" Madrean species are those that are (1) found in 20 or more of the local floras used by McLaughlin (1992) to develop the classification, and (2) centered on the Madrean Floristic Province. "Regional" Madrean species are those with more restricted distributions (found in 10 to 19 of 101 local floras from the western United States) that are centered within the Madrean Floristic Province. "Central Arizonan," "Chihuahuan," and "Apachian" species are narrowly distributed in

Table 1.—Floristic elements in the Huachuca, Rincon and Pinaleño mountains. Values in the table are the percentage of the total native flora assigned to each floristic element.

Floristic Elements	Huachuca Mountains	Rincon Mountains	Pinaleño Mountains
Madrean			
Widespread	5.6	5.1	6.6
Regional	17.8	19.0	20.5
Central Arizonan	1.3	1.5	2.3
Chihuahuan	6.4	4.3	2.4
Apachian	38.8	31.6	20.9
Total Madrean	69.9	61.5	52.7
Sonoran	5.0	19.4	10.7
Cordilleran	18.0	10.6	27.2
Intermountain	3.5	2.9	4.6
Californian	3.6	5.6	4.8

the western United States (found in 9 or fewer of the sample of 101 local floras) and are centered, respectively, within the Central Arizona, Chihuahuan and Apachian floristic districts.

The Huachuca, Rincon and Pinaleño mountains all lie within the Madrean Floristic Province, since the majority of their species belong to Madrean elements. All three floras are placed within the Apachian district, since the Apachian element is the largest narrow-species element in their respective floras. The Huachuca Mountains flora has the highest percentage of Apachian species, and all species with Madrean affinities constitute nearly 70% of the flora. The Cordilleran element accounts for 18% of the Huachuca Mountains flora; species with Sonoran and Californian affinities are better represented in the flora of the Rincon Mountains, and those with Cordilleran and Intermountain affinities are better represented in the Pinaleño Mountains. The Chihuhuan element is somewhat better represented in the Huachuca Mountains than in the Rincon or Pinaleño mountains.

The importance of Madrean floristic elements in the Huachuca Mountains is not unexpected. The Apachian element is particularly large. Genera notably rich in Apachian species (5 or more) in our study area include *Asclepias, Bidens, Brickellia, Ipomoea, Dalea, Desmodium, Cyperus,* and *Muhlenbergia*. The Apachian element is most strongly associated with oak and pine-oak woodlands, plant communities that are particularly well represented in the Huachuca Mountains.

The low percentage of Sonoran elements in the Huachuca Mountains contrasts with that of the Rincon Mountains. The base elevation of the Rincon Mountains is 2000 feet (610 m) lower than that of the Huachuca Mountains, resulting in hotter summers, milder winters and lower rainfall, all conducive to a higher representation of species with Sonoran affinities. Those Sonoran species within the flora of the Huachuca Mountains are mostly species with widespread and regional distributions. Some are spring-flowering annuals, a group that is not well represented in the Huachuca Mountains.

The Cordilleran elements are of much greater importance in the Pinaleño Mountains, especially above 9000 feet (2743 m) (McLaughlin 1993), than in the Huachuca Mountains (Table 1). Species with Cordilleran affinities are found mostly in the mixed-conifer and spruce-fir forests in the Pinaleño Mountains, where moisture-loving, cold-tolerant plants thrive under high winter precipitation and low winter temperatures. In the Huachuca Mountains, where winters are neither as cold nor as wet, there is no spruce-fir forest, and the mixed-conifer forest is of limited extent. In the sky island region in general, and in the Huachuca Mountains in particular, the Cordilleran elements include both many widespread taxa and many narrowly distributed species with Mogollon affinities (centered in the Mogollon Rim of Arizona and the Mogollon highlands of New Mexico). In the Huachuca Mountains, species with Cordilleran and Mogollon affinities are found mostly at high elevations or in moist, shaded canyons.

SPECIES DIVERSITY

The plant species diversity of the Huachuca Mountains was evaluated in two ways. First, based on the elevational range of the study area and the collecting effort invested in compiling its flora, we compared the actual number of species observed with the number expected to occur (Bowers and McLaughlin 1982). The elevational range of our study area is 4466 feet (1361 m). For collecting time, we estimated low and high values based on the number of years in which 50 or more specimens were collected (22 years) and the number of years in which 75 or more specimens were collected (16 years). The results showed that, compared to other local floras from throughout Arizona, the Huachuca Mountains have 29-39% more species than would be predicted based on elevational range and collecting history.

We plotted number of species versus elevational range for the Huachuca Mountains and 23 other local floras from Arizona and New Mexico (fig. 3). The regression line in figure 3 shows the relationship between elevational range and richness in this sample of 24 floras [$S = 264 + 0.274(\Delta E)$, $R^2 = 0.502$, $p < .001$)]. The flora for the Huachuca Mountains is the farthest above the regression line, that is, it has the highest residual value. Of the mountain ranges from the southwestern United States whose floras have been investigated in detail, the Huachuca Mountains appear to be exceptional in their high species diversity.

In local floras from the western United States, elevational range is closely correlated with habitat diversity, since both temperature and precipitation vary with elevation, often over short distances. Habitat diversity in turn is a major determinant of species diversity. Thus local floras from areas spanning a large elevational range (such as the Huachuca Mountains) tend to have higher species diversity (fig. 3). The Huachuca Mountains also have many aquatic habitats and much variation in gelogical substrates, and these factors probably also contribute to high species diversity in the range. The complex topography of the range, with its numerous deep canyons cutting nearly to the ridge lines, makes a topographically patchy landscape that may promote high species diversity. Bennett and Kunzmann (1992) attempted to quantify topographic "roughness" and found that their index was correlated with species diversity among a small set of floras from the sky island region. In some sky island floras, a pronounced biseasonal rainfall regime allows both a spring and a summer flora to flourish (Bowers and McLaughlin 1987, McLaughlin and Bowers 1990). In the Huachuca Mountains, where winters are rather dry, spring-flowering species are not well represented.

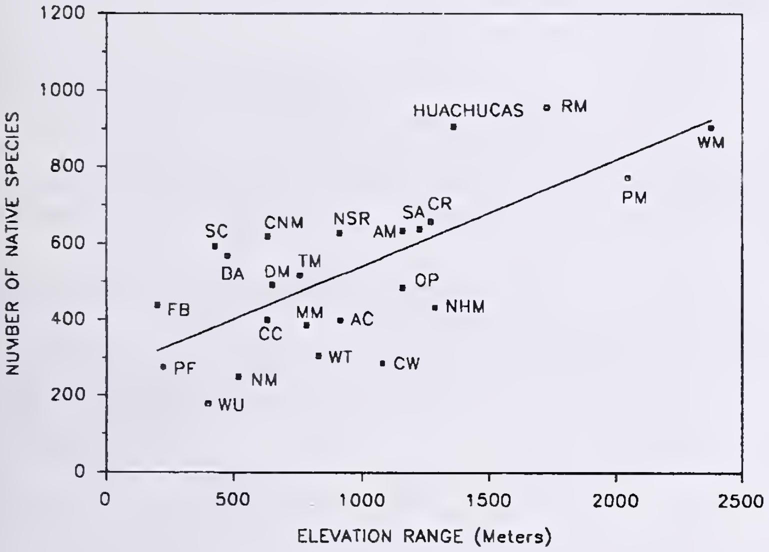

Figure 3.—Relationship between elevational range (difference between highest and lowest elevations) and species diversity among 24 local floras from Arizona and New Mexico. In addition to the Huachucas, the floras plotted are: AC, Aravaipa Canyon, AZ (Warren and Anderson 1980); AM, Animas Mountains, NM (Wagner 1973); BA, Buenos Aires National Wildlife Refuge, AZ (McLaughlin 1992b); CC, Canyon de Chelly National Monument, AZ (Halse 1973); CNM, Chiricahua National Monument, AZ (Reeves 1976); CR, Cooke's Range, NM (Columbus 1988); CW, Chiricahua Wilderness, AZ (Leithliter 1980); DM, Datil Mountains, NM (Fletcher 1972); FB, Fort Bowie National Historic Site, AZ (Warren et al. 1992); MM, Mule Mountains, AZ (Wentworth 1982); NHM, Northern Hualapai Mountains, AZ (Butterwick et al. 1991); NM, Navajo National Monument, AZ (Brotherson et al. 1978); NSR, Northern Santa Rita Mountains, AZ (McLaughlin and Bowers 1990); OP, Organ Pipe Cactus National Monument, AZ (Bowers 1980); PF, Petrified Forest National Park, AZ (Petrified Forest National Park 1976); PM, Pinaleño Mountains, AZ (McLaughlin 1993); RM, Rincon Mountains, AZ (Bowers and McLaughlin 1987); SC, Sycamore Canyon, AZ (Toolin et al. 1980); SA, Sierra Ancha, AZ (Pase and Johnson 1968); TM, Tucson Mountains, AZ (Rondeau 1991); WM, White Mountains, NM (Hutchins 1974); WT, White Tank Mountain Regional Park, AZ (Keil 1973); WU, Wupatki National Monument, AZ (McDougall 1962).

Groombridge (1992) lists the "Apachian/ Madrean" region as one of 164 global centers of plant diversity. Floras from the sky island region are inherently richer than other floras from the western United States (McLaughlin, this symposium). For example, the floras of the Huachuca Mountains, Rincon Mountains, Sycamore Canyon, Chiricahua National Monument and Buenos Aires National Wildlife Refuge, all in the sky island region, are farthest above the regression line in Figure 3. Much of the high species diversity of the Huachuca Mountains is due to the presence of a large Apachian component. Although it is clear that certain floristic elements and floristic areas are richer than others, the environmental, historical and ecological factors that determine these inherent differences are not yet well understood.

CONCLUSIONS

After 112 years of plant collection, the flora of the Huachuca Mountains is well known. Local floras can never be completely collected. Additional field work inevitably turns up species that had been overlooked. Ornamental and crop plants invade from nearby settlements, sometimes becoming naturalized. Native plants, too, may occupy new territory. Natural disasters such as fire, flood, and drought may extirpate some species, especially those with small populations in limited habitats. Human-induced disasters such as grazing and plant introduction may also take a toll. Inevitably, some species will be overlooked by collectors and mistakenly assumed to be extirpated. Between 1882 and 1994, additions (144) to the Huachuca Mountains greatly exceeded subtractions (31). Plant checklists serve as a baseline for assessing floristic change in future decades.

In a region known for its biological diversity, the Huachuca Mountains are exceptionally rich in plant species. Contributing factors include a large Apachian floristic element, complex topography, a wide elevational range, and a diversity of geological substrates and aquatic habitats.

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Flora of the Woodlands of the Sierra de La Laguna, Baja California Sur, México

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Abstract.—The Sierra de la Laguna is the main high mountain range in the arid state of Baja California Sur, Mexico. It is high and narrow, rising boldly from coastal lowlands, with many precipitous and rocky slopes. Its peaks reach up to 2200 m. Above 1500 m this mountains are occupied by the only woodland community in hundreds of kilometers away, and it is believed to have been one island in the geologic past, and in fact now it is in environmental sense. Because the recegtive high altitude of the range, plant communities on the tops has been historically less arids than those on the lowlands, such environment has permited the establishment of woodlands as today.

Origins of the current vegetation seems to amount to middle tertiary period, when some types of montane woodlands in SW United States and NW Mexico were developed under xeric conditions.

The flora of this community is part of a project leading to establishment of an ecological reserve on such area, because the importance as wild recreative area, which was finally decreed in 1993. Number of species of the vascular flora is 272, most of the species (65%) are herbs, both annual and perennial; 43 species are considered endemics (15.8%), including two monospecific genera. This work describes the flora arranged in two communities: the oak-pine and the oak woodland, the first one comprises four plant associations and the later two.

A phytogeographical analysis of this flora shows that the community has high levels of affinity with the tropical element, at both family and genus level (40% and 59% respectively), followed by the cosmopolitan (39% and 20% respectively), this last levels of affinity could suggest a relative recent conformation of the flora.

INTRODUCTION

The woodlands of the Sierra de la Laguna mountains were referred by Axelrod (1950, 1958) in his classification of the Madro-Tertiary Flora as part of the Sierra Madrean Woodland Element, specifically as the Sierra Laguna Component. Table 1 shows the original classification of such Element.

The woodlands of the Cape Region, or Sierra Laguna oak and oak-pine woodlands, differs as much from those of southern California and Arizona, such differences are interpreted as a reflection of the dry climate prevailing along the Baja California peninsula. These woodlands represent one of the southern limits of the Madrean Element.

The Sierra Madrean Woodland Element find their nearest modern representatives in the woodlands of summer-wet and relatively winter-mild climate, regions now located at the southern mountains in California and Arizona in United States, and mountains of medium altitude in the Mexican states of Baja California Sur, Sinaloa, Durango, and Coahuila (see Table 1).

The Sierra Laguna Component was conceptualized by Axelrod (1950) by the fossil analysis of plants of the Miocene of California, and Pliocene of California and Nevada. Fossils and living representatives are shown in Table 2.

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According with his hipothesis, Axelrod states that the associated species during those epochs included plants whose descendants are now found in the woodland associations elsewhere in southwestern United States and northern Mexico.

The Cape Component, see Table 3, a member of the North Mexican Element, a complex which comprises the arid subtropical scrub, currently ocurrs inmediatly below the woodlands ot the Sierra de la Laguna, and anothers localities not well documented today. This same couple of communities are found in the Miocene and Pliocene fossil floras of southern California.

STUDY AREA

The mountains of the Cape Region extend in a south-north from 23° to 23°35'N Lat. It is crossed by the Tropic of Cancer. About 500 km^2 (200 mi^2) of these mountains are estimated to be occur above 1000 m of elevation. The Sierra de La Laguna woodlands are located in the northern part of the Cape Region mountains, it harbors the highest peak at 2200 m. It is conformed by five major canyons (fig. 1); the oak woodland (1000 to 1500 m) has an estimated surface of about 350 km^2, meanwhile the oak-pine woodland (> 1500 m) around 150 km^2.

Table 1.—Original classificacion of Madro-tertiary Geoflora by Axelrod (1950) is based in the assumption of Complexes (biomes), Elements (present climax communities) and Components (fossil groups).

	Madro Tertiary Geoflora:
elements:	current climax communities woodland, chaparral, subtropical scrub, sage & desert.
component:	group of fossil plants, ancestors of the elements

Table 2.—The Sierra Laguna Component was conceptualized by Axelrod (1950) by the fossil analysis of plants of the Miocene of California, and Pliocene of California and Nevada.

Fossils from California	Living Representatives In Sierra de la Laguna Woodlands
Arbutus tehachapiensis	*A. peninsularis*
Ilex sonomiensis	*I. brandegeana*
Populus mohavensis	*P. brandegeana*
Quercus mohavensis	*Q. brandegeei* *Q. albocincta*
Garrya	*Garrya salicifolia*
Rhus	*Rhus laurina*

Table 3.—Floristic Units In the Madro-Tertiary Geoflora according Axelrod (1950).

WOODLAND COMPLEX
  Elements (7):
  1 California Woodland
  2 Conifer Woodland
  3 Sierra Madrean Woodland
    Components
      a) Arizona
      b) **Sierra Laguna**
      c) Edwards Plateau
      d) Durango
      e) Coahuila

CHAPARRAL COMPLEX
  4 California Chaparral

SAGE COMPLEX
  5 Coastal Sage

ARID SUBTROPICAL SCRUB COMPLEX
  6 North Mexican
    Components
      a) Sinaloan
      b) Cape
      c) Tamaulipan

DESERT COMPLEX
  7 North American Desert

Methods

Thirty eight visits has been made in all the four seasons to the area between 1984 to 1993. Almost 3000 of voucher specimens has been prepared and are housed at Centro de Investigaciones Biológicas del Noroeste Herbarium (HCIB). Most of the determinations has been cheked by comparison with the correspondent stored at CAS and UC Herbariums. Some papers has been published, León de la Luz & Domínguez (1989), Breedlove & León de la Luz (1989) and León de la Luz & Coria (1993). An annotated catalog is provided in such papers. Nomenclature follows mainly that of Wiggins (1980).

The Cape Region, and in particular the montane areas, has an incomplete representation in Wiggin's Flora. About 25 % of the plants listed in our papers were omitted from such Flora, or in the same cases, reported to other areas of the Peninsula but not in the woodlands of the Sierra de la Laguna.

Geology and Soils

The Sierra de la Laguna is composed totally of massive intrusive rocks, granites the most part. It is an extension of a great batholith of upper

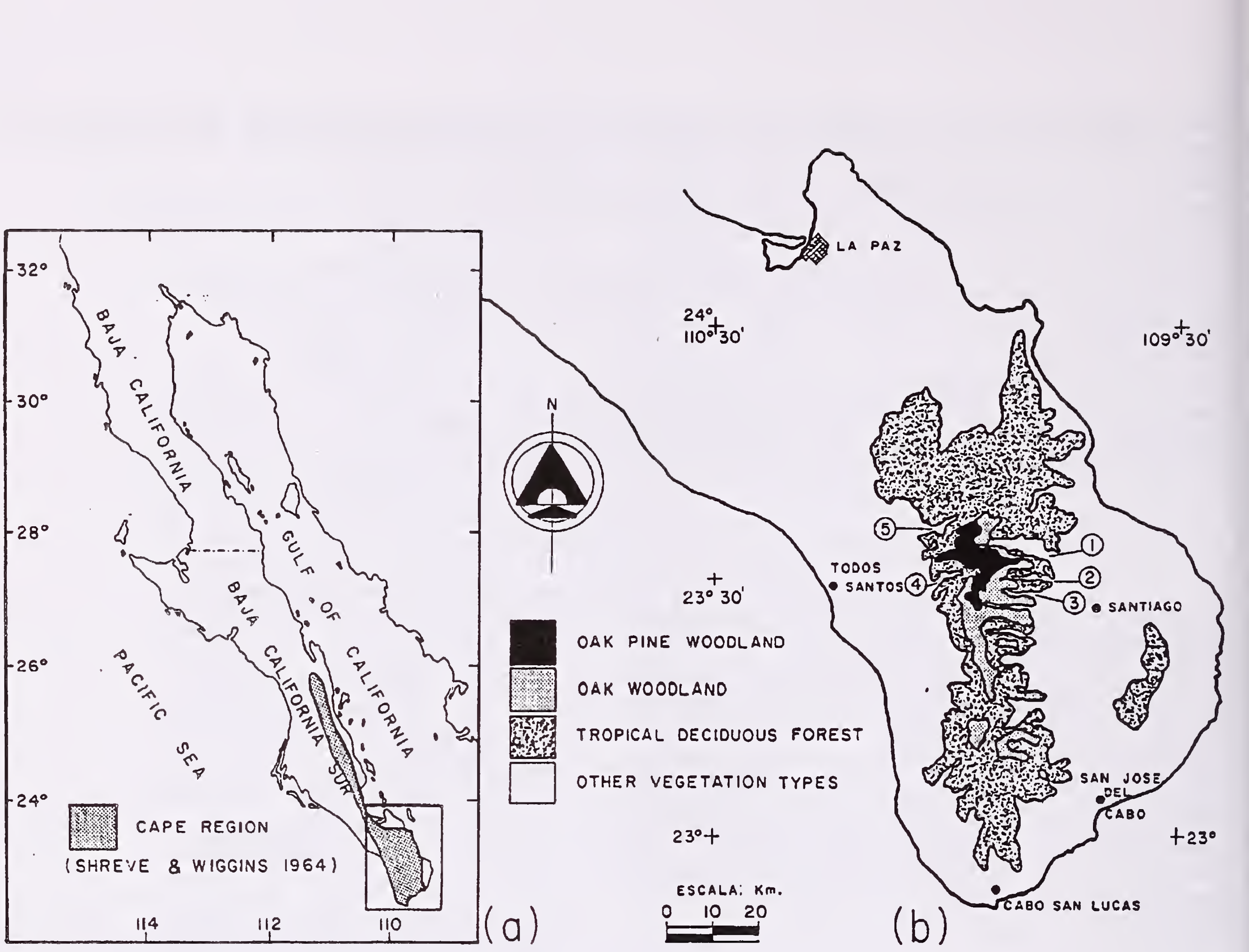

Figure 1.—The Sierra de La Laguna woodlands are located in the northern part of the Cape Region mountains, Baja California Sur, Mexico. It includes five major canyons, having an estimated surface of about 250 km², which aproximately 100 correspond to the oak-pine and the rest to the oak forest.

jurasic or lower cretaceous age, which underlies most of the peninsula and presumably also parts of the Gulf of California (Beal 1948; Durham and Allison 1960). Most of these rocks are moderately coarse grained and subject to rapid disintegration. The derivated soil is sandy, with a thin layer of litter; the content of loam and clay is relatively low. On slopes, foothills, and alluvial plains there are no differentiated soil layers. These are classified as Regosols (FAO-UNESCO system modified by Mexican government; SPP 1981a). At the bottom of brooks and canyons some permanent pools occur on the hard rock bed.

The courses of the canyons are a direct consequence of active erosion along their escarpments (López Ramos 1973; Hammond 1954). The eastern face of this sierra is more precipitous than the western slopes. Similar patterns are present also in the Sierra de la Giganta and other ranges much further kilometers to the north, such as San Pedro Mártir, Juárez and several others in California, USA.

Climate

Foothills and adjacent low areas, where the arid subtropical scrub develops, have a warm and dry climate. But the climate of the woodland is relatively cool, and light frosts occur during winter nights. Figure 2 shows both yearly temperature and precipitation obtained from García (1973) at a location at 1620 m and three others at lower elevations (350-368m). Climate in the summits, C(w1), is temperate, subhumid, with main rains in summer, but some also ocurring in winter. Precipitation is scarse in some years. At middle and low elevations occurs several BS and BW types respectively; the first one is semiarid climate, with rains mainly in the summer but

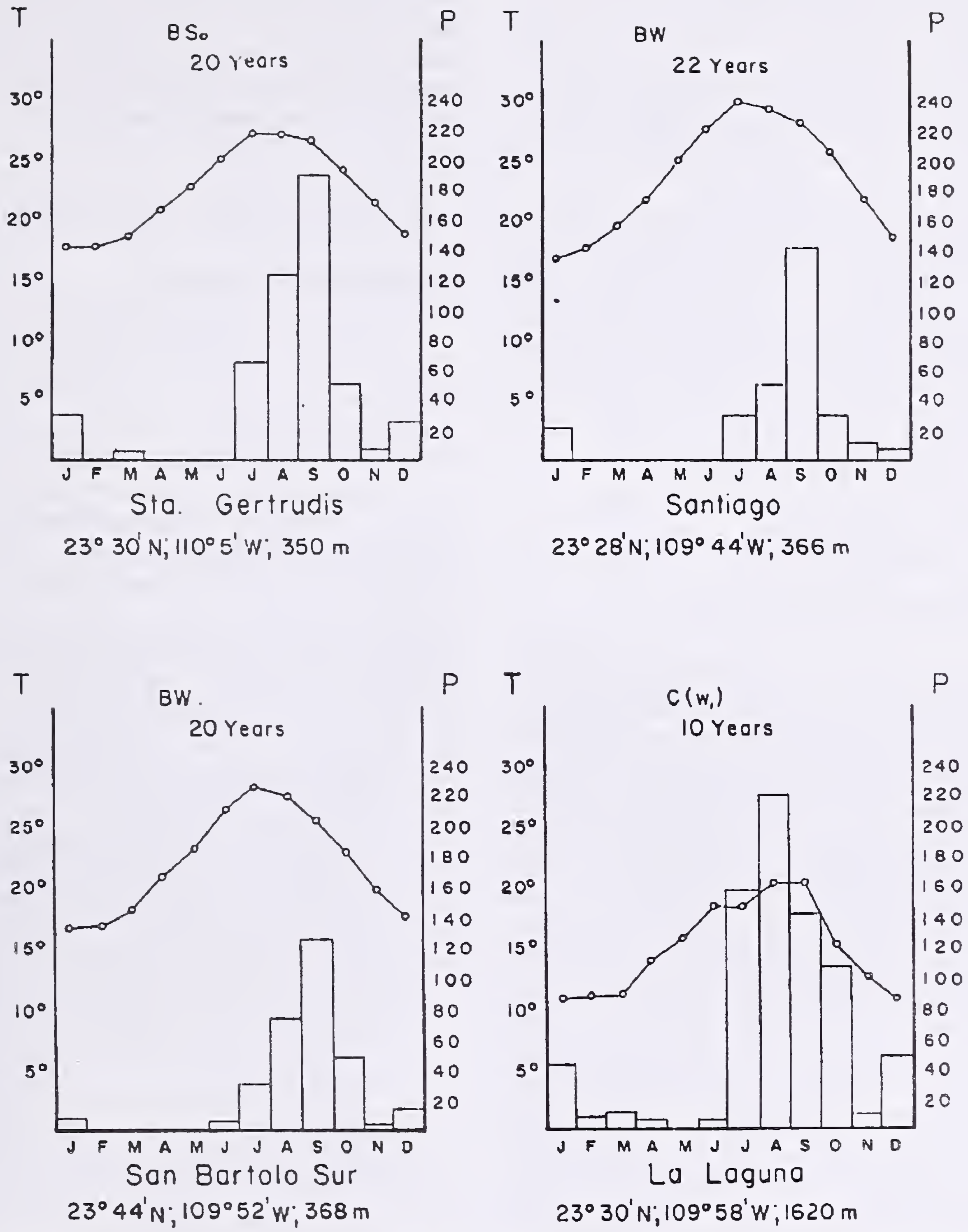

Figure 2.—Annual courses in mean monthly temperature (°C) and total monthly precipitation (mm) in three localities at foothills of the Sierra de la Laguna mountains (Sta. Gertrudis, Santiago and Sn. Bartolo Sur), and one in the woodland (La Laguna).

scattered through the year, the second refers to a very dry and warm climate, with rains occurring mainly also in the summer. Generally precipitation in winter is low, but during the summer months rains occur as thunderstorms caused by cyclone perturbations originating in the Pacific Ocean. Late winter to early summer are usually the driest season.

The high elevations of the mountains receive the highest levels of precipitation in all of the state. Probably, these regions supply the aquifers that provide for many ranches, urban and suburban populations, and some small agricultural areas in one of the most arid regions of our continent.

Problematic

Within the Cape Region, the Sierra de la Laguna resembles an island. A vegetation of less arid affinities is now restricted to its highest elevations, above the 1500 m. The oak and oak-pine woodlands communities that occurs in such elevations contains a relative high proportions of both, endemic and disjunct taxa. Increasing human settlement in the vicinities has been resulting in destructive use of this natural resource, and thus the plant communities may be at risk of losing their natural balance.

Rural and urban populations as well as tourism activities around the area of Sierra de la Laguna are increasing rapidly. Recent human population derived from census data, indicate aproximately 250,000 inhabitants in the region. This population demands more water to satisfy its primary needs; it is obtained totally from underground aquifers by pumping.

RESULTS

Botanical Collections

In the southern tip of the peninsula botanical explorations have been not so extensive as others xerophitic and mesic areas in the central and northern regions of the same peninsula. This area has been designated as a natural unit by Bryant (1891) as "Cape Region of Baja California". The early reports on its plant composition were published at the end of the last century by Brandegee (1891, 1892a, 1892b, 1894, 1903). Nelson (1921), and Shreve (1937) published vegetational descriptions of this region. Two decades ago, Gilmartin and Neighbours (1978) undertook field work in hopes of preparing a flora of the same, but their project was never completed. Recently, Lenz (1992) compiled a flora for the Cape; our team has also collected on it, and surpassed Lenz's catalogue in almost a 15% because a major field work.

Plant Communities

Vegetation in the Cape Region adjacent areas are here organized into three major plant communities (see fig. 1). The nearly level alluvial lands and valleys with scattered low hills that surround the mountain body contain a "desert scrubland" or "sarcocaulescent scrubland" that following modern Mexican systems (SPP 1981b) it designated as a "matorral sarcocaule". The pediplains with prominent hills and canyons from 400 to 1000 m elevation, support a vegetation called "selva baja caducifolia" (low deciduous forest, or the arid subtropical scrubland). The middle elevations (1000 to 1500 m) is covered by a oak woodland, and the upper elevations (1500 to 2200 m) by a oak-pine woodland. These woodlands represent the southernmost Sierra Madrean Woodland Elements.

Plant Associations

1) Oak-pine Woodland

This community can be divided into four types of associations or habitats, according to floristic composition and physiognomy. We are termed: "Valleys", "Stream Bottoms", "True Woodland", and "Open Areas".

The dominant species in this community are *Pinus cembroides* var. *lagunae* (pino piñonero), *Quercus devia* (encino negro), *Arbutus peninsularis* (madroño) and *Nolina beldingii* (sotol). Their relative densities vary within different habitats, Table 4 illustrates the composition of the higher stratum of this woodland; the data were taken from "True Woodland" habitat.

- Valleys: These are open sunny areas in which both annual and short-lived perennial herbs are the components. These areas are scattered through the Sierra. The largest, known as *La Laguna* (to which this range owes its name), it is located at 1820 m, and is crossed by permanent streams derived from the nearby mountain peaks. It is a flat-bottomed basin of almost 4 square km in surface. It is possible that in the recent past La Laguna was a marsh, rather than a lagoon (Nelson, 1921). An association of pinyon pine occurs at the valley margins, and it is here that the pines exhibit their maximum vigor. Two habitats can be distinguished in the valleys: **a**) streams and banks, and **b**) meadows. Some species typical of this association are listed below.

Streams & Banks	**Meadows**
Bacopa monieri	*Bidens nudata*
Hydrocotyle umbellata	*Centaurium nudicaule*
Mimulus guttatus	*Cosmos parviflorus*
Nasturtium officinale	*Lepechinia hastata*
Polygonum punctatum	*Lychurus phleoides*
Potamogeton foliosus	*Oxalis albicans*
Tinantia modesta	*Tagetes micrantha*

- Stream Bottoms: These areas are characterized by high soil moisture and low radiation. Trees and shrubs here are generally taller than elsewhere in the range. The environmental conditions of this habitat has favored the presence of some species which are supposed relictuals, such as: *Quercus reticulata* (encino blanco), *Q. arizonica, Q. laeta, Ilex brandegeana* (manzanita), *I. californica* (palo extraño) and *Prunus serotina* subsp. *virens* (cerezo), all of which also occur in the Sierra Madre Occidental in north Mexico and some ranges in Arizona in not so restricted conditions. In addition there are disjointed species such as *Heteromeles arbutifolia* (toyon), whose main distributional area is in California chaparral and woodlands. Some species of this association includes:

Adiantum capillus-veneris
Rhus radicans
Cyperus pallidicolor
Epipactis giganteum
Equisetum hyemale var. *afine*
Polypodium guttatum
Arethusa rosea
Ribes brandegeei
Rubus scolocaulon
Styrax argenteus
Thelypteris puberula
Tripsacum lanceolatum

- True oak-pine woodland. This is the most common habitat. It contains many annuals, short-lived herbs, and woody species that vary in relative density from one site to another. This can be attributed to such features as steepness of the slope, exposure to light, elevation, and succesional stage of the area. It is opportune to mention that this plant association is constantly disturbed by fire; there are practically no areas of forest without recent evidence of fire from both natural and human origins. Selected shrubby and woody species include:

  Calliandra peninsularis
  Helianthemum glomeratum
  Helianthus similis
  Heterotoma aurita
  Hypericum peninsularis
  Lepechinia hastata
  Mimosa xantii
  Perezia pinetorum
  Rumfordia connata
  Verbesina pustulata

  Some short-lived herbs are:

  Arracacia brandegeei
  Desmodium prostratum
  Gibasis heterolhylla
  Gnaphalium bicolor
  Malaxis unifolia
  Linanthus nuttalli subsp. *nuttalli*
  Oenothera tetraptera
  Stachys coccinea
  Tagetes lacera
  Verbena carolina

- Open Areas: These widely distributed surfaces are of two types; one consists of an early successional stage induced by fire and contains such species as *Muhlenbergia emersleyi, Rhynchelytrum repens, Bernardia lagunensis, Dodonaea viscosa* and *Tephrosia cana*. Other open areas occur on prominent rocks, with high exposure to sun and thin soil. These areas contain endemics species as *Morangaya pensilis, Mamillaria petrophylla, Daphnopsis lagunae, Myrtillocactus cochal, Dudleya nubigena, Agave promontorii* and *Russelia retrorsa*.

2) Oak woodland.

The area occupied by this community is very precipitous, with the slopes ranging from 30° to 40° in steepness. The strata consist of trees, low shrubs, and both annual and perennial herbs. Trees are scattered, *Quercus tuberculata* (encino roble) and *Q. albocincta* (encino laurel) characterizes this community. Also, it is common to find some species coming from the Arid Subtropical Scrub and other from the lowlands.

Low shrubs usually are scattered, but grow more densely in some areas. Common species are: *Mimosa xantii, Arracacia brandegeei, Dodonaea viscosa, Bernardia lagunensis* and *Tephrosia cana*. Herbs are typically represented by bunchgrasses as *Muhlenbergia emersleyi, Heteropogon contortus* and *Schizachyrium sanguineum* var. *brevipedicellatum*, and small annual herbs such as *Tagetes subulata, Crotalaria saggitalis, Heterosperma xantii* and *Zornia reticulata*. Vines such as *Phaseolus filiformis* and *Quamoclit coccinea* var. *coccinea* are abundant after the rainy season.

Finally, a local riparian plant association occupies the bottom of the brooks and canyons, descending with the streams until these disappear at elevations of 300 to 500 m. This association is characterized by *Populus brandegeei* var. *glabra* (gueribo), *Salix lasiolepis* (sauce), and the fan palms *Erythea brandegeei* and *Washingtonia robusta* at middle elevations.

Table 4.—Basical dasonomycal characteristics of the woody plants on a slope of 20-30° of steepness, in the Sierra de la Laguna Oak-Pine Woodland in a 3000 m² plot at 1700 m of altitude. Only individuals with dhb 3 cm were considered.

Species	Sampled Individuals	Avg. Cover m²	Avg. height m
Quercus devia	68	24.1	11.5
Arbutus peninsula	6	21.3	6.8
Pinus cembroides var. *lagunae*	4	7.6	6.9
Nolina beldinguii	14	2.5	3.3
Prunus serotina subsp. *virens*	2	7.4	6.4
Ilex brandegeana	2	5.8	4.3
Heteromeles arbutifolia	1	6.6	3.1

The Flora of the Woodlands

A total of 272 taxa of vascular plants have been identified from this region to date. These represent 69 families and 184 genera. Table 5 shows the major taxa of such flora. Excluding large families as Graminae, Compositae, and Leguminosae, the rest of the families have a genus to species ratio of about 1 to 1.5 . Forthy three species and infraspecific taxa are considered to be endemic (aproximately 16%). The area contains two endemic monospecific genera: *Behria* (Amaryllidaceae) and *Morangaya* (Cactaceae). The proportion of endemic species is moderate as compared with the closest biotic provinces: the Californian with around 48% and the Sonoran Desert with about 23%, but these are hundreds of times greater in total surface (Wiggins 1980).

Table 6 shows the frequency of life forms in the woodland. Both, annual and perennial herbs includes plants with herbaceous stem. Hydrophytes are all those plants which grow in or close to streams. Climbing includes herbaceous and woody.

Table 5.—Distribution of the 272 species of vascular plants which form the recognized flora of the woodland communities of the Sierra de la Laguna.

	Families	Genera	Species & infra categories
Pteridophytes	4	14	19
Gymnoesperms	1	1	1
Angiosperms	64	169	252
TOTAL	69	184	272

Table 6.—Absolute and relative proportions of life forms in the Sierra de la laguna woodlands.

Life form	No. of species	%
Trees	17	6.25
Shrubs & subshrubs	30	11.02
Annual & perennial herbs	176	64.71
Hydrophytes	34	12.51
Succulents	8	2.94
Climbing vines	5	1.83
Saprophites & parasites	2	0.74
	272	100.00

Rare Species

Almost a century ago T. S. Brandegee described *Faxonia pusilla* from a single plant from the locality "Sierra de la Laguna", but it is uncertain if the specimen came from some place in the woodland or the arid tropical scrub, this taxa has not been collected again and may well be extinct. In the same status may be *Pectis uniaristata* var. *uniaristata*, *Muhlenbergia wolfii* and *M. ciliata*, all of them collected only by Brandegee. Specimens of *Ilex californica* are very scarce, only a dozen living trees are known. Others species with very restricted localities, with relatively few individuals, or scarcely collected are:

Aralia scopulorum
Arenaria lanuginos
Epipactis gigantea
Heteromeles arbutifolia
Hypericum anagalloides
Ilex brandegeana
Opuntia lagunae
Quercus albocincta
Quercus arizonica
Quercus laeta
Quercus reticulata
Rhus schiediana

Some of these rare species are probably relictuals, small populations has remained in places with a relatively less arid environment. Most of the herbaceous endemics are founded in restricted habitats.

DISCUSSION AND CONCLUSIONS

Phytogeography

Table 7 shows the geographical affinity of the floral groups (families and genera) with the elements tropical, temperate, cosmopolite (worldwide and pantropical), disjointed (some of the tropics, subtropics, or both tropical and temperate) and endemic. The geographical affinities were taken from Willis (1985).

Table 7.—Geographical affinity of floral groups of families and genera of the vascular flora of the Sierra de la Laguna woodlands (oak and oak-pine) and their numerical contribution.

	Families No.	(%)	Genera No.	(%)
Tropical	28	(40.5)	109	(59.2)
Temperate	9	(13.1)	29	(15.7)
Cosmopolite	27	(39.2)	37	(20.1)
Disjointed	5	(7.2)	8	(4.4)
Endemic	0		1	(0.6)
	69	(100)	184	(100)

According with this same table, it is possible to observe that the major affinity at family and genus level is with the tropical element. This result is not surprising because this surface has been influenced by tropical climate since its geological development through tertiary epochs (Moore and Curray 1982). The temperate element only has moderate participation, the presence of these could be considered as remnants of a pleistocene flora.

A paleobotanical study, based on palinological sample, was carried out in the woodland area; preliminary results provide important information on its natural history. Then, 9000 years before present, pollen of *Pinus* and *Quercus* is dominant in the profile, as well those of several grasses, forbs and undeterminated Compositae family species.

Conservation

The woodlands and the arid subtropical scrub support several human activities without efficient control including hunting, gathering firewood or harvesting trees, and both intensive and extensive livestock breeding. For 1990, the number of all kind of cattle in the south tip of the peninsula was estimated in no less than 30,000 heads.

For these reasons, it is necessary that simultaneously with the investigations of the flora and vegetation, another studies must be made of its ecological aspects, both basic and applied. Mexican institutions and organizations have realized the importance of ecological preservation of the communities of this range in order to protect the area from the destructive human activities noted above. Late last year an ample area wich comprises the woodland was decree as Biosphere Reserve by the Mexican Government.

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Forests and Woodlands of the Sky Islands: Stand Characteristics and Silvicultural Prescriptions

Gerald J. Gottfried[1], Peter F. Ffolliott[2], and Leonard F. DeBano[3]

Abstract.—The mountains of the Sky Islands or Madrean Archipelago are noted for their biological diversity. The higher elevations support pine, mixed conifer, and spruce-fir forests, while encinal and pinyon-juniper woodlands are found at more intermediate elevations. The highest forest zones are representative of the Rocky Mountain flora and the woodlands are representative of the Madrean flora of Mexico. Local and regional climatic patterns over the past 24,000 years have influenced the establishment and survival of these ecosystems. Past natural and human disturbances have affected stand conditions. The diversity of forest and woodlands can be observed on the five highest and largest mountain ranges in southeastern Arizona, namely, the Santa Catalina, Santa Rita, Huachuca, Chiricahua, and Pinaleno Mountains.

Human activities in the forests and woodlands have changed over time. Some traditional industries have declined while demands for other activities, such as recreation, have increased. There are concerns about the condition of these mountain ecosystems. Silviculture can be used as a ecosystem management tool to enhance long-term productivity of a variety of resources and amenities, to enhance biological diversity, and to help ensure forest and woodland health.

INTRODUCTION

The mountains of the Madrean Archipelago, or Sky Islands of southern Arizona, New Mexico, and northern Mexico are recognized for their diverse mixtures of plants and animals. Variety characterizes the region, which includes an area approximately 160 to 175 km on each side of the international border (Gehlbach 1981). The highest mountains support pine, mixed conifer, and spruce-fir forests, while encinal and pinyon-juniper woodlands are common at more intermediate elevations. The varied plant communities and their animal populations reflect the meeting, mergence, and coexistence of species representative of the northern Rocky Mountain flora or the Madrean flora of Mexico. Some species find their northern or southern limits in these mountains. The mountains have allowed for the migration of some species to the north or south (Gehlbach 1981). The northern mountain ranges in the Madrean Archipelago of Arizona have more components of the Rocky Mountain flora and fauna than those further south, where Mexican affinities are greater. Local and regional climatic patterns and the natural impacts of fire, wind, and insects have influenced the establishment and survival of the forests and woodlands.

Human activities since pre-historic times have affected the distribution, characteristics, and health of the region's forests and woodlands. Although these lands have been heavily utilized, especially since European settlement, 96 percent of the original postglacial forests and woodlands still exist (Gehlbach 1981). Utilization of these lands continues to change; traditional land uses to supply wood for forest products or mining industries or forage for livestock grazing are often perceived to be in conflict with increasing de-

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mands for recreation, landscape preservation, watershed protection, and habitats and site requirements of rare species. Demands for fuelwood have increased. Privately owned woodlands are increasingly being converted to home sites, causing land management conflicts, fragmentation of wildlife habitats, and potential fire control problems. There are concerns about the sustainability and health of the mountain ecosystems under pressure from human activities and natural effects of fires and insect infestations, and the impacts of past fire suppression activities.

Silvicultural prescriptions can be developed to help ensure long-term sustainability and to provide for forest and woodland health. Silviculture can be used as an ecosystem management tool to enhance wildlife habitat, the production of herbaceous species for both livestock and wildlife, and watershed protection. It can also be used to enhance and maintain biological diversity within the region.

The objectives of the paper are to review the characteristics of the forests and woodlands of the Madrean Archipelago, some of their historical land uses, and some appropriate silvicultural prescriptions. Riparian woodlands, an extremely important ecosystem within the Sky Islands, will not be covered here; they are covered elsewhere in these proceedings. Although the region contains numerous isolated mountain ranges that vary in physical size and vegetational associations, the current effort will concentrate on the five largest and highest mountain ranges: Santa Catalina, Huachuca, Santa Rita, Chiricahua, and the Pinaleno or Graham Mountains.

GENERAL DESCRIPTION

Physiography

The five mountain ranges are within the mountain subdivision of the Basin and Range Geological Province that crosses Arizona in a northwest to southeast belt (Wilson 1962). The Province is characterized by elongated mountain ranges trending northwest to southeast, separated by broad, generally alluvial valleys (Nations and Stump 1981). Peaks range from Mt. Lemmon in the Santa Catalina Mountains with an elevation of 2,791 m to Mt. Graham, the highest peak in the zone, with an elevation of 3,265 m. Mt. Graham is over 2,377 m above the Gila Valley at Safford. Most other peaks in the region do not extend above 2,438 m. The ranges tend to be elongated, for example, the Chiricahua Mountains are approximately 64 km long and between 6 and 32 km wide (Jackson 1970).

Climate

The regional climate in southeastern Arizona is semiarid, and precipitation is bimodal. Winter precipitation is associated with frontal storms originating in the Pacific Ocean that move westerly over the State. Winter conditions generally prevail from October through May, but most intense storms occur between mid-November and mid-April. Late spring and early summer are typically dry. Summer monsoon moisture begins to enter the region in late June or July; storms are convective resulting from the flow of tropical air over heated mountain terrain. Intense summer thunderstorms, which are common over mountains, result from a combination of thermal heating, orographic uplifting, and conveyance of air on the windward side of the mountains (Gottfried 1989). Late summer and early autumn tend to be dry, although tropical cyclones during this season may push moisture into the State producing record rainfalls. Summer precipitation may account for up to 70 percent of the annual total in southeastern parts of Arizona (Bahre 1991). Records at the Chiricahua National Monument indicate that 50 percent of the precipitation occurs in July and August, and that May is the driest month. Annual precipitation ranges from 230 to 635 mm, although higher elevations can receive over 890 mm, often as snows in December and January. Bahre (1991) indicated that average temperatures at higher elevations can average 1.6° C in January and 18.3° C in July.

The amounts of precipitation, available moisture, and the resulting distribution of vegetation zones within the Madrean Archipelago are influenced by mountain physiography. Elevation affects precipitation and temperature; however, Lowe (1961) indicated that mountain geomass is more important than elevation in determining vegetation. He reported a different vertical displacement of vegetation types and species on adjacent peaks of different mass. He referred to this phenomenon as the Merriam effect. This may be one reason for the absence of Engelmann spruce (*Picea engelmannii*) at 2,740 m in the Santa Catalina Mountains, while it is common at that elevation in the more massive Pinaleno Mountains (Lowe 1961). Gehlbach (1981) stated that less massive mountains tend to be more arid. He indicated that because the Huachuca Mountains are lower and a third smaller in area than the Chiricahua Mountains, coniferous forests are displaced 305 m upward there. The Merriam effect may be related to drying winds (Hanks and Dick-Peddie 1974), or to the influence of geomass on orographic precipitation. Gehlbach (1981) indicated that mass may be linked to the speed that mountains heat and cool during the summer, since slower changes reduce evaporation rates and allow for more efficient utilization of summer moisture.

Geology and Soils

The mountains of the Madrean Archipelago consist of tilted, and sometimes structurally deformed blocks of rocks that are bounded by faults and have been severely eroded (Nations and Stump 1981). Precambrian and Tertiary granites are common in the Basin and Range Province, as are volcanic rocks from the Mesozoic to Quaternary (Hendricks 1985). The Chiricahua Mountains were an important volcanic center about 26 million years ago, characterized by explosive production of large quantities of ash and the formation of caldera complexes (Nations and Stump 1981). The orogeny which had the greatest impact on the Province began about 13 million years ago, and may have ended in southeastern Arizona about 6 to 3 million years ago (Hendricks 1985).

Mountain soils within the Province are generally shallow, rocky and gravelly (Hendricks 1985). Soil development depends on parent material and erosional surface stability. Weathering of granitic material tends to produce soils with coarse surface material and little profile development, and subsurface soils that are gravelly sandy loams or gravelly loams. Volcanic rocks weather into fine-grained material; soil development depends largely upon erosional dynamics on the site, although relatively deep soils are possible where particle removal is low. Higher elevation mountain soils tend to be more acidic and contain more organic matter than soils at lower elevations.

Hendricks (1985) classified most of the soils within the five mountain ranges as Mesic Subhumid soils. These soils are found at about 2,135 m in southeastern Arizona, where mean annual soil temperatures of 8.3 to 15.0° C and more than 405 mm of mean annual precipitation occur. Most of these soils, except for some areas in the Huachuca Range, are within the Lithic Haplustolls-Lithic Argiustolls-Rock Outcrop Association. The soils are shallow, gravelly and cobbly, moderately coarse to moderately fine-textured. Slopes are variable; rock outcrops are found in the hills and mountains. They usually support woodlands of oak, pinyon, and juniper. The Huachuca Mountains contain some areas of the Casto-Martinez-Canelo Association. These soils are found on mesas and valley slopes between 1,675 and 1,890 m in elevation, and are deep, gravelly, moderately fine or fine-textured. The Casto and Canelo soils support woodlands while the Martinez soils support grasslands. The Casto and Martinez soils are Udic Haplustalfs and the Canelo is an Aeric Ochraqualf.

Hendricks (1985) identified Frigid Subhumid soils at the highest elevations in the Pinaleno and Santa Catalina Mountains. These soils occur at elevations of from 2,075 to 3,290 m, where the mean annual soil temperature is less than 8.3° C and mean annual precipitation is over 405 mm. They are associated with pine, mixed conifer, and spruce-fir forests, and are representative of the Mirabal-Baldy-Rock Outcrop Association. The soils are classified as Typic Ustorthents and Typic Cryorthents, and are shallow to deep, gravelly and cobbly, and moderately coarse-textured; rock outcrops are characteristic of some sites.

FOREST AND WOODLAND VEGETATION

General Distribution Patterns

The elevational zonation of woodlands and forests within the Madrean Archipelago has been described by a number of authors (Lowe 1964, Whittaker and Niering 1965, Brady and Bonham 1976, Gehlbach 1981, Niering and Lowe 1984, Hendricks 1985, Bahre 1991). Whittaker and Niering (1965) and Niering and Lowe (1984), in their studies on a south slope of the Santa Catalina Mountains and in the highest elevations of the Pinaleno Mountains, listed the plant communities and their elevational distributions. These can be regrouped, based on Niering and Lowe (1984), as: Sonoran Desert scrub (below 1,220 m), semi-desert grassland (1,220 to 1,700 m), open oak woodland (1,400 to 1,700 m), pygmy conifer-oak woodlands (1,520 to 2,130 m), pinyon-oak woodland (1,830-2,130 m), Chihuahua pine-oak woodlands (1,830 to 2,130 m), ponderosa pine-oak forest (2,130 to 2,440 m), ponderosa pine forest (2,440 to 2,740 m), montane fir forest (2,440 to 2,740), mixed conifer forest (2,740 to 2,920 m) and subalpine forest communities (above 2,920 m).

Whittaker and Niering (1965) indicated how community distribution also varied by aspect. The drier the site, the higher the elevational displacement. Species distribution patterns by aspect and elevation in the Huachuca Mountains and in the Santa Catalina Mountains are similar (Brady and Bonham 1976), although there appear to be differences between the Huachuca and Chiricahua Mountains (Gehlbach 1981). In the current review, we have grouped Niering and Lowe's open oak and Chihuahua pine-oak woodland as the encinal woodlands, the pygmy conifer-oak and pinyon-oak woodlands as the pinyon-juniper woodlands, and the five forest zones together as the high elevation coniferous forests.

VEGETATION CHANGES OVER TIME

Biogeography

The current distribution of woodlands and forests on the isolated mountains of the region is the result of shifts in the climate conditions over the past 24,000 years (Jackson 1970). Merrill and Pewe (1977) indicated that temperatures in the Southwest were 5 to 6° C cooler and precipitation was 20 to 25 percent greater during the late Quaternary when glaciers occurred on Mount Baldy in the White Mountains (8,000 to 35,000 B.P.). Palynological evidence from the Willcox Playa indicates a vertical displacement of vegetation zones of at least 915 to 1,220 m during pluvial times (Hevly and Martin 1961). This displacement allowed Rocky Mountain forest flora to spread from the Colorado Plateau into the sub-Mogollon mountain ranges and into the Sierra Madre Occidental. The changing distributions of vegetation types in the Southwest over the past 22,000 years and their relationships to climate have been document by analyses of packrat (*Neotoma* spp.) middens (Van Devender and Spaulding 1979).

The Hypsithermal Interval, also called the Medieval Warm Period, brought warmer and drier conditions and a rise in the elevational distribution of vegetation zones; the vegetational links between mountain ranges and the Colorado Plateau were broken and xerophytic species invaded the lower elevations within the Basin and Range Province. Climatic conditions over the past 4,000 years have been moderately cool and moist although extended periods of drought have occurred (Jackson 1970).

Historical

Fire, wind, and insects are the main natural disturbances in the region. Changes in the characteristics and timing of natural fires affect the current distribution of vegetation zones. Increased fires during the Hypsithermal may have eliminated some vegetation types on marginal sites (Jones and Rietveld 1974). American Indians probably set some fires, but lightning was the main factor. Most fires were localized or ground fires that tended to reduce understory vegetation. Forests and woodlands were less densely stocked with trees prior to European settlement (Moody et al. 1992, Covington and Moore 1994). Fire suppression has eliminated most fires and allowed for potentially dangerous fuel accumulations and fire ladders to develop. Stand replacing crown fires are becoming more common because of these changes (Covington and Moore 1994).

Prior to European settlement, under natural fire regimes, upper mixed conifer forests may have contained less spruce, and ponderosa pine (*Pinus ponderosa*) forests less Douglas-fir (*Pseudotsuga menziesii* var. *glauca*). Overgrazing in the woodlands, which eliminated the herbaceous layer, also prevented the spread of wildfires and reduced competition for tree establishment. The movement of oaks and junipers into grasslands and the increased tree densities in juniper savannahs have been attributed to these two factors.

Although there are a large number of forest insect species within the area, they were not considered to be a major problem (Shupe and Solether 1973), although the evaluation may be different now, especially on Mt. Graham. Wind may have had a significant impact within the coniferous forests.

HUMAN USE OF FORESTS AND WOODLANDS

The encinal woodlands of the Madrean Archipelago have been important to prehistoric and historic people (Propper 1992). The prehistoric people gathered acorns for food and ceremonial purposes, and pinyon nuts and juniper berries for winter food. American Indians also collected fuelwood and construction materials and hunted game in the woodlands and forests.

The Apache Indians and Spaniards entered the region in the late 1600 (Propper 1992). The Spanish used the wooded areas primarily for fuelwood and construction material for their homes, mines, and ranching activities. However, intensive development in the region did not begin until the 1870s and 1880s, when hostilities with the Apaches began to decline and the railroad entered the region. Large herds of cattle were moved into the area from Texas and Sonora during this period; Bahre (1991) indicated that there were over 200,000 head in southeastern Arizona in 1890. The major impact on the woodlands during the late 19 century was the cutting of wood to support mining activities. The Tombstone Mining Region contained over 50 silver mines and 7 stamp mills in 1878 (Bahre 1991). Fuelwood, mostly oak (*Quercus* spp.), pinyon, juniper (*Juniperus* spp.), and mesquite (*Prosopis juliflora*), was cut to run the steam engines and meet the cooking and heating needs of the inhabitants (Bahre 1991). Over-cutting adjacent to settlements caused fuelwood shortages that resulted in increased transportation costs to bring in supplies from more distant mountains and in increased prices.

Sawmills in the Santa Rita Mountains supplied ponderosa pine and Douglas-fir to Tucson and neighboring mines before 1870. Logging began in the other mountain ranges after the settlement of the Upper Gila Valley and the beginning of the mining booms. The Huachuca and Chiricahua Mountains supplied much of the construction timber for Tombstone. Historic records indicate that only the five largest mountain ranges had significant logging activities, mostly prior to 1900 (Bahre 1991). Only the Pinaleno and Santa Catalina Mountains have had limited harvesting since that time. Most of the logging in the Pinaleno Mountains occurred after 1893; however, early activities were confined to isolated pockets of timber on the lower third of the mountain (Shupe and Solether 1973).

ENCINAL WOODLANDS

Information on the distribution, characteristics, and uses of encinal woodlands of the southwestern United States and northern Mexico has been obtained largely from Brown (1982). The encinals, also referred to as the Madrean evergreen woodland formation (Brown and Lowe 1980), are concentrated in the Sierra Madre Occidental of Mexico, from where they extend northward into southeastern Arizona, southern New Mexico, and Texas. Encinal woodlands cover approximately 80,300 km^2 in aggregate, although a precise delineation of this biotic community is difficult, since inconsistent criteria for classification have been employed (Gottfried and Ffolliott 1993).

Annual precipitation in the woodlands exceeds 405 mm; generally, half falls during the growing season of May through August. Extremes in annual precipitation range from 305 to over 1,015 m. Freezing temperatures are rare in the southern portions of the woodlands but increase to an average of almost 125 days at the northern limits.

The woodlands occur between 1,200 and 2,200 m in elevation. Structural development of the encinals is apparently determined by soil type and depth. Stands commonly are located in a variety of sites including along drainages, on rocky slopes, and on alluvial basin fill and fans (USDA Forest Service 1987).

Characteristics

A large variety of oak species are found in the encinal woodlands. Mexican blue (*Q. oblongifolia*) is found at the lowest elevations to the north. Among the oaks in the mountainous regions of southeastern Arizona, southwestern New Mexico, and Texas are Emory (*Q. emoryi*), Arizona white (*Q. arizonica*), Mexican blue, and gray (*Q. grisea*). Silverleaf oak (*Q. hypoleucoides*) and netleaf oak (*Q. rugosa*) are found at the intermediate elevations. Border pinyon (*P. discolor*) and juniper species are found intermixed with the oaks on many sites throughout the encinals. Other important pines within the encinal woodlands are: Chihuahua pine (*Pinus leiophylla* var. *chihuahuana*) and Apache pine (*P. engelmannii*).

At its upper elevations in the southwestern United States and in Mexico, the encinals often grade into the interior ponderosa pine type. They can merge with the pinyon-juniper woodlands with complex transitional forms.

Encinal woodlands contain relatively small, often multiple-stemmed, irregularly formed trees. Species compositions and stand densities depend largely upon specific site characteristics (Gottfried and Ffolliott 1993). One-, two-, or occasionally three-aged stand structures are found. Intermingled with these trees are shrubs, grasses and grass-like plants, forbs, and succulents, often in parks and savanna-like mosaics. Stand density is related to soil properties, site characteristics, and fire and land use histories.

Tree densities in the encinals vary considerably. The numbers of trees range from a few scattered individuals to several hundred stems/ha. Volumes of stemwood vary from less than 2 to over 100 m^3/ha (Ffolliott and Gottfried 1992). Annual growth rate is relatively slow, ranging from 0.25 to 0.50 m^3/ha, an annual growth rate of less than 1 percent. Mortality generally is low, likely because the long history of utilization in some areas has reduced the number of old trees (Conner et al. 1990).

Twelve habitat types in the Southwest are dominated by encinal oak species (USDA Forest Service 1987). A predominant habitat type of the encinals in southeastern Arizona is *Quercus emoryi/Bouteloua curtipendula*. In addition, a general scarp woodland habitat type is recognized on sites with slopes in excess of 40 percent.

PINYON-JUNIPER WOODLANDS

Pinyon-juniper woodlands cover approximately 19 million hectares in the western United States. The climate in the woodlands is classified as arid or dry sub-humid (Gottfried and Ffolliott 1993). In the Southwest, stands generally are found at elevations from 1,370 to 2,290 m where annual precipitation ranges from 305 to 560 mm.

Although Whittaker and Niering (1965) and Niering and Lowe (1984) did not identify a separate a pinyon-juniper community, these stands are unique and easily differentiated. Pollisco et al. (this volume), in a study of woodlands in three Sky Island mountain ranges, found numerous sites where pinyon and juniper constituted at least 80 percent of the tree basal area. The seasonal distribution of precipitation, particularly the relative amounts of winter and summer moisture, influences stand composition. The woodlands grade into grasslands, brushlands, and encinal woodlands on drier sites, and into ponderosa pine forests on more moist sites. They are found on soils associated with different parent materials and characterized as being shallow, well-drained, and generally of low fertility, although exceptions occur.

Characteristics

Although the two-needled Colorado pinyon (*P. edulis*) is the most characteristic pinyon of the woodlands of the Southwest, the three-needled border pinyon is associated with most pinyon-juniper and encinal woodlands of southern Arizona and New Mexico. A single-needled pinyon, *P. californiarum* var. *fallax*, also is found in the pinyon-juniper stands located south of the Mogollon Rim, including parts of the Madrean Archipelago. The Mexican pinyon (*P. cembroides*) is widespread at lower elevations in the mountains of northern Mexico, (Critchfield and Little 1966), and in the rain shadows of the eastern and western Sierra Madre mountain ranges (Segura and Snook 1992). Border pinyon is often classified as Mexican pinyon in some of the older literature.

Junipers are the other major tree group in the southwestern woodlands. The major species in the Madrean Archipelago are: alligator (*J. deppeana*), one-seed (*J. monosperma*), and red berry juniper (*J. erythrocarpa*). Utah (*J. osteosperma*) and Rocky Mountain (*J. scopulorum*) are important in other parts of the Southwest. Alligator juniper is an important component of many encinal stands in the southwestern United States and in the Mexican pinyon forests. Red berry juniper (*J. erythrocarpa*) is found on drier sites in southern Arizona and New Mexico.

A typical pinyon-juniper stand in the Southwest is uneven-aged and contains about 1,150 trees and 21 m^2 of basal area per hectare (Barger and Ffolliott 1972). Niering and Lowe (1984) reported that an average Mexican pine-oak woodland on the south slope of the Santa Catalina Mountains contained 1,124 trees/ha. Although oak species dominated the smaller size classes, 46 percent of the total number of trees and 95 percent of the trees 15 cm and larger at breast height (bh) were pinyon and alligator juniper. Pinyons are more common in a typical stand in the Southwest and tend to dominate in the smaller size classes, while junipers are an important component of the larger size classes and contribute almost half of the wood volume. However, some pinyons in the Santa Catalina Mountains were over 60 cm in diameter (Niering and Lowe 1984). Even-aged stands develop after disturbances such as fire and tree control operations for range improvement or agricultural activities.

Pinyon-juniper woodlands are not homogeneous and consist of a large number of habitat types or plant associations (Moir and Carleton 1987). The USDA Forest Service (1987), for example, recognizes six habitat types in southern Arizona and New Mexico where border pinyon dominates and four where either alligator or red berry junipers dominate. Available soil moisture is the most critical factor controlling the distribution of woodlands, and the composition and density on undisturbed sites. Junipers, which are more drought-tolerant than pinyon, dominate on drier sites, but pinyons increase in importance as available moisture increases. The distribution of juniper species is influenced by the proportion of winter precipitation. Alligator, one-seed, red berry, and Rocky Mountain junipers dominate in summer moisture areas, while Utah juniper occurs in winter moisture areas. Temperature extremes also affect the upper and lower elevational distribution of woodland species.

THE HIGH ELEVATION CONIFEROUS FORESTS

Community Distribution

High elevation coniferous forests generally occur above 2,130 m. Niering and Lowe (1984) recognized six community types in the Santa Catalina Mountains and an additional two types in the higher Pinaleno Mountains. Spruce-fir forests, which are confined to the highest elevations within the Pinaleno Mountains, contain Engelmann spruce and corkbark fir (*Abies lasiocarpa* var. *arizonica*). These are usually found above 2,920 m. Mixed conifer forests, which includes montane forest communities described by Niering and Lowe (1984), are found from 2,440 to 2,920 m. These are diverse forests that can contain up to seven major tree species: Douglas-fir, Engelmann spruce, corkbark fir, white fir (*A. concolor*), ponderosa pine, southwestern white pine (*P. strobiformis*), and quaking aspen (*Populus tremuloides*). The mix of species and habitat types will vary throughout the Madrean Archipelago. Corkbark fir, for example, is found at one location in the Santa Catalina Mountains, where it occurs with aspen, Douglas-fir, and white fir, and is absent in the Santa Rita, Chiricahua, and Huachuca Mountains. Some mixed conifer stands can be dominated by Douglas-fir and white fir with minor components of other tree species.

The third major category of forests is dominated by ponderosa pine and is found from 2,130 to 2,740 m. Silverleaf and Arizona oaks are common in pine stands between 2,130 and 2,440 m, while Gambel oak (*Quercus gambelii*) is common at elevations between 2,440 and 2,740 m. Southwestern white pine with some Douglas-fir are found in stands between 2,590 and 2,740 m (Niering and Lowe 1984). The five-needled Arizona ponderosa pine (*P. ponderosa* var. *arizonica,* also classified as *P. arizonica*) replaces the Rocky Mountain variety (*P. ponderosa* var. *scopulorum*) on many southern Arizona sites (Lowe 1964). The spruce-fir, mixed conifer, and ponderosa pine forests respectively correspond to Merriam's Hudsonian, Canadian, and Transition Life-zones (Lowe 1964).

Habitat Types

The USDA Forest Service (1987) recognizes a large number of forest habitat types within southeastern Arizona that are found at a variety of elevations and in different mountains. For example, a partial list of spruce-fir habitat types would include:

Abies lasiocarpa / Carex foenea	3,050 m	Pinaleno
A. lasiocarpa / Erigeron eximius	2,865-3,110 m	Pinaleno
A. lasiocarpa / Jamesia americana	2,650 m	Catalina
A. lasiocarpa / moss	2,985-3,505 m	Pinaleno
Picea engelmannii / Acer glabrum	2,745 m	Chiricahua

Some other common habitat types are *Pseudotsuga menziesii*/ *Quercus hypoleucoides,* which is found in the Chiricahua, Pinaleno, Huachuca, and Animas Mountains between 1,980 to 2,620 m, and *Pinus ponderosa*/ *Quercus hypoleucoides,* which is found in the Chiricahua, Pinaleno, Santa Rita, Santa Catalina, and Galiuro Mountains between 2,100 and 2,450 m.

Amount of Area Covered by Forest

Almost all of the forests within the United States portion of the Madrean Archipelago are administered by the Coronado National Forest. There are about approximately 2,020 ha in the Santa Catalina and 4,050 ha in the Chiricahua Mountains that could be classified as commercial forest based on stand conditions and accessibility (Shupe and Solether 1973). The Pinaleno Mountains contain 3,410 ha of operable commercial forest land, including 440 ha of ponderosa pine, 2,260 ha of mixed conifer, and 710 ha of spruce-fir; in addition, there are 1,920 ha of commercial forest that is inoperable (Shupe and Solether 1973). The Pinaleno Mountains also contain pockets of forest vegetation and forested steep slopes and rocklands that are not commercially operable.

Stand Characteristics

A typical spruce-fir stand in the Pinaleno Mountains contains approximately 2,773 conifer and aspen trees/ha that are 2.5 cm dbh and larger; 95 percent of the stand consists of corkbark fir and spruce, in almost equal proportions (Niering and

Lowe 1984). However, the proportions of spruce and fir vary depending on the stage of development following major disturbance (Stromberg and Patten 1991). In old-growth stands, spruce will have a greater basal area and density of large trees, while corkbark fir will dominate the smaller trees and sapling size classes (Niering and Lowe 1984, Stromberg and Patten 1991). Thirteen percent of the spruce in the Niering and Lowe sample, for example, were greater than 30 cm, while only 2 percent of the fir was in the larger size classes.

The mixed conifer forest in the Pinaleno Mountains contained about 2,330 trees per hectare (Niering and Lowe 1984). Over 50 percent of the average stand consisted of white fir, mainly because of the large number of trees in the smaller dbh classes (less than 15 cm). Spruce and fir comprised 34 percent of the density, and Douglas-fir was about 10 percent. Some of the old-growth Douglas-fir had diameters of 152 to 178 cm (Shupe and Solether 1973).

The Douglas-fir and white fir forest in the Santa Catalina Mountains only contained 455 conifers/ha but supported an additional 425 trees/ha of *Acer* spp., *Jamesia americana*, and *Robinia neomexicana*. The ponderosa pine forest contained 1,375 conifers/ha, 74 percent ponderosa pine and the other being southwestern white pine, Douglas-fir and white fir. Oaks and *Robinia* made up an additional 450 trees/ha.

SILVICULTURE

Silviculture Prescriptions

One part of the definition of silviculture states that it is the application of a knowledge of silvics to the treatment of a forest or woodland (Gottfried and Ffolliott 1993). One key objective of traditional silviculture is to ensure adequate tree regeneration for the future. There is growing interest and public demand for ecosystem management that will create and maintain healthy and sustainable forest and woodland ecosystems. Health is defined as the ability of a forest to recover from natural or human-caused stressors (Haack and Byler 1993), while sustainability refers to the long-term production of all forest values. Silviculture is a tool for ecosystem or multiresource management of any forest or woodland ecosystem. Silvics or tree ecology must serve as the basis for management activities if ecosystem management goals are to be achieved. Managers, with public input, must determine the desired future condition and mix of resources to be favored on a site, and modify their prescriptions.

Encinal Woodlands

Ecological research to support silvicultural prescriptions in the encinal woodlands, is relatively limited (McPherson 1992). Natural regeneration from seed is apparently episodic; oak seedlings were 19 percent of the regeneration in one study; sprouting from roots and stumps was a more common regenerative mechanism (Borelli et al. 1994). Only nine percent of the plots contained any tree regeneration, and, as a consequence, the encinals might not be reproducing in sufficient numbers to sustain themselves if they continue to be heavily harvested (Borelli et al. 1994). On many sites, encinal stands sprout vigorously after cutting, indicating that coppicing might form a basis to obtain regeneration in silvicultural prescriptions. Furthermore, harvesting cycles can be reduced through proper thinning of the resultant coppice (Touchan et al. 1992). Sustainability of vegetative reproduction is unknown, however.

A silvicultural prescription for sustained productivity of fuelwood, based largely upon on the studies mentioned above and management procedures of the USDA Forest Service in southeastern Arizona, might involve the following scenario. Trees to be harvested are marked for removal by managers (Bennett 1992). A subsequent thinning of the resultant coppice to retain 1, 2, or 3 of the largest and most vigorous residuals is scheduled for 5 years after harvesting. Delaying thinning beyond this time can reduce growth of the residuals (Touchan et al. 1992). Residual trees are selected for harvesting after they attain a specified size. For example, a diameter of 15 to 20 centimeters drc (diameter at root collar) likely can be reached in 20 to 30 years after the coppice thinning on some sites. The USDA Forest Service specifies a 15-centimeter stump height and about a 45-centimeter slash height in southeastern Arizona. Other silvicultural prescriptions based upon clearcutting, shelterwood, seed tree, and selection cuttings have not been widely tested.

Removal of trees in any silvicultural treatment changes landscape diversity, which can affect habitats for wildlife. Unfortunately, there have been no studies on the effects of harvesting in encinal woodlands on deer habitats (Smith and

Anthony 1992) or those of other big game species, although an increase in diversity might be beneficial if sufficient cover is retained. Encinal woodlands provide resources for unique assemblages of neotropical migratory birds (Block et al. 1992), and it is likely that different management approaches will be needed for different situations. Actual impacts of silvicultural treatments on nongame bird and many other wildlife species remain to be evaluated.

Although livestock production is important, encinal woodlands have not been subjected to large-scale range improvement practices (Ffolliott and Guertin 1987, McClaran et al. 1992). Haworth and McPherson (1994) indicated that production levels and species compositions of herbaceous plants might not be affected greatly by range improvement practices consisting of the removal of trees in fuelwood harvesting. However, more research is necessary to assess overstory-understory relationships over the broad range of sites found in the encinal woodlands (McPherson 1992).

Pinyon-juniper Woodlands

Although knowledge of pinyon-juniper woodland ecology is increasing, it still is incomplete (Gottfried and Ffolliott 1993). However, managers recognize that heavy, wingless seeds of pinyons and junipers, and dryland environmental conditions require special consideration when preparing silvicultural prescriptions. It would be ideal if treatments could be linked to good seed crops, but this is difficult considering the relatively long period between good years, and the inability to confidently forecast them. Silvicultural prescriptions must be linked to habitat type in order to succeed.

Bassett (1987), in reviewing the potential applicability of common silvicultural prescriptions to pinyon-juniper woodlands in the Southwest, concluded that single-tree selection and two-step shelterwood methods best sustain stand health and productivity for tree products or for a mix of resources. These cutting methods are compatible with the dispersal patterns of heavy tree seed, provide protected micro-sites for regeneration, and are esthetically acceptable. The single-tree selection method reduces stand density, but still retains the uneven-aged structure and horizontal and vertical diversity important for some wildlife species. Initial harvesting by the shelterwood method, which leaves the best trees for seed production, also tends to retain a diverse cover. However, there are some disadvantages with both methods, especially the costs associated with intensive management and potential damage to residual trees during subsequent harvests. Bassett (1987) discussed the trade-offs that must be evaluated in preparing a silvicultural prescription. Success from a forestry perspective will depend largely upon achieving satisfactory regeneration.

The shelterwood method is used to regenerate even-aged stands and can be used in existing even-aged and uneven-aged pinyon-juniper woodlands. Bassett (1987) recommended the two-step shelterwood method. A modified one-cut shelterwood method, which removes the entire overstory, can be used where advance tree regeneration is satisfactory. However, it is important to protect the younger trees from harvesting damage.

Bassett's (1987) recommendations are valid for stands within the Madrean Archipelago, especially if regeneration of pine or non-sprouting juniper species is important. The clearcut or seed-tree methods would favor alligator juniper and oak regeneration, but generally result in unsatisfactory regeneration of species with short seed dispersal distances.

Current management is attempting to integrate livestock and wildlife with tree production (Gottfried and Severson 1993). Silvicultural methods can also be used to enhance forage production for livestock and forage and cover for wildlife. A common treatment is designed to clear small dispersed areas of trees. This practice has been shown to benefit elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*) (Short et al. 1977). However, care must be taken to insure that openings are not too large (Gottfried and Severson 1993) or that the woodlands not become too fragmented. Wildlife and other needs must be assessed to ensure tradeoffs in resource allocation are acceptable. Openings create a more diverse landscape that should favor other wildlife species such as small mammals (Gottfried and Severson 1993). In many cases, the size of the openings might not be critical, if continuous corridors of adequate width are maintained. Managers must decide if cleared wildlife-livestock openings should be maintained, or trees should be allowed to reoccupy the sites. A management scheme could be created which would involve a variety of seral stands in space and time. This strategy would enhance biological diversity within woodland landscapes.

Treatments that reduce tree densities should benefit livestock and native ungulates by providing additional forage while maintaining thermal and hiding cover. However, the impacts of residual trees on understory dynamics are unclear. Some questions concern the quantity and quality of herbaceous vegetation which can be achieved, and the longevity of any increases. Relationships among overstory cover, tree regeneration, and forage yields need better definition.

Conifer Forests

The only remaining commercial forests in the United States portion of the Madrean Archipelago are found in the Santa Catalina, Chiricahua, and Pinaleno Mountains (Shupe and Solether 1973). However, because of conflicting land uses in the Santa Catalina Mountains and poor site and low stand densities in the Chiricahua Mountains, these two areas could not support a commercial timber management program. The Pinaleno Mountains contain commercial stands of spruce-fir, mixed conifer, and ponderosa pine. The silviculture of these forest types in the central and southern Rocky Mountains has been reviewed by Alexander (1974). This review covered the various even-aged and uneven-aged systems that are applicable to achieve satisfactory regeneration of these forests. Silviculture for multiple-use was covered, but in less detail.

Shupe and Solether (1973) indicated that the most successful regeneration prescriptions on Mount Graham were light selection cuts or small patch clearcuts of from 0.8 to 2.0 ha. Blowdown was a problem in some stands if overstory removals were heavy, and dwarf mistletoe (*Arceuthobium vaginatum* var. *cryptopodum*) was a problem in some ponderosa pine stands. Ice damage has been a periodic problem. Multiple-use silviculture for a variety of resources and for sustained stand health is the main concern in the Sky Islands today. The USDA Forest Service overall management objective for Mount Graham is to maintain and enhance esthetics and outdoor recreational values (Shupe and Solether 1973).

Silvicultural treatments anticipated in 1973 were: salvage of poor risk and overmature trees; light commercial thinning of sawtimber and subsawtimber stands; overstory removal (simulated shelterwood) where satisfactory regeneration has become established under overmature trees; and stand regeneration according to a single-tree or group selection prescription (Shupe and Solether 1973). Many of the Mt. Graham stands are fairly old and natural mortality is increasing; individual tree growth is also lower in dense stands. The goal was to maintain tree vigor and reduce insect and disease damage. These prescriptions may not be feasible today unless there is a market for the timber. More importantly, public attitudes do not support commercial harvesting solely for wood products; harvesting would have to be related to forest health considerations.

Slash cleanup to reduce fire hazard was an important component of most treatments (Shupe and Solether 1973). Slash disposal policies are under review, since ecosystem benefits must be compared to increased fire and insect hazards. However, Moody et al. (1992) indicate that a high percentage of the forest on the Coronado National Forest is at high risk of catastrophic wildfires because of high fuel loading and lack of management to alleviate the situation. If conditions have changed drastically since 1973, the Forest Service may have to evaluate the need for fuel reduction activities, sanitation or salvage logging, and eventually, prescribed fire. The latter would be difficult because of the fuel loading and fuel ladders. Any activities to correct the condition would draw public comment.

Insect and fire control activities in the old-growth stands within non-wilderness areas will also have to be evaluated. The public may endorse natural forest dynamics in a remote wilderness area but be less tolerant when they can see its effects on their way to a favorite campground. Large areas of dead and dying trees or of burned snags often are the results of unhealthy stand conditions. Silvicultural treatments may become necessary to open dense stands where tree vigor, and resistance to insects and diseases, has been reduced or where unacceptable insect and disease damage has been identified. Regeneration or improvement treatments would be used to improve stand health prior to insect or disease attack, while sanitation treatments would be used to prevent a pest from spreading.

The roundheaded pine beetle (*Dendroctonus adjunctus*) currently is causing considerable mortality in ponderosa pine forests on Mount Graham, especially adjacent to Riggs Lake. Coronado National Forest crews have cut infected and dead trees in hopes of removing potential hazards and containing the problem. Many cut trees have been bucked and left as firewood for recreational visitors. Some were sold to a sawmill in Alamogordo, New Mexico.

CONCLUSIONS

The mountains of the Madrean Archipelago or Sky Islands support a diverse mixture of forest and woodland ecosystems representing the Rocky Mountain and Madrean floras. Regional and local climatic conditions over last 24,000 years have influenced the present distribution of vegetation communities. These lands have been used by humans since prehistoric times.

Demands for the forest and woodland resources have changed over time. However, there currently are conflicts among different interest groups as to how intensively the land should be managed. To this end, silvicultural prescriptions, matched to habitat type, provide one tool for ecosystem management in the Madrean Archipelago. The Coronado National Forest is charged with ecosystem management that will ensure sustainability and health of the region's forests and woodlands. The various interest groups should work together to achieve these goals.

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Temperate Pines of Northern Mexico: Their Use, Abuse, and Regeneration

James T. Fisher, Patrick A. Glass, and John T. Harrington[1]

Abstract.—The pines of northern Mexico contribute greatly to regional economies and biodiversity. This paper examines their distribution, ownership and principal uses. It also explores their present and future integrity in view of present and projected forest practices. In particular, the paper addresses the necessity for developing effective forest regeneration strategies which do not diminish genetic diversity. Some of these pines have a potential role in the genetic improvement of commercial, select gene pools maintained in the United States. Cooperative efforts to establish *ex situ* plantations for conserving germ plasm therefore deserve attention, especially in the case of endangered species.

INTRODUCTION

Mexico's geographic location, diverse topography and vast coastal areas have made its land rich in biological diversity (Bye, 1993; Rzedowski, 1993; WCMC, 1992). Its forests are especially rich in flora and fauna, with some groups having ancestral lines traceable to taxa existing today deep within South America or latitudes far to the north (Brown and Gibson, 1983) . Our aim is to examine the importance of Mexico's principal pine forests to its people and to describe some of the factors threatening their ecological integrity. We will also discuss efforts to regenerate deforested areas and how this work might be accelerated. We will see that the United States and Canada can indirectly exert both positive and negative influences on Mexico's biological resources. Opportunities for expanding positive U.S.-Mexico interactions should become obvious as we discuss Mexico's efforts to develop its resources without compromising ecological integrity.

Our focus will be two madrean regions (fig. 1), as recognized by Peet (1988), and three Mexican states. In a geological context , these regions are two of Mexico's 11 morphotectonic provinces, identified according to their physiographic and geologic-tectonic features (Ferrusquia-Villafranca, 1993). We will discuss the forests of two of these provinces, the Sierra Madre Occidental and Trans-Mexican Volcanic Belt. The Mexican states of Chihuahua and Durango have forests in the Sierra Madre whereas Michoacan has forests in the Volcanic Belt. The approach will be to describe the forest resources of each state followed by descriptions of their productivity and factors leading to deforestation. Forest regeneration needs and practices will be discussed with the issue of biodiversity in full view.

Figure 1.—Map of the Madrean regions within Mexico and southwestern United States.

Pines of these regions occur in pure stands, be they forests or woodlands, or mixed with oaks at

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lower elevations. Several species of *Abies* and *Picea* (Gordon, 1968) occur on the highest slopes but are increasingly threatened by human encroachment owing to their meager abundance. *Picea chihuahuana* occurring in the Creel, Mexico area is clearly an endangered species (National Research Council, 1991).

The forests of the Sierra Madre and Volcanic Belt are unusually rich in numbers of pine (Table 1, after Perry, 1991; Styles, 1993) and oak species and subspecies (Martinez, 1981; Nixon, 1993) . Numerous pine and oak species extend northward into the madrean regions of New Mexico, Arizona and western Texas. A reasonable estimate of oak species for the entire western Hemisphere is 200-225 species. About 135 *Quercus* species occur wholly or partly in Mexico and montane Mexico is recognized as the center of diversity for this genus in our hemisphere. The Sierra Madre Occidental is estimated to have 41 oak species and a species list is available for this area (Nixon, 1993).

The pine forests of the three states generally occur above 2000 m (Table 1) with extensive, uninterrupted areas of heavily stock stands being present in some areas of Chihuahua and Durango from 2200-2500 m. Compared to the neighboring forests of New Mexico and Arizona, forests of the Sierra Madre and the Volcanic Belt are more productive. Within Mexico, growth increases from north to south along the Sierra Madre Occidental range into the state of Michoacan. This can be attributed to several factors but is clearly related to increasing precipitation from 30 to 18 degrees latitude (Mosino-Aleman and Garcia, 1974). It must also be related to the briefer intervals of moisture deficit which are determined by the seasonal flow of monsoonal rains. Rains begin earlier and end later in the southern parts, nearer to the equator. A decisive point is that forests further south can be managed on shorter rotations which on better sites can be as brief as 12 years for pulpwood (Garcia Magana and Munoz Flores, 1993) production or more conventionally about 18-20 years. In northern Chihuahua, rotations require 80-100 years or longer depending on site factors (Arteaga Martinez, 1989).

Table 1.—Key features of the pine forests of Mexico's three principal pine wood producing states. Demographic data from INEGI (1991a, 1991b and 1992; production data from FAO (1992); information on pines from Perry (1991).

	Chihuahua	Durango	Michoacan
Total area (Km^2)	244,938	123,181	59,928
Forested Area (Ha)	464,100	407,300	129,200
Elevational band of pine forest (masl)	2000 - 3500	2000 - 3500	2000 - 3700
Pine roundwood production in 1993 (m^3)	1,049,000	1,695,000	634,000
Minimum and maximum temperatures (C°)	5 - 30	10 - 25	15 - 25
No. of pine species	15	21	21
No. of pine subspecies	1	5	6

FOREST PRODUCTS AND UTILIZATION

According to Camara Nacional de la Industria Forestal (CNF, 1994), Mexico produces almost 25 million cubic meters of roundwood each year and production was rather steady from 1982-1992 (fig. 2). The three states of interest contribute greatly to pine roundwood production (Table 1), accounting for 68.2% of Mexico's total pine wood production. Durango leads production (33.5%) followed by Chihuahua (20.7%) and Michoacan (12.6%) (CNF, 1994). The products obtained from these forests are numerous and reflect both industrial and communal uses (Gonzalez Hernandez, 1986). In each of the three states conventional industrial products are obtained as shown for the state of Durango (fig. 3).

Most of the volume (60.5%) is utilized in the production of lumber for local, national and export consumption. Pulp and paper production consumes 29% followed by plywood production (5.9%), pressure treated products (4.1%) and chipped products (0.5%) (CNF, 1994). Forests also provide commercially important resins (Moncayo Ruiz and Gonzalez Lopez, 1979) fuelwood for mountain communities and a host of products needed for furniture manufacturing and artist guilds. Michoacan is especially well known for its artistic use of wood in carved furniture.

Pulp mills consume mostly pines but also utilize oaks where they are abundant. (e.g., Michoacan). Pulp and paper mills tend to be few in number in each of the states owing to infrastructure requirements and wood supply. Sawmills can be found throughout the intensely forested areas in Michoacan , for example, and closely follow the east to west belt of forests in the upper third of the state (Moncayo Ruiz and Gonzalez Lopez. 1979). Each state has centers of more intense utilization as shown for the state of Chihuahua (fig. 4). Utilization is particularly intense in the municipios of Guachochi, Guerrero andUrique (Gonzalez Hernandez, 1986; INEGI, 1991b).

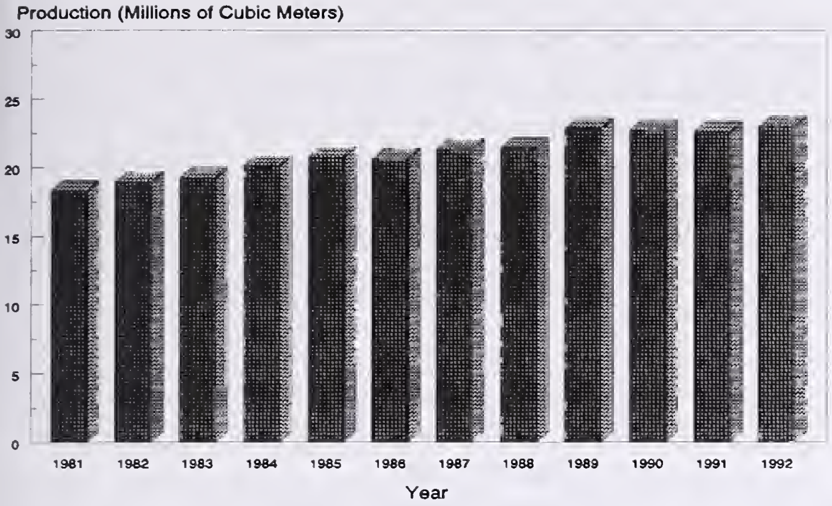

Figure 2.—Total roundwood production for Mexico from 1981 through 1992 (Source: FAO).

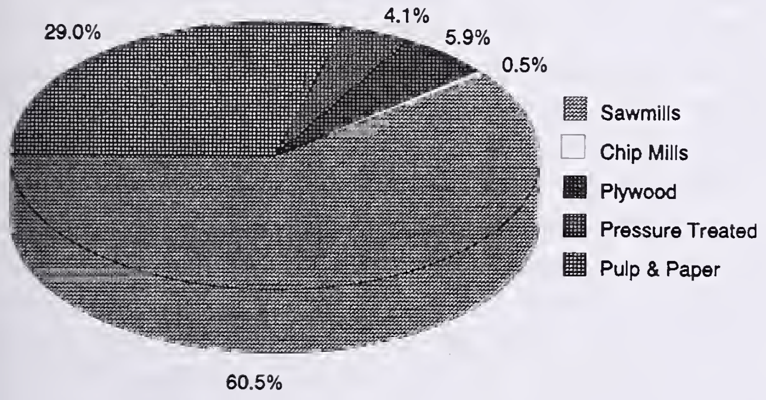

Figure 3.—Product utilization by industry for the state of Durango.

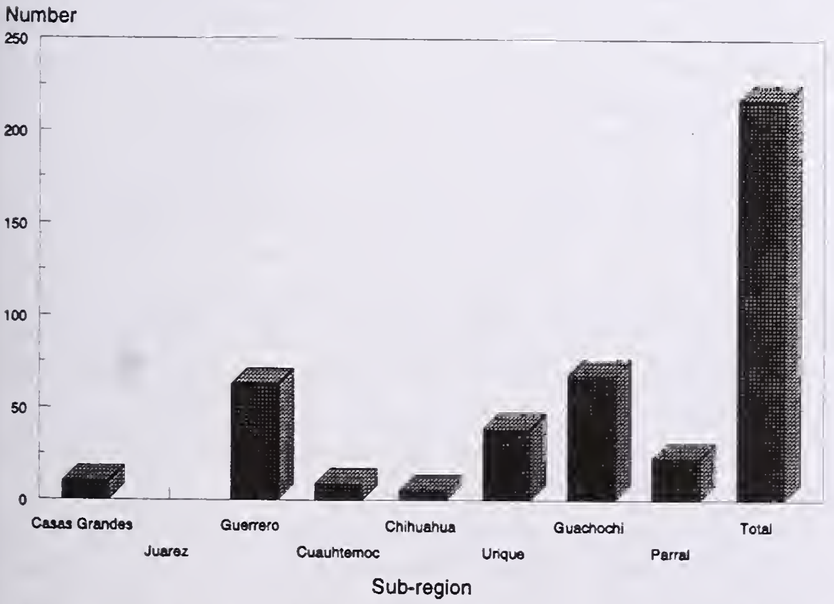

Figure 4.—Sawmill distribution by sub-region within the state of Chihuahua (Source:SARH).

Table 2.—Forestry related employment for the states of Chihuahua, Durango, and Michoacan.

	Chihuahua	Durango	Michoacan
People employed	17,854	15,229	10,133
Percent of total population	1.00%	1.10%	0.30%
Total population	2,238,542	1,384,518	3,377,732

Owing to Mexico's historical dependence on rural-based agriculture economies, forestry employment plays a critical role in the livelihood of communities existing outside the economic mainstream of the larger cities (table 2). No where is this more obvious than in the state of Durango where no less than 1% of the population is employed in forestry-related activities (Hernandez Diaz et al, 1991). In Chihuahua, ranching gives way to forestry as one moves from the natural pastures of the plains into the sierras. Forest land use increases from 15.2% to 47.7% from plains to sierras (INEGI, 1991a) and the importance of forestry employment becomes outwardly obvious. In areas such as Creel, forest industry employs a member of one of every third or fourth household.

DEFORESTATION

Numerous factors threaten the forests serving Mexico's forest-based communities. On a local scale, fire takes a heavy toll on forests. From 1983-1988, as much as 125,000 Ha of Mexico's forest have been lost in a given year with rangeland fires covering twice that amount (e.g., 1988) (fig. 5).

Fire is particularly destructive in Durango(fig. 6 (Hernandez Diaz et al., 1991) and Chihuahua (fig. 7 (INEGI, 1991b) where pine growth is less rapid. Owing to the concentration of forests in these states, forested lands often exceed rangelands in total areas burned. Figure 7 also illustrates one of the underlying reasons for Mexico's steady decline in forest cover.; regeneration simply falls woefully short of replacing forests lost to fire.

We see a similar pattern in Chihuahua which also shows a fire-regeneration mismatch but also that fire consumes as much timber as harvest.

For the entire country the net rate of deforestation from 1980-1992 has shown a steady increase and in 1992 exceeded 1 million hectares. Fire and an inability to regenerate forests therefore does not fully explain Mexico's forest decline. Here, the issues become exceedingly complex with opinions differing among economists and sociologists as to root causes.

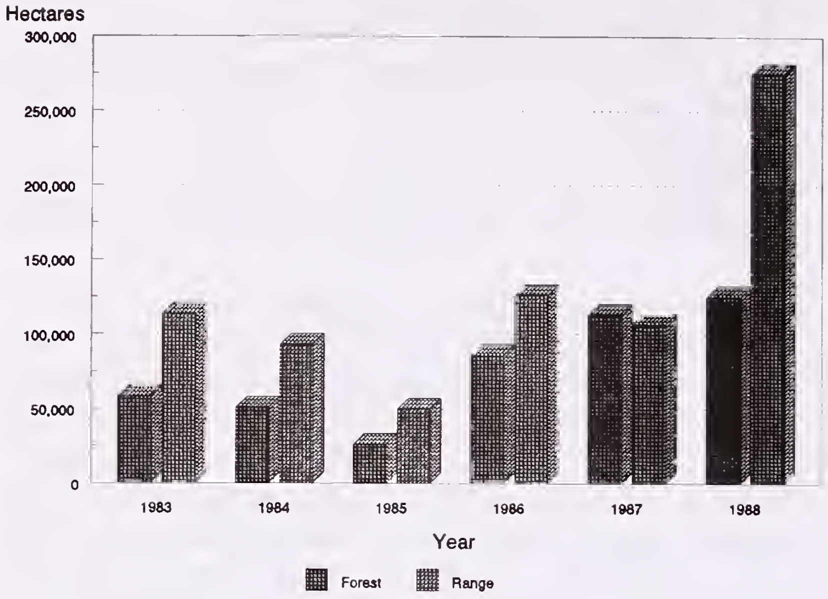

Figure 5.—Mexican forest and range area lost to fire.

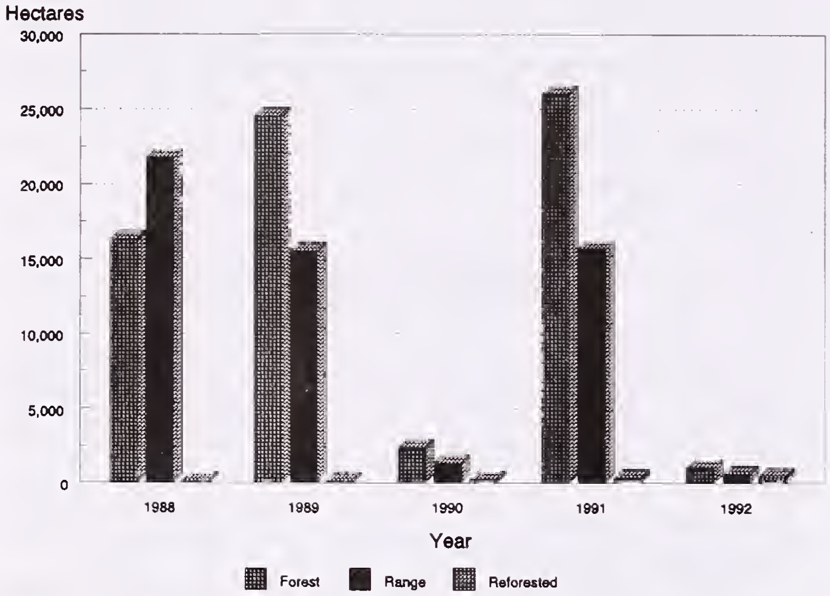

Figure 6.—Fire and reforestation areas for the state of Durango.

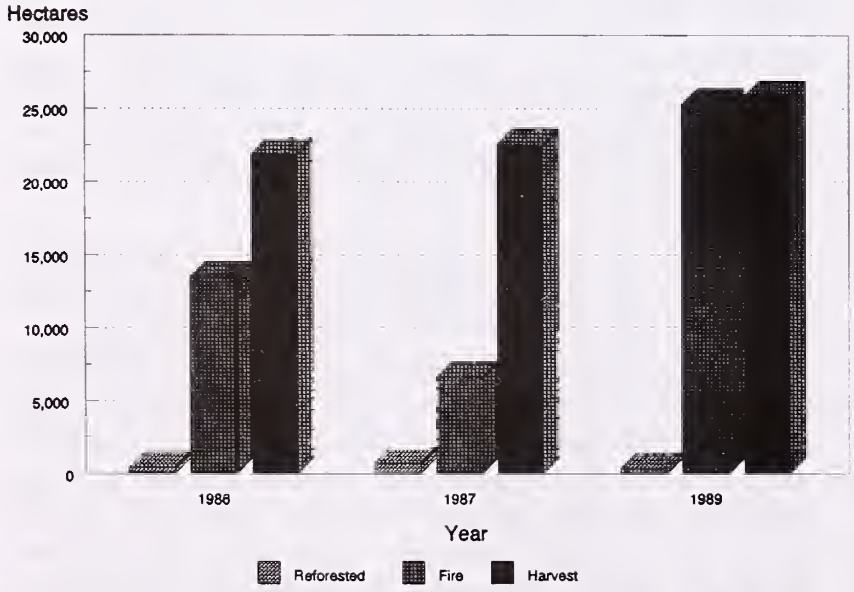

Figure 7.—Harvest, fire and reforestation areas for the state of Chihuahua. (Assumption of 100% loss due to fire.)

One approach toward understanding Mexico's forest-related dilemmas is to examine the broader issue of ecosystem health. As we identify threatened resources and why they are being challenged, we will see that many problems , including deforestation, have similar root causes. We will also be better able to understand why Mexico's land management priorities are gradually changing.

One economist (Mumme, 1992) characterized Mexico's ecosystem health as undergoing steady degradation. He listed as symptoms of decline:

- Loss of biodiversity
- Damaged aquatic ecosystems
- Decline in sustainable agricultural practices
- Deforestation

Economists have attributed ecosysten degradation primarily to political, economic and social factors (Barkin, 1990; Mumme, 1992; Nuccio et al., 1990; Nuccio, 1991). Political factors are largely associated with the need to stress economic recovery to the electorate with other causes and reforms remaining secondary to this chief aim. This is understandable in view of the financial stresses imposed on Mexico since the oil bust of the 1980s. Economic recovery would mean an increase in real wage earnings. It would also mean that finances needed for public works and the environment would become available. In particular, Mexico's industrial plants are severely lacking in environmental control equipment (Herrera Toledano, 1992).

Economic strategies dating back to the 1950s are often cited as creating Mexico's financial crisis, and as indirectly creating social pressures leading to environmental decline. In particular, rural areas are said to have suffered at the hands of policies lacking economic incentives for the production of basic foods. As farmers abandoned the production of basic foods such as corn and beans due to price controls, they moved to urban areas to seek higher wages. Cd. Mexico now has more than 20% of the country's population (Wilkie, 1993). Unable to keep pace with an inflation economy, peasants remaining in rural areas progressively cleared land for agriculture or cattle. Southern Mexico has been heavily impacted by cattle.

Hoping to balance its trade deficits, Mexico poured large subsidies into intensive irrigated agriculture for the purpose of bolstering its exports of high value crops. Unsubsidized rain-fed lands cultivated and cropped continuously lost their productivity owing to nutrient decline and erosion. In Oaxaca, some areas (e.g., Mexteca) arable land has been reduced 70%. The removal of trees from watersheds to make room for crops and cattle has been blamed for erosion, flooding and the loss of biodiversity. One concern is that peasant migration could erase the existence of endemic forest species occurring at lower elevations where mountains join farming valleys. Forests at these locations are at high risk in terms of intentional burning. Deforestation has led to further desertification in the drier areas, and in the humid subtropical areas extensive biologically diverse forests have been lost. For example, the Lacandon jungle area has been reduced 70% over the past 40 years. The overall loss of Mexico's forested areas has been estimated to be 66%.

The net result of migration from rural to urban areas has intensified the need for industrialization to create employment. Effects associated with urbanization and industrialization have combined to create problems of waste management, air pollution, coastal oil spills and sanitation handling. More than 60% of Mexico's rivers and streams and many of its largest and best known lakes (*e.g.* Chapal & Patzcuaro) are reported to be contaminated (Mumme, 1992) by pollution from concentrated populations and industry.

These issues received considerable debate during the NAFTA debates which directed attention to Mexico's lax enforcement of environmental laws, transborder pollution from maquiladoras, and potentially negative effects of the trade agreement on Mexico's environmental quality.

Mexico's response to these issues has been to overhaul its environmental oversight agency (SEDESOL). It stiffened enforcement and now requires environmental impact statements for all construction projects. Mexico has also declared its commitment to sustainable development (Manzanilla, 1992) and has entered numerous multi-lateral agreements to protect biodiversity. One of Mexico's immediate aims is to develop a thorough inventory of its biotic resources and to put risk assessment at the top of its development criteria.

Rural economic development has been dealt with by a massive restructuring of the ejido system (Kuenzler, 1992) through which the majority of agricultural and forest lands were previously managed. Reorganization will encourage further intensification of agriculture under varying types of land ownership. The goal is to connect capital investment, domestic or foreign, with land and labor previously managed exclusively under ejido domain. For example, foreign capital has enabled Mexico to expand production of winter export vegetables and fruit crops offering comparative advantage. Forestry may also prove attractive to foreign companies.

Effects of Mexico's polices and NAFTA on timber harvest *per se* have received minor attention compared to the staggering environmental problems of the Federal District and border towns. In domestic terms, Mexico clearly will have to harvest or import more trees to meet the needs of its expanding population (fig. 8) . Anticipating this need, the American Plywood Association and the Forest Products Association both voiced support for NAFTA. According to one economic model, both U.S. and Mexican consumers of softwood lumber will benefit (Boyd, et al., 1993).

The attention given trade negotiations and global ecology clearly intensified cooperation among the NAFTA participants. The U.S. Forest Service has worked closely with the Mexican government to meet needs for reforestation training while continuing efforts to provide assistance in fire management (Gonzalez-Caban and Sandberg, 1989). New Mexico State University has worked with the Forest Service to deliver nursery management training over the past four years. Canada is currently extending its "model forest" concept (Brand and LeClaire, 1994) to a project near Creel, Mexico. Creel is a somewhat remote forest-dependent community with an unresolved future owing to the growing needs of the community for potable water, sanitation facilities and transportation. Responding to concerns that road development would adversely affect the area, the World Bank apparently is not going forward with road construction assistance. Development impacts on the future of the Tarahumarans, numbering in excess of 40,000., and maintaining the scenic value of Copper Canyon were among the principal concerns. Forest Guardians, a conservation group based in Santa Fe, New Mexico , is providing financial assistance for developing Tarahumaran community nature reserves and agro-ecology training centers. Clearly This region clearly is attracting international attention and resource management case studies addressing its complex problems should be greatly rewarded.

Forest Regeneration

With a fuller understanding of issues impacting the pine forests of Mexico, we return to the need to close the gap between forest loss and reforestation. Mexico's commitment to reforestation is most evident in the work being done by nursery specialists at community, state and national levels. It is also apparent in the cooperation among these groups in finding solutions to difficult technical problems. The fact remains, however, that reforestation must become increasingly efficient and this can be achieved more rapidly by overcoming existing limitations. Factors constraining reforestation include available finances, technical services and the shortage of professionals capable of handling the diverse problems encountered in nursery operations. The technical problems encountered would tax the capabilities of the most advanced nursery research centers in the U.S. owing to the absence of published information about Mexico's diverse tree species. The absence of soil, plant and water testing laboratories with advanced testing equipment poses another limitation. Tree seed testing facilities are especially needed.

Although some Mexican nurseries have greenhouse facilities, most grow seedlings in containers outdoors. Bare root nurseries are rare. The nurseries observed thus far frequently have problems associated with crop salinity caused directly by water supplies or soil media, or indirectly by crop management. Probably the most frequent cause of poor seedling growth is the container medium used. Media frequently have poor physical properties owing to the large amounts of soil used in them. Reliable substitutes for unaffordable Canadian peat are needed. Severe labor problems are created by the large number of blank containers caused by poor seed germination. Most nurseries avoid this problem by investing considerable labor in transplanting germinants. This practice is even used in bare root nurseries where transplanting is back breaking. Fertility management problems are severe in some nurseries with deficiencies in nitrogen, phosphorus and iron being most common. Sometimes bareroot crops show striking growth reductions as fertility declines. Green manure rotation practices could alleviate many fertility and disease related problems. Production can also be accelerated by using pest and weed control chemicals within integrated management schemes recognizing the need for safe application.

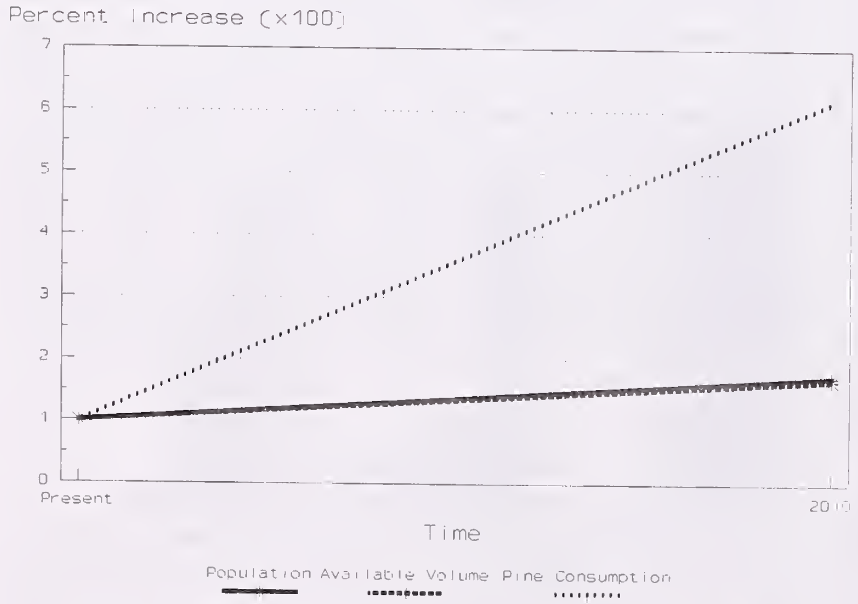

Figure 8.—Projected trends for population growth, pine volume consumption and available pine volume for the state of Michoacan.

More needs to be known about basic growth patterns of Mexican forest species as related to nursery production and outplanting success. The diversity of Mexican species magnifies the need for such information while representing a conservation issue deserving separate attention. In view of Mexico's biodiversity, a rich store of tree genotypes can be lost as nursery and reforestation practices inadvertently deselect them. Practices should therefore be examined to identify steps where potentially valuable genotypes are being lost (Jasso, 1970; Kleinschmidt, 1979; Ledig, 1986). In particular, reductions in seed and seedling mortality would promote gene conservation. Some of Mexico's temperate tree species may deserve germ plasm preservation efforts similar to those presently directed toward its tropical conifer species (Dvorak and Laarman, 1986). Pine seed production appears to be quite reliable for some species and areas (e.g., Michoacan (Guzman et al, 1979). Mexican forest researchers are testing methods for improving long term storage for species offering only rare collection opportunities. They are also discussing provisional seed zones as a means of protecting pine diversity. Oaks and other endemic hardwoods should receive attention as well as pines and other conifers.

Mexican nurseries could operate at higher efficiency levels through the centralization of facilities. Also, fixed geometry container systems permitting mechanized precision sowing could be used, and bare root nurseries could be developed to reduce seedling costs (Carrillo Sanchez, 1980). At present, the few bareroot nurseries existing in Mexico struggle with a brief lifting window created by mild climate, and presently do not offer much of a cost advantage, if any. Compared to the USA, Mexico presently has fewer options for safely transporting and storing bare root stock owing to its infrastructure limitations.

There clearly is a need to view issues such as production centralization and mechanization within social and environmental contexts. Because

Mexico must provide 300,000 new jobs in agriculture each year to stay even with population growth, rural employment cannot be neglected. Also, one dollar earned in a rural community translates to almost four dollars of benefit to the local economy. Steps toward production centralization and mechanization therefore must be taken in a responsible manner. However, these steps may provide the only means of accelerating seedling production to achieve specific goals. Proper treatment of these issues, belongs in our opinion, in the hands of managers having thorough knowledge of rural economics and Mexico's infrastructure.

With its nurseries working at a high level of efficiency, intensively managed plantations could be developed rapidly for the purpose of sparing, not replacing, its natural forests . Strategically located plantations could provide a more steady flow of supply to Mexico's forest industry. In the past, industry has been plagued with flow interruptions created by difficult harvest access, lack of machinery and transportation net works. NAFTA could play major role in developing such plantations by providing the capital and technology needed. Research is needed to identify plantation approaches featuring contributions to genetic, ecological, and landscape diversity as discussed by Kanowski et al., (1992). In some areas (e.g., Michoacan (Esparza and Trujillo, 1986), extensive surveys are available for matching species and forest types with soils, topography and land uses.

We will conclude our topics by asking what importance do the forests of Mexico have for the U.S. beyond the immediate issues. As we asked this question it became apparent that global warming could make us directly dependent on some Mexican forest species sometime in the future.

Global climatic models (GCMs) enable us to predict how global warming could increase the United State's dependency upon Mexican forest species. Under the assumption that the concentration of atmospheric CO_2 is doubled from 0.03% (Sagan and Turco, 1990) the effects on forest communities might include:

- A 200 - 1,500 km shift to the northwest of some tree species,
- A 1 - 5 degree Celsius rise in mean annual temperature,
- Increased plant stress,
- Species composition changes,
- Decrease in productive areas (Andrasko, 1990; Ledig and Kitzmiller 1992).

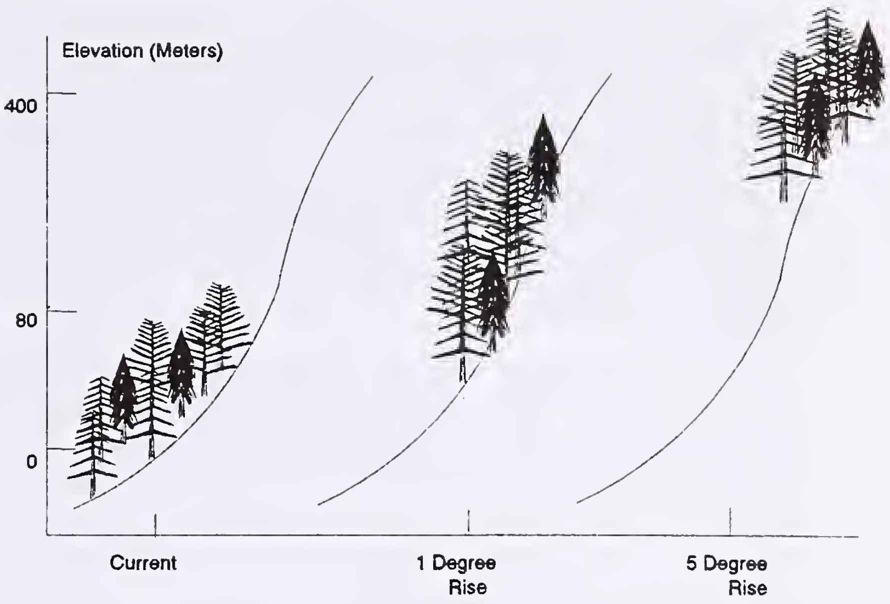

Figure 9.—Elevational and spatial change in forest community with global warming.

The easiest transition for a forest community to make is elevationally (Ledig and Kitzmiller 1992). Figure 9 illustrates the outcome of a forest community adapting to increased temperatures elevationally. The relatively small distances in elevation that need to be traversed are within the capability of the natural transport vectors (e.g., animal and wind). However, elevational transition is limited by the narrow range existing between the current timberline and the apex of the mountain. At many locations more than a 2° to 3° C rise in temperature would cause the upper boundary of the forest to shift upward beyond the top of the mountain it occupied.

Unlike elevational transition, however, latitudinal movement is hampered by geography, habitat and territory conflicts (Ledig and Kitzmiller 1992). The migration rate utilizing natural dispersion vectors will be incapable of keeping pace with the expected displacement of isotherms (Table 3). Forest ecosystems in the Madrean archipelago and the southwestern United States are faced with an extreme challenge in adapting to climatic change. Because of the isolation of the range peaks, latitudinal migration is improbable without intervention by man.

Table 3.—Expected migration rates and isotherm displacement under assumptions of global warming.

Vector Class	
Anemophilous	25 kilometers per century
Zoophilous	12 kilometers per century
Mean Temperature Increase (Celsius)	
1 degree rise	200 kilometers northwest
5 degree rise	1,000 kilometers northwest

What this portends for the Madrean region as a whole and the United States in particular is the loss of forest species that are commercially valuable as those species migrate northward to adapt to changing climatic conditions. The forest species that occupy the lower latitudes (18° -30°) can be used to replace those species lost in the southwestern United States as the dominant commercial species.

Global climatic change is an ongoing process. Changes that would be considered catastrophic to a forest ecosystem are not going to occur "overnight", however, the effects are cumulative and accrue rapidly relative to a systems ability to respond. Utilizing available technology in conjunction with foresight, proper planning, and the inherent adaptability of forest species, man can mitigate the consequences of global climatic change through forest regeneration efforts.

CONCLUSIONS AND RECOMMENDATIONS

The information presented shows that the madrean forests in the states of Chihuahua, Durango and Michoacan are major contributors to Mexico's people, economy and biodiversity. However, Mexico's national rate of deforestation threatens the livelihood of rural communities and industries, while posing a serious threat to Mexico's rich biodiversity. Impacts on Mexico's biodiversity will be felt much beyond its borders. Effective regeneration practices, as discussed, can reverse current trends in deforestation, thereby preserving ecological integrity and sustainable economic development.

Our recommendation is for North American countries to continue building cooperative strengths to overcome factors threatening the biota of this hemisphere. The assistance being provided to Mexico by the U.S. Forest Service and Canada is commendable and represents several productive approaches. Non-governmental organizations on both sides of the border are also becoming increasingly involved. Mexico's most pressing problem obviously centers on its ability to develop its resources without damaging its environment. In this context, there have been too few studies on the economic values derived from its natural ecosystems, particularly its forests. More effort should be directed to this area. Finally, it is clearly in the best interest of the U.S. to foster ecological, economical and political stability in Mexico. Our lives are not separate, now or in the future.

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Dynamics of the Landscape Patches in the Old Growth Forest on Mt. Graham (Pinaleno Mountains), Arizona

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Abstract.—The old growth forest on Mt. Graham (Pinaleno Mountains) of eastern Arizona is comprised of forest patches rather than being homogeneous in composition. These patches reflect the heterogeneity of disturbances that occur on the mountain. The two primary disturbances have been fire and wind, although clearing for road construction and recently for an astronomical observatory also are important. The forest patches represent different stages in forest succession following disturbance. Patches can be described as open, forest edge, and mature and old growth forest. With these categories, composition and demography of dominant tree species varies and creates smaller patches within the general categories. Variability results from the relative success of pioneer species and the consequent invasion of other species. There appear to be four recovery patterns following disturbance within the Engelmann spruce-corkbark fir (*Picea engelmannii-Abies lasiocarpa* var. *arizonica*) forest. These include (1) initial spruce invasion closely followed by fir with a second surge of fir recruitment in about 80 years, found more on level topography sites; (2) initial invasion by spruce with fir establishment about 40 years later and a second surge of spruce recruitment about 100 years after recovery initiation, found on moderate topography sites; (3) initial spruce invasion with fir following in about 40-80 years with no second recruitment surge by either species, found on moderate to steep topography sites; and (4) initial spruce invasion with fir recruitment following in about 120 years and surging only in the past 50-60 years, found on steep topographic sites. For all locations there is a conifer recruitment period initiating about 140 BP and lasting about 50 years. This closely corresponds with a wet climatic period following a drought period. Sites with similar recovery patterns are clustered together indicating the forest is composed of large patches rather than a heterogeneous mix of small patches. The locations of large forest patches with particular recovery patterns could be used to project possible successional patterns of recently reforested areas on the mountain.

INTRODUCTION

Many mountains of the Southwest are isolated peaks surrounded by contiguous desert ecosystems. These peaks, often referred to as "sky islands" (Gelbach 1981), have functioned as refugium for the montane and subalpine flora and fauna during climatic fluctuations over the past 10,000 years (Martin 1963). Climatic changes have caused vertical migrations of the mountain flora resulting in extirpation of species. For example, the Engelmann spruce (*Picea engelmannii* Parry)-corkbark fir (*Abies lasiocarpa* var. *arizonica* (Merriam) Lemmon) forest association found on Mt. Graham (Pinaleno Mountains) does not occur on any other sky island in southern Arizona al-

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though the species may be found separately on other mountain tops. Many of the high elevation forests of the sky islands have not been lumbered because of their limited area and therefore have attained "old growth" status.

Old growth forests are becoming increasingly rare in the Southwest. The old growth spruce-fir forest on the Pinaleno Mountains only covers about 360 ha, and occurs primarily above 3,100 m. This is a very small portion of the thousands of hectares of forest on the mountain, most of which has been impacted by timbering. The remainder of the conifer dominated forest communities on the Pinalenos include, in descending order, mixed conifer forest immediately below the spruce-fir forest with the upper stands part of the old growth forest characterized by Douglas fir (*Pseudotsuga menziesii* var. *glauca* (Breissn.) Franco), southwestern white pine (*Pinus strobiformis* Engelm.) and white fir (*Abies concolor* (Gordon et Glendinning) Hoopes); ponderosa pine (*Pinus ponderosa* Laws.) forest; and pinyon-juniper forests. These forests have been described by Johnson (1988) for the Pinalenos and Whittaker and Niering (1965) for the Santa Catalina Mountains near Tucson, Arizona. Whittaker and Niering used the top of the Pinalenos to complete their description of vegetational zonation on a southwestern mountain because the spruce-fir forest did not occur on the Santa Catalinas. In this description they demonstrated how different environments found at different elevations and aspects, and within drainages greatly influenced the pattern of vegetation on the mountain. This was an extension of the early work of Shreve (1915) in his description of distribution of vegetation in relation to climate on a desert mountain.

These studies of desert mountain vegetation along with ours on the Pinalenos (Stromberg and Patten 1991) describe the high elevation forest communities not as one homogeneous forest stand, but rather as a heterogenous stand of forest patches, each a consequence of site conditions and external disturbance factors. Old growth spruce-fir forests in Colorado have also been shown to be a function of the interaction of these factors (Rebertus et al. 1992). Most landscapes are affected by natural or anthropogenic disturbances which operate in a heterogenous manner resulting in a heterogenous landscape. Frequency and severity of disturbance events are often controlled by site conditions, resulting in a mosaic of forest patches, each a consequence of the resistance and resilience of the community to the type of disturbance.

The forest on the top of the Pinaleno Mountains is a mosaic of patches resulting primarily from two natural disturbance factors and one anthropogenic disturbance. These are fire (lightning strikes), wind, and strip clearing for fire roads (now abandoned). Very limited cutting has occurred along the edges of cienegas, and more recently road building and clearing has occurred for an astronomical observatory. These disturbances have created (1) burned areas of various sizes in which some trees may have survived, (2) windthrow areas with down timber, (3) openings with no trees, and (4) edge communities. There are also a few open areas for which the cause is not known, although fire is suspected. The topography of the mountain top varies in aspect, with all aspects represented. Soil development appears to be the result of topographic steepness and aspect.

The objectives of this paper are to describe the demographics of different forest patches in the old growth spruce-fir forest of the Pinalenos and to show how they are a result of the temporal and spatial influences of the various disturbance factors acting in concert with site conditions and recovery processes of the different communities.

METHODS

Thirty sites were delineated for study within the high elevation old growth forest area on the Pinaleno Mountains . Of these, 15 were in the spruce-fir zone (3,130 to 3,270 m) and 15 in the spruce-fir, mixed conifer transition zone (2,930 to 3,100 m). Five of the sites were open stands recovering from disturbance and 5 were edges between forest and recently disturbed areas. At each site, trees were sampled for density, dbh and basal area, and cover using ten 20 m^2 plots on randomly placed transects within about a one hectare forest stand. A representative sample of trees was cored for age determination. Shrub and herbaceous cover was determined. The forest floor was sampled for rock and litter cover. Slope and aspect were measured for each site.

RESULTS AND DISCUSSION

Results presented here are limited to spruce-fir stands, especially old growth stands. A more detailed description of all of the study sites has been presented in earlier papers (Stromberg and

Patten 1991, 1994) including cone and seed productivity (Stromberg and Patten 1993).

The oldest spruce-fir stands were about 340 years old. In most cases the oldest trees were Engelmann spruce, while in only a few cases did the corkbark fir achieve nearly this age. Old stands were located throughout the old growth spruce-fir study area. Interspersed among the old stands, where there had been road building or recent windthrow, were younger stands of various ages depending on the time of the disturbance.

The density of different age classes of spruce and fir differs between locations. The pattern of age classes over time is an indicator of the recruitment dynamics of each stand. Because the oldest age of the trees within the spruce-fir forest is about 340 years for most of the old growth stands (an age younger than the maximum age reported for Engelmann spruce of 500-600 years (Alexander 1987)), we assume that there was a major disturbance at that time; most likely an extensive fire. The presence of a few younger stands indicates there also have been more recent disturbances, and road building and winds have created very recent disturbances.

We have suggested that there are two general patterns of recovery from disturbance within the old growth spruce-fir forest depending on the disturbance mechanism (Stromberg and Patten 1994). For a major disturbance that clears a site, for example fire or timber cutting, initial recovery results from invasion of spruce. This is followed in time by either a second spruce recruitment period, or establishment of a young population of fir. In areas that are only partially cleared (e.g., windthrow), both spruce and fir may invade the site but fir more commonly is the pioneer species. Other studies of spruce-fir forests in the Rocky Mountains have shown similar staggered or bimodal recovery patterns following disturbances (Aplet et al. 1988, Rebertus et al. 1992).

A review of age class data for each site indicates that, although each site has its individual pattern that follows the general patterns we have described, there are secondary patterns among sites (fig. 1). The following patterns are based on existing age class densities. We recognize, however, that present trees only represent survivors from past recovery cycles and recruitment events.

Pattern A (fig. 1) shows initial spruce establishment about 340 years BP with a fir establishment surge from about 200 to 100 years BP. Spruce shows another small surge from 100 years BP to near present. This pattern is exemplified by sites 11 and 14 in our study (Site 11 presented).

Pattern B shows spruce establishment about 260 years BP with a second spruce recruitment surge about 180 to 100 years BP. A fir recruitment period occurred in this latter period with most recruitment of fir occurring in the past few decades. This pattern is exemplified by sites 10 and 12 (Site 10 presented).

Pattern C shows a low to moderate level of recruitment of spruce starting about 300 years BP with very limited fir recruitment. About 140 years BP fir had a high recruitment surge which has lasted until the present. This pattern is exemplified by sites 7 and 9 (Site 9 presented).

Pattern D has a low level of spruce recruitment starting about 340 years BP. Fir did not have any recruitment for nearly 160 years until 180 to 140 years BP and has shown a moderate to high establishment rate in the past century. This pattern is exemplified by sites 15 and 16 (Site 15 presented).

In an attempt to explain the different patterns of forest patch development over time, we looked at general site conditions for each pattern (fig. 2). The number of sites for each pattern were too limited to permit statistical analysis, however, there were some differences among the recovery patterns. The pattern with nearly synchronous early recruitment for spruce and fir occurred on sites with nearly level topography (Pattern A). This pattern also had the earliest surge of fir recruitment. The pattern with delayed fir recruitment following spruce initiation occurred on the steepest sites (Pattern D).

To determine what factors might influence seedling establishment of spruce and fir, we ran a correlation between seedlings and various site conditions, especially those that influence the microenvironment near ground surface (Table 1). The presence of an existing canopy, especially of older trees (i.e., high basal area), appears to have the greatest positive relationship with establishment of spruce and fir seedlings. As expected, a dense spruce canopy cover and/or basal area improved conditions for fir. In open sites where herbaceous cover had established, spruce and fir seedling recruitment was low. Steeper slopes also played a negative role in conifer seedling recruitment.

There are common trends among the recovery patterns. Spruce initiates establishment of the spruce-fir forest following an area-clearing disturbance. A few of the study sites that were open meadows now have scattered spruce trees, in most cases less than 60 years old. There also are periods which show higher recruitment rates,

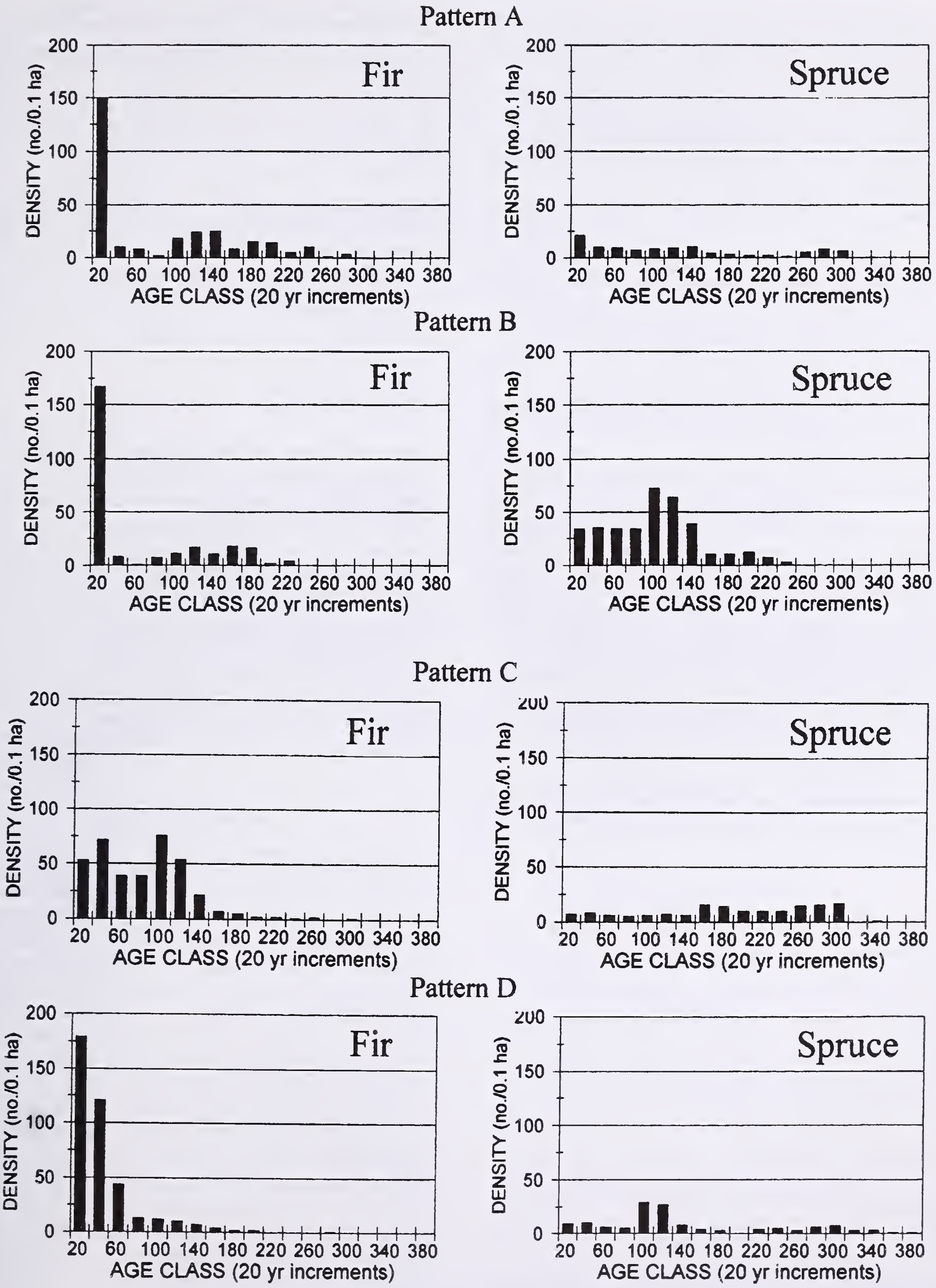

Figure 1.—Four recovery patterns of spruce-fir old growth forest showing different time responses of corkbark fir and Engelmann spruce based on age class demographics of representative forest stands on the Pinaleno Mountains.

often for both spruce and fir. The most obvious of these is the period 140 to 100 years BP, and the last 40 years (see fig. 2). The latter period may just represent short-term survival of young trees; however, the first period may be tied to past climatic cycles. The initiation of many of the present forest stands, around 300 to 350 years BP, also may be climatically influenced.

A study on "severe, sustained drought" funded by the State Department Man and the Biosphere Program and the U.S. Geological Survey in the late 1980s and early 1990s, reviewed tree ring chronologies of the West and Southwest, using studies by H.C. Fritts of the University of Arizona Tree Ring Laboratory (see Fritts 1991), to determine periods of severe drought over the past 400 years. The chronologies for the Southwest indicate several drought periods, but only two that where considered severe and sustained. These were 1667-1670 (ca. 320 years BP) and 1822-1826 (ca. 165 years BP). The drought period of the late 1980s was not included. Wet periods identified through tree ring chronologies (e.g., Buckley's 1989 spruce tree-ring chronology from Mt. Graham) included 1740-1750 (ca. 250 years BP), 1830 to 1840 (a very wet period ca. 150 years BP), 1850-1860 (ca. 130 years BP) and 1904-1934 (ca. 70 year BP). In general, Buckley's chronology indicates that the period 1755-1825 (ca. 245-165 years BP) had below normal tree-rings, while the period 1825-1870 (ca. 165-120 years BP) had above normal tree-rings.

The drought period in the 1600s may have created conditions for initiating forest disturbance and recovery such as enhancing the potential for extensive fires. Apparently, the only extensive evidence of fires in the spruce-fir zone of the Pinalenos is about 340 BP (Thomas Swetnam, pers. comm.). On the other hand, the wet period in the 1800s may have triggered extensive masting of the conifers and thus seedling recruitment. If this wet period followed a relatively dry period, the masting could be extensive as occurred with the breaking of the drought of the late 1980s (Stromberg and Patten 1993). The lengthy wet period in the early 1900s might also have maintained a moderate level of conifer recruitment following the recruitment surge in the 1860s.

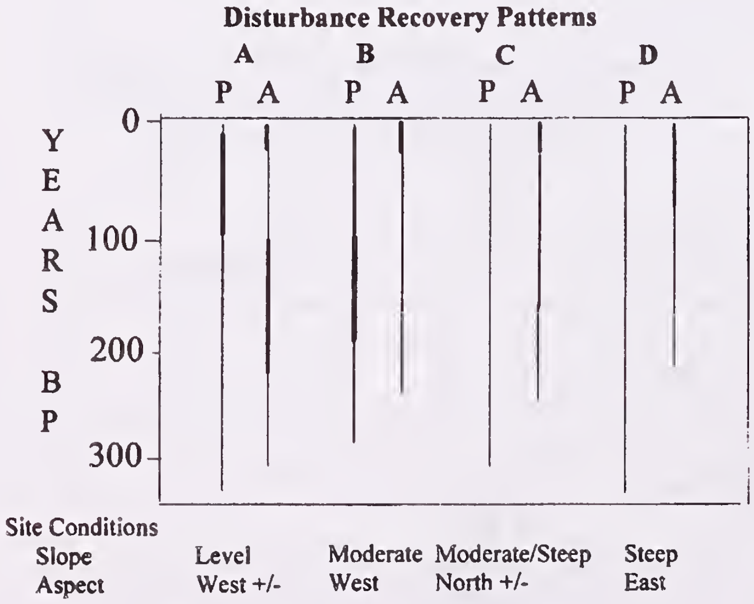

Figure 2.—Comparison of disturbance recovery patterns indicating recruitment initiation and "surges" of spruce (P) and fir (A). Line thickness indicates relative rates of conifer recruitment.

Table 1.—Correlation coefficients between densities of conifer seedlings (plants <1.5 m tall) with selected site factors.

	Picea engelmannii	*Abies lasiocarpa*
Rock cover	-0.31	-0.09
Slope	-0.36*	-0.33
Litter depth	0.23	0.21
Herbaceous cover	-0.46**	-0.47**
Shrub cover	0.03	0.03
P. engelmannii canopy cover	0.62**	0.37
A. lasiocarpa canopy cover	0.18	0.59**
Total canopy cover	0.37	0.43**
P. engelmannii basal area	0.61**	0.50**
A. lasiocarpa basal area	0.34	0.73**
Total basal area	0.40*	0.50**

Sample size n=30
*Significant at P<0.05
**Significant at P<0.01

CONCLUSIONS

Although each site in the old growth spruce-fir forest on the Pinaleno Mountains has its own recovery pattern, we have shown what appears to be four general patterns. Our hypothesis is the forest is not composed of a highly heterogenous mix of forest patches, but that there is some spatial relationship among those patches with similar recovery patterns. There were not enough sites within the old growth spruce-fir forest area of our Pinaleno Mountain study area to test these relationships through ordination; however, through aggregating sites with similar recovery patterns (including younger recovery sites), we found that similar sites do occur in groups (fig. 3). This appears to indicate that areas of the mountain top with similar environmental conditions will give rise to similar disturbance recovery patterns. Disturbance history may also play a role, however, it appears as though much of the mountain top, with exception of recent disturbances, experienced extensive fires at about the same time period.

The spruce-fir forest, with its limited area on the Pinaleno Mountains, is composed of a few large patches within which the environmental conditions are causing similar responses of the two dominant forest species to produce predictable compositional changes following major disturbances. Using these recovery patterns, it might be possible to project future forest age class composition on sites where reforestation was initiated with transplants of young spruce trees, such as near the astronomical observatory site.

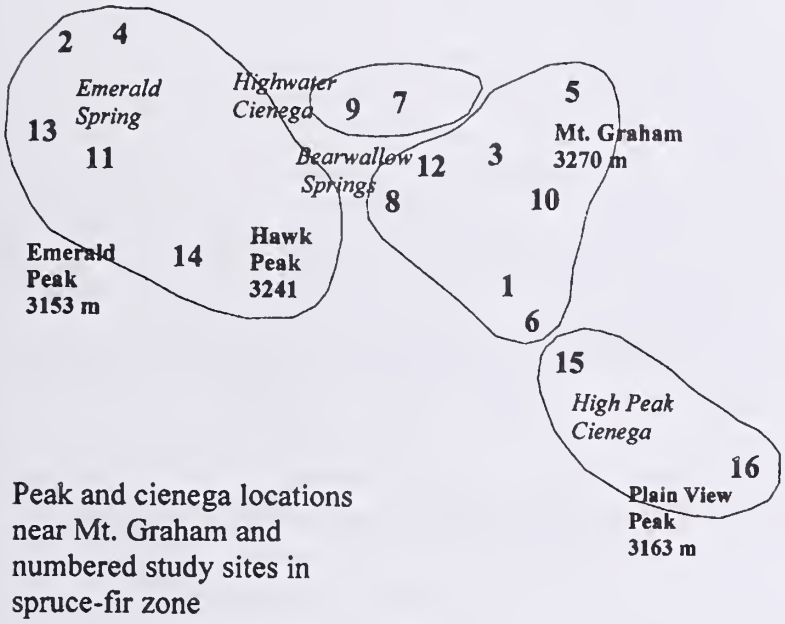

Figure 3.—Groupings of study sites with similar recovery patterns in the Mt. Graham area.

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Potential Effects of Climate Change on Lower Treelines in the Southwestern United States

Jake F. Weltzin and Guy R. McPherson[1]

Abstract.—Oak (*Quercus*) woodland and savanna biomes occupy several million hectares in the southwestern United States and northern Mexico. Despite their regional importance, our understanding of mechanisms that control their component vegetation populations is limited. Descriptive research to date has provided little predictive power to managers, and thus has had limited applicability to ecosystem management. Ongoing experimental investigations of constraints on seedling establishment suggest that vertebrate and invertebrate herbivory, interference from herbaceous plants, and climatic and edaphic conditions interact to produce low seedling establishment rates. These biotic and abiotic factors may be overwhelmed by predicted, directional changes in climate caused by anthropogenically-induced increases in atmospheric trace gas concentrations. For example, CO_2-induced increases in surface temperatures, and changes in amounts and seasonalities of precipitation may affect vegetation at the individual, population, or community level, with subsequent ramifications for ecosystem structure and function. As such, direct and indirect effects of increased CO_2 concentrations (e.g. CO_2 fertilization, changes in fire frequency and extent) may replace grazing and fire suppression as important regulators of plant community change in these biomes. We argue that knowledge gained from appropriately designed experimental research should enable managers to predict effects of management activities on oak woodlands and savannas, within the context of changing regional and global climatic conditions.

INTRODUCTION

Oak (*Quercus*) woodland and savanna biomes in the southwestern United States and northern Mexico occupy several million hectares of arid and semi-arid wildlands. Oak woodlands in Arizona have been utilized by settlers, miners, explorers and pastoralists for over a century. Oak trees provided mine timbers and smelter fuelwood between 1890-1910 (Bahre and Hutchinson 1985). Woodlands and savannas were heavily grazed by livestock in the 1880s, and grazing continues today, though at much lower stocking rates. Fire suppression and grazing-induced removal of fine fuels have altered historical fire frequencies.

Despite their areal extent, and economic, ecologic, and historic importance, we know little about the dynamics and processes of their component vegetation populations and communities. Although scientific knowledge about these areas is increasing, research to date has been largely descriptive (e.g. Brown 1982). One area of relatively recent scientific interest has focused on changes in plant community distributions.

Woody plant abundance has increased substantially during the last 50 to 300 years in many of the world's grasslands (e.g. Buffington and Herbel 1965, Archer et al. 1988, Walker et al. 1989). Although encroachment of woody plants into grasslands is widely recognized, the rates, patterns, and mechanisms of the process are not well quantified (Archer 1989), or are inconclusive. For example, increased woody plant abundance in

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North American grasslands has been attributed to climate change, reduced fire frequency, increased grazing by cattle, or combinations of these factors (as reviewed by Archer 1994).

Changes in vegetation physiognomy (e.g. from grassland to woodland) have broad implications for management and land use throughout the world. Life form changes in plant communities affect virtually all resources, including wildlife, water, livestock, fuelwood, and recreation. Proper management of these and other systems depends on the accurate prediction of ecosystem response to perturbation and management.

The purpose of this paper is to review the current state of knowledge regarding changes in the distribution and boundaries of Madraen oak woodlands in the southwestern United States. We will focus on shifts in lower treeline, and the biotic and abiotic factors that constrain vegetation establishment and distribution. Further, since anthropogenically-induced changes in climate are an ongoing and increasingly important control over vegetation distribution, we will examine the effect of climate change on vegetation, and subsequent effects on vegetation distribution. Finally, we discuss possible directions for future research.

PRESENT STATE OF KNOWLEDGE

Shifts in Lower Treeline

Recent ecological research in the southwestern United States has focused on shifts in the oak woodland/semi-desert grassland boundary (e.g. Hastings and Turner 1965, Bahre 1977, 1991, McPherson et al. 1993; figs. 1,2). Reports of historical changes in this ecotone are varied. Paleoecological data suggest that oak woodlands have shifted upslope in concert with warmer and drier conditions since the Pleistocene. This interpretation is consistent with upslope movement of most woody species in the last 40,000 years (Betancourt et al. 1990).

On a more contemporary temporal scale, Hastings and Turner (1965) examined matched, historical ground photographs from the southwestern United States, and concluded that the oak woodland/semi-desert grassland boundary moved upslope over the last century. They attributed oak mortality at this ecotone to an increasingly xeric climate. However, Hastings and Turner's interpretations were questioned by Cooke and Reeves (1976), whose analysis of precipitation patterns for the southwest indicated that precipitation had not varied significantly during the previous 100 years. Further, Hastings and Turner's latest photographs, taken soon after the severe regional drought of the 1950s, portrayed widespread top-kill among mature oak trees. This episodic event with relatively ephemeral effects may have colored their conclusions about ecotone shifts. Thus, their interpretation of treeline shifts was probably more suited to a scale of years rather than decades or centuries. In contrast with Hastings and Turner (1965), Bahre (1991) concluded that the distribution of oak woodlands has been stable since the 1860s, regardless of changes in livestock densities.

Traditional technologies for assessing changes in woody vegetation distribution include dendrochronology, historical accounts, and

Figure 1.—Oblique aerial photograph of Emory oak-dominated woodland/semi-desert grassland boundary.

Figure 2.—Emory-oak savanna at lower treeline.

repeat-photography. Dendrochronology is limited to woody species, usually trees, and is based on correlations between tree age and cross-sectional ring number. However, ages of trees that dominate woodlands and savannas at the tree/grass boundary in southeastern Arizona cannot be determined with current technology (McPherson 1992). First, since these species resprout after top removal, stem age does not necessarily represent individual plant age. Further, current dendrochronological techniques are not able to determine stem age. And finally, tree ages cannot be used to describe the vegetation history of sites currently unoccupied by trees.

Historical accounts of vegetation change are usually anecdotal and imprecise, and thus do not allow accurate determination of historic (let alone prehistoric) vegetation physiognomy or plant community composition. Repeat ground photography has a limited and oblique field of view, and historic photographs usually portray anthropogenic manipulation of landscapes, all of which limits their usefulness for determining changes in plant distribution. Repeat aerial photography is limited in that even the earliest photographs (ca. 1930) were obtained after broadscale vegetation change had already occurred.

Recently, quantitative chemical analysis has provided yet another interpretation of vegetation boundary shifts in southeastern Arizona. McPherson et al. (1993) used stable carbon isotope analysis to investigate the direction and magnitude of vegetation change along oak-dominated woodland/semi-desert grassland boundaries. Their investigation focused on the two dominant woody species, velvet mesquite (*Prosopis juliflora* (Swartz) DC.) and Emory oak (*Quercus emoryi* Torr.) at lower treeline ecotones in the southwestern United States and northwestern Mexico. Emory oak and velvet mesquite, like almost all woody plants, have the C_3 metabolic pathway of photosynthesis. The grassland below the lower woodland boundary, as characterized and described by Brown (1982), is dominated by perennial bunchgrass species, all of which have the C_4 metabolic pathway (Gurevitch 1986). These two metabolic pathways ultimately affect the stable carbon isotope ($^{13}C/^{12}C$) ratio of living plant tissue, which is retained and incorporated into soil organic material after plant mortality and decomposition.

McPherson et al.'s (1993) analysis of $\delta^{13}C$ values of soil organic matter and roots from the woodland/grassland boundary indicated that both velvet mesquite and Emory oak were recent components of former grasslands. Their results were consistent with other reports of recent increases in woody plant abundance in grasslands and savannas throughout the world (e.g. Archer et al. 1988, Steuter et al. 1990, Tieszen and Archer 1990). Further, their interpretation of vegetation change was of similar temporal and spatial magnitudes relative to downslope shifts in lower limits of *Coleogyne ramosissima* (Cole and Webb 1985) and *Pinus longaeva* (LaMarche 1973) in eastern California.

Results of a subsequent investigation of within-savanna vegetation dynamics support the conclusions of McPherson et al. (1993), and indicate that grasslands immediately below existing woodland boundaries have been stable for at least 1700 years (McPherson and McClaran in review). In addition, this most recent data suggests that within-savanna dynamics are complex and not necessarily directional (e.g. grassland shifting to woodland). For example, $\delta^{13}C$ values of soil organic matter indicate that within the savanna proper, trees have established on sites not previously occupied by trees, but that some sites dominated by grasses previously supported trees. Results indicate that there is redistribution of trees over time within these savannas, and suggests that periodic disturbances (Whittaker 1975, Gillon 1983, Trollope 1984, Frost and Robertson 1987, Medina 1987) and soil resource partitioning by trees and grasses (Walter 1954, Walker and Noy-Meir 1982) contribute to long-term persistence of savannas.

Constraints on Seedling Establishment

Ultimately, shifts in lower treeline reflect temporal integration of tree seedling establishment and persistence at the woodland/grassland boundary. Thus, assessments of treeline shifts are dependent upon an understanding of the mechanisms that limit or constrain seedling establishment at lower treeline.

In southern Arizona, oak seedling establishment occurs infrequently in grasslands below current lower treeline and in the grassland phase of low-elevation savannas (Weltzin and McPherson 1994; fig. 3). Factors that may be responsible for low recruitment include herbivory, interference from herbaceous plants, and climatic and edaphic constraints. These factors, and possibly others, probably interact to produce low seedling establishment rates. For clarity, their effects on oak seedling establishment will be discussed individually.

Invertebrate herbivory is a potentially important source of seedling mortality that is commonly overlooked in field studies. Although it is rarely mentioned in studies of semi-arid woody plant establishment (e.g., Neilson and Wullstein 1983, Borchert et al. 1989, Brown & Archer 1989, Davis et al. 1991, Williams et al. 1991, Allen-Diaz & Bartolome 1992, Callaway 1992, Hall et al. 1992; but see Adams et al. 1992), invertebrate herbivory is the most common source of mortality in the low-elevation oaks of southern Arizona (McPherson 1993, Peck and McPherson 1994). In Arizona, invertebrates defoliate seedlings primarily during the summer (Peck and McPherson 1994, Eggleston and McPherson unpubl. data). Similarly, mesh exclosures over seedlings during the summer increased survival of *Quercus douglasii* and *Q. lobata* in California (Adams et al. 1992), but effects of exclosures on invertebrate herbivory and water stress could not be separated; evidence from another experiment indicates that shade is critical for establishment of at least the former species (Callaway 1992). Vertebrates kill *Q. emoryi* seedlings primarily during autumn and winter months (Eggleston and McPherson unpubl. data). Temporal and spatial variability in herbivory (McPherson 1993, Peck and McPherson 1994, Eggleston and McPherson unpubl. data), combined with differential population dynamics of different animal species, doubtless contribute to the variability of invertebrates and vertebrates as sources of mortality.

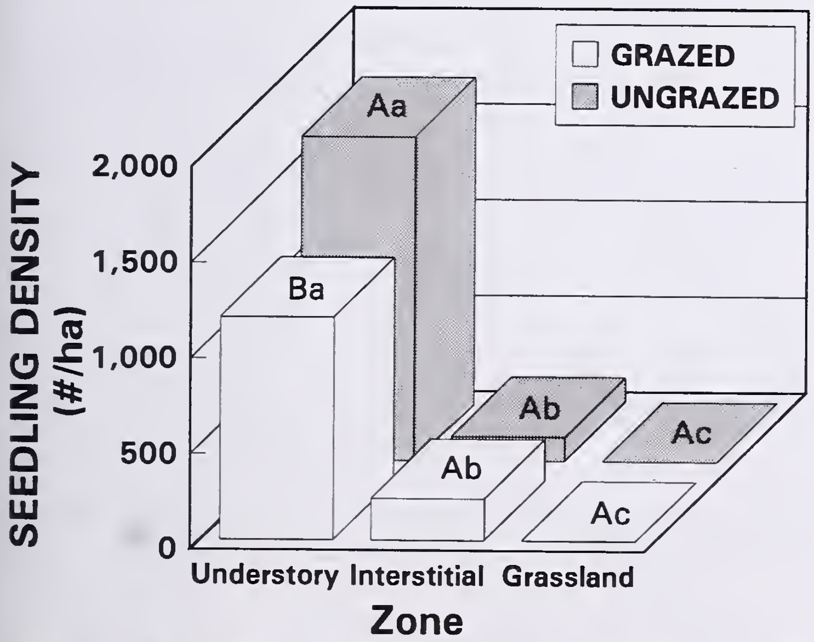

Figure 3.—Mean Emory oak (*Quercus emoryi*) seedling densities (#/ha) under mature Emory oak trees, in grass-dominated interstitial zones between trees, and in semi-desert grassland below lower treeline, for three grazed and three ungrazed sites in the Huachuca mountains of southeastern Arizona (from Weltzin and McPherson 1994). Means within grazing treatment with the same lower-case letter and means within zone with the same upper-case letter were not different (P 0.05).

Interference from herbaceous plants also constrains oak establishment. Aboveground interference from herbs slightly reduced seedling survival, but had no effect on growth (McPherson 1993). More importantly, removal of all interference (above- and belowground) substantially increased survival and growth of Emory oak seedlings. Belowground interference impedes survival and growth of oak seedlings in southern Arizona, underscoring the importance of accessing soil resources. Emory oak, like many semi-arid woody species, allocates significant resources belowground in the seedling stage. Rapid early root growth (exceeding 90 cm/year for some individuals; unpubl. data) allows oak seedlings to access soil moisture largely unavailable to herbs (Richards 1986) within a year after germination.

The combination of herbivory and interference from herbs constrains oak seedling survival in the field, and may account for infrequent recruitment beyond the seedling stage in these (e.g., Ffolliott et al. 1992, Borelli et al. 1994) and other (e.g., Griffin 1971, McClaran & Bartolome 1989, Davis et al. 1991) oak woodlands. Other factors (especially climatic and edaphic) have been the subject of considerable speculation, but no experimentation. Thus, interpretation of the relative importance of the latter factors should be conducted with considerable caution.

Drought is one of the principal factors limiting seedling establishment (Osmond et al. 1987) and forest productivity on a world-wide basis (Schulze et al. 1987). Moisture-controlled differences in recruitment and establishment form an important control on vegetation physiognomy and pattern (e.g. Cornelius et al. 1991, Bowman and Panton 1993, Neilson and Wullstein 1983). For example, the distribution and extent of some oak-dominated woodlands and savannas is thought to be controlled primarily by gradients in soil available moisture (e.g. Griffin 1977, Pigott and Pigott 1993).

Precipitation and temperature are often considered the climatic factors that most constrain woody plant establishment in grasslands and savannas. McPherson (1993) concluded that during most years in southern Arizona, oak germination and early survival are not constrained by low soil moisture. Subsequent research suggests that variability between sites contributes substantially to differential emergence and early survival (Eggleston and McPherson unpubl. data, Weltzin and

McPherson unpubl. data). These data hint at the importance of meso-climatic, edaphic and geomorphic factors (and their interactions) in the constraint of woody plant establishment.

The fact that the oak woodland/semi-desert grassland boundary occurs at a wide variety of elevational limits within Arizona (1,200-1,800 m; Brown 1982), coupled with the ability of oak seedlings to establish at locations below the current treeline during some years (McPherson et al. 1993, McPherson 1993, Peck and McPherson 1994, Weltzin and McPherson unpubl. data) suggests that temperature alone does not constrain seedling establishment. However, the influence of temperature on soil water balance is probably critical to seedling establishment. Again, interactions between various factors are doubtless more important than single effects.

It has been suggested that soil argillic horizons constrain establishment of woody plants. McAuliffe (1994) hypothesized that water-impermeable argillic horizons (1) reduce water availability to woody plants in summer below thresholds necessary for survival, or (2) result in perched water tables in the winter, which may contribute to woody plant mortality. Although these hypotheses are intuitively palatable, and are often cited, they have not been tested.

It should be noted that high rates of woody plant recruitment occur in some systems even when invertebrates are not excluded and herb interference is high. McPherson et al. (1993) demonstrated that Emory oak trees have recently encroached into former grasslands in southern Arizona. Their study investigated the net outcome of various mortality factors interacting on a site (i.e., it was not designed to partition out the relative contributions of various factors), and clearly demonstrated that Emory oak, like many other woody plants throughout the world, has overcome the many constraints on establishment at some time during the past. In fact, preliminary results of a large-scale manipulative experiment in southern Arizona indicate that Emory oak is capable of establishing in the presence of herbaceous vegetation and invertebrates under existing climatic conditions (Eggleston and McPherson unpubl. data).

EFFECTS OF CLIMATE CHANGE

Directional climatic change is often cited as an important factor affecting recent and future redistribution of vegetation types (e.g. Hastings and Turner 1965, Neilson 1986, Mayeux et al. 1991). For example, the world's grasslands may become increasingly susceptible to succession toward woodland as a consequence of anticipated global climate change (Emanuel et al. 1985). Conversely, vegetation communities may shift upslope, with grasslands expanding into woodlands (e.g. Bolin et al. 1986). Results of empirical studies that indicate North American savannas and grasslands have recently converted to woodland (e.g. Archer et al. 1988, Steuter et al. 1990, McPherson et al. 1993) are contrary to those expected from changes in global climate alone: global warming and drying since the Pleistocene has generally caused woody plant species to shift upslope (Betancourt et al. 1990). Further, Neilson and Wullstein (1983) argue that an actual cause-effect relationship between climatic change and biogeographic dynamics has rarely been demonstrated. However, changes in climate, whether similar to or different than those predicted by general circulation models, are almost certain to occur on either local, regional, or global scales (Houghton et al. 1990, 1992).

Climate change will likely affect competitive interactions between species coexisting under current equilibrium conditions (Ehleringer et al. 1991); changes in interactions between plant species may be manifested at the community level of ecosystem organization, and vegetation distribution may be affected on regional scales (e.g. Emanuel et al. 1985, Neilson et al. 1989, Melillo et al. 1993, Neilson 1993).

Although climate change has great potential to change the physiognomy of many southwestern landscapes over relatively short time scales (e.g. decades), research to date has focused on historic and geologic shifts in vegetation distribution (e.g. Betancourt et al. 1990, Van Devender and Spaulding 1979). The potential for future vegetation change in the southwestern United States has been largely ignored (with the exception of general circulation models that are too coarse-scaled to be useful for management decisions). Therefore, the following sections describe predicted climate changes, and possible subsequent effects on vegetation and vegetation distribution.

Global and Regional Climate Change

Since the beginning of the 19th century, fossil fuel consumption and agricultural conversion have increased atmospheric carbon dioxide concentrations ([CO_2]) ca. 27% (Neftel et al. 1985, Keeling et al. 1989) and are expected to cause [CO_2] to double by the mid- to late-21st century (Trabalka et al. 1985). Such increases in atmospheric [CO_2] will cause global- and regional-scale changes in environmental conditions (e.g. climate).

Increases in atmospheric [CO_2] are expected to produce an increase in mean global surface temperatures of between 1.5δC and 4.5δC, with a "best guess" of 2.5δC "in the light of current knowledge" (Mitchell et al. 1990, Houghton et al. 1992). CO_2-induced changes in the amount and distribution (or seasonality) of precipitation have also been predicted (Houghton et al. 1990, 1992). General circulation models for central North America predict precipitation increases of 0-15% in winter and decreases of 5-10% in summer. Perhaps more importantly, summer soil moistures may decrease by 15-20% (Mitchell et al. 1990). Although there is broad consensus that seasonal precipitation patterns will change, there is considerable uncertainty about the direction and magnitude of these changes, especially on a regional basis. For example, although Manabe and Wetherald (1986) predict a decrease in summer soil moisture, Schlesinger and Mitchell (1987) suggest that summer precipitation in desert regions may increase.

The potential temporal and spatial magnitude of anthropogenically-induced changes in climate is debated (e.g. Lindzen 1993). For example, there is considerable uncertainty in predictions at local or regional scales (Mitchell et al. 1990). Further, anthropogenically-induced changes in climate may not be directional. For example, changes in climate may result in increased frequency of extreme events (Wigley 1985, Katz and Brown 1992). Also, climate may become more serially correlated which will result in sequences of warm or cold (wet and dry) years and greater overall climate variability (Cohen and Pastor 1991). Almost any change in climate, however, is likely to affect vegetation at the plant, population, or community level, with subsequent ramifications for ecosystem structure and function.

Climate Change and Vegetation

Physiological effects of increasing [CO_2] on vegetation include increased net photosynthesis, reduced photorespiration, changes in dark respiration, and reduced stomatal conductance which decreases transpiration and increases water use efficiency (as reviewed by Patterson and Flint 1990, Rozema et al. 1993). Ambient temperature affects plants directly and indirectly at each stage in their life cycle (as reviewed in Long and Woodward 1988). Water (i.e. soil moisture) is usually the abiotic factor most limiting to vegetation, especially in arid and semi-arid regions. CO_2, temperature, and soil moisture effects on plant physiology are exhibited at the whole-plant level in terms of growth and resource acquisition. For example, elevated atmospheric [CO_2] enhances growth of tree seedlings, even under conditions of water and nutrient stress (Mooney et al. 1991), but heat stress may increase seedling mortality rates (Nobel 1984).

Responses to [CO_2], temperature and soil moisture vary among species, particularly between plants with C_3 and C_4 photosynthetic metabolisms (Bazzaz and Carlson 1984, Patterson and Flint 1990, Johnson et al. 1993). C_3 plants exposed to elevated [CO_2] exhibit greater increases in growth and photosynthesis than do C_4 plants grown under the same conditions (as reviewed by Bazzaz 1990 and Patterson and Flint 1990). Growth and photosynthesis of plant species with the C_4 metabolic pathway are limited by cool temperatures (Long 1983, Potvin and Strain 1985). When grown with elevated [CO_2], water use efficiency (WUE) of C_3 plants generally is affected more than WUE of C_4 plants (Sionit et al. 1981, Polley et al. 1992, Polley et al. 1993). When temperatures are consistent, physiological changes favor C_3 plants over their C_4 counterparts in multi-species competition experiments in controlled environments with elevated [CO_2] (Wray and Strain 1987, Bazzaz 1990, Patterson and Flint 1990).

Perhaps more important than individual effects of increasing atmospheric [CO_2] and increasing temperatures, however, is their interactive effect on photosynthetic productivity and ecosystem-level process (Long 1991). Unfortunately, the relatively few studies of interactive effects of temperature and CO_2 on vegetation (Bazzaz 1990, Farrar and Williams 1991) have conflicting, poorly understood results (Gifford 1990). For example, photosynthesis and growth of plants in elevated atmospheric [CO_2] may be stimulated by increases in temperature (Sionit et al. 1987, Allen et al. 1989, Grulke et al. 1990, Idso et al. 1987, Idso et al. 1993). Alternatively, temperature may have little or no effect on CO_2-enriched plant growth (Jones et al. 1985, Tissue and Oechel 1987). Nonetheless, *a posteriori* analysis of vegetation response to CO_2 as mediated by atmospheric temperatures suggests that relative effects of CO_2

increase with temperature (Drake and Leadly 1991, Idso et al. 1993), perhaps because of upward shifts in photosynthesis temperature optima with increasing CO_2 (Pearcy and Bjorkman 1983). For example, Mooney et al. (1991) predict that elevated CO_2 will amplify the effect of CO_2 enrichment on ecosystem productivity when daytime temperatures are above 30δC, as in the middle-latitude grasslands. Conversely, low temperatures may attenuate CO_2-induced growth enhancement (Hofstra and Hesketh 1975, Sage and Sharkey 1987, Idso et al. 1993). Thus, interactive effects of changing abiotic conditions may be of greater importance than main effects in terms of changes in plant response and subsequent changes in vegetation distribution.

Climate Change and Vegetation Distribution

Shifts in the relative competitive ability of plants that experience changes in [CO_2], surface temperatures, or soil moisture may result in changes in their spatial distribution (Curtis et al. 1989, Davis 1989, Bazzaz 1990, Long and Hutchin 1991, Neilson 1993, Neilson and Marks 1994). For example, it has been hypothesized that increases in [CO_2] may enhance growth and establishment of C_3 shrubs in C_4-dominated grasslands of the southwestern United States. (Mayeux et al. 1991, Idso 1992, Johnson et al. 1993, Polley et al. 1994). CO_2-induced increases in WUE or fine root biomass (e.g. Norby et al. 1986, Idso and Kimball 1992, Polley et al. 1994) of C_3 shrubs suggest they may be able to expand their distribution into ecosystems where water is otherwise a limiting factor (Long and Hutchin 1991, *sensu* Mellilo et al. 1993). This is supported by correlative evidence that higher WUE is positively correlated with growth and survival of plants in dry habitats (Ehleringer and Cooper 1988). A simple WUE model developed by Idso and Quinn (1983) suggested that a doubling of [CO_2] would cause oak woodlands dominated by Emory oak in the southwestern United States to shift downslope and displace extensive regions of semidesert grassland. However, their hypothesis has not been tested in this, or any other, system.

Conversely, global increases in temperature may enhance the competitive ability of C_4 plants (such as grasses) relative to C_3 plants (e.g. shrubs and trees), especially where soil moisture (Neilson 1993) or temperatures (Esser 1992) are currently limiting. This could result in regional, upslope shifts of semidesert grasslands at the expense of woodlands (*sensu* Long and Hutchin 1991).

Changes in quantity and seasonality of precipitation will also affect competitive interactions between species coexisting under current equilibrium conditions (Ehleringer et al. 1991). For example, increased summer precipitation is hypothesized to favor shallow-rooted grasses over more deeply rooted woody perennials (Eissenstat and Caldwell 1988, Ehleringer et al. 1991). Conversely, predicted increases in winter soil moisture (Manabe and Wetherald 1986, Mitchell and Warrilow 1987) may contribute to the expansion of C_3-dominated shrublands into C_4-dominated grasslands in the southwestern United States (*sensu* Neilson 1986, Melillo et al. 1993). It is hypothesized that the present distribution of vegetation in the southwest is highly dependent on precipitation (Van Devender and Spaulding 1979). Thus, minor changes in precipitation pattern in this region, especially at ecotones (Neilson 1993), may cause major shifts in plant distribution (*sensu* Stephenson 1990).

Already-observed increases in post-industrial atmospheric [CO_2] have greatly increased production of some plants (Baker et al. 1990, Allen et al. 1991, Polley et al. 1992), although this is debated (Archer 1994, Archer et al. 1994). Further, one explanation for recent increased C_3 woody plant abundance in C_4 grasslands is based on changes in atmospheric [CO_2] over the last century (e.g. Mayeux et al. 1991, Idso 1992, Idso and Kimball 1992, Johnson et al. 1993). Invasion of woody plants (with the C_3 photosynthetic pathway) into C_4 grasslands has been accompanied by a 30% increase in atmospheric [CO_2] over the past 200 years. Increases in atmospheric [CO_2] are said to have conferred a significant advantage to C_3 species relative to C_4 species in terms of physiological activity, growth rates, and competitive ability.

In contrast, Archer et al. (1994) argue that changes in [CO_2] alone are not the proximate cause for observed shifts in woody plant distribution, because (among other arguments) 1) substantial increases in woody plant abundance in grasslands occurred before [CO_2] rose more than ca. 11% over levels of the 1700s; 2) widespread replacement of C_3 grasses by C_3 shrubs has occurred in temperate zones and cold deserts; and 3) C_4 species have quantum yields, photosynthetic rates, and water use efficiencies that are still greater than C_3 species, even under current atmospheric [CO_2]--thus, there is no historic ecophysiological basis for a change in competitive interactions that favored C_3 over C_4 plants.

Elsewhere, Archer (1994) has argued that direct and indirect effects of grazing by domestic livestock are the proximate cause of woody plant encroachment into arid and semi-arid ecosystems throughout the world. However, Archer et al. (1994) do suggest that interactive effects of post-industrial atmospheric CO_2 enrichment and domestic livestock grazing may have facilitated observed increases in woody vegetation abundance.

In concord with these arguments, we suggest that increased atmospheric [CO_2] has not contributed significantly to historic shifts in lower treelines in the southwestern United States, especially relative to the effects of livestock grazing and fire suppression (Bahre and Shelton 1993, Archer et al. 1994). However, it is unlikely that pre-settlement fire or livestock grazing regimes will be restored in the foreseeable future. Even if changes in fire regimes and livestock grazing were instituted, former grasslands now dominated by woody plants are relatively stable in the absence of major cultural inputs, which are not feasible (Archer 1989, Westoby et al. 1989, Archer and Smeins 1991). Thus, whereas past increases in [CO_2] may have had little or no impact on vegetation interactions, continued increases in [CO_2] may contribute to increased abundance of woody plants in southwestern grasslands, particularly if these increases are accompanied by shifts in seasonal precipitation or other climatic factors. Thus, we argue that rising atmospheric [CO_2] has the potential to replace grazing and fire suppression as an important regulator of plant community change.

In summary, predicted changes in climate that may occur in the southwestern United States include increased atmospheric concentrations of CO_2, increased surface temperatures, changes in the amount, seasonality, and distribution of precipitation, more frequent climatic extremes, and a greater variability in climate patterns. Increases in atmospheric [CO_2] and possible increases in winter precipitation should favor woody plant establishment and growth at the expense of grasses, and may cause woodland boundaries to shift downslope. Alternatively, increases in temperature and possible increases in summer precipitation would favor C_4 grasslands at the expense of C_3 woodlands. However, increases in monsoonal (July through September) precipitation may favor germination and establishment of plant species that reproduce coincident with the monsoon (e.g. Emory oak).

Climate-Induced Changes in Fire Frequency and Extent

Prior to settlement, fire frequencies in semi-desert grasslands were on the order of 10-20 years (Wright and Bailey 1982). Over the last 130 years, however, fire regimes have changed considerably, due to changes in biological, political, and managerial factors and activities. Inadequate fine fuel is the most common constraint on fire spread in semi-desert grasslands--ignition sources are plentiful, and an extended drying period occurs virtually every year (McPherson in press).

Within the last 150 years, cattle grazing has reduced biomass enough to limit fire spread during most years. However, the number of cattle grazing southwestern ranges has declined in the last few decades (Allen 1992), and this trend is expected to continue for the foreseeable future (McClaran et al. 1992). Exotic species such as Boer lovegrass (*Eragrostis chloromelas*), buffelgrass (*Pennisetum ciliare*), and Lehmann lovegrass (*Eragrostis lehmanniana*) produce more fine fuel than native species (Cable 1971, Cox et al. 1984), which suggests that the recent (and continuing) spread of these species (e.g. Cox and Ruyle 1986, Cox et al. 1988, Anable et al. 1992) may contribute to increased fire frequency and spread. At least one of these species (Lehmann lovegrass, the most common introduced species) increases after fire (Ruyle et al. 1988, Sumrall et al. 1991), suggesting that a positive feedback pattern may develop (Anable et al. 1992). Therefore, decreased cattle stocking rates coupled with the introduction of exotic grasses could result in more frequent, widespread fires than those that occurred over the last century. Alternatively, the fragmented nature of semi-desert grasslands and more efficient and effective fire suppression activities may constrain the frequency and extent of contemporary and future fires relative to those that occurred a century ago.

Anthropogenically-induced changes in climate are also likely to affect fire frequency and extent. Previously reviewed changes in community structure caused by changes in atmospheric composition or climate may have substantial effects on fire regimes (*sensu* Clark 1990). A shift from grassland to woodland will reduce herbaceous biomass (Haworth and McPherson 1994), and subsequently reduce fire frequency because of decreased accumulation of fine fuel. Conversely, increased surface temperatures may either increase fire frequency (because hotter, drier conditions cure fuel more quickly), or decrease fire frequency (because of decreased fine fuel production caused by hotter, drier conditions). Increases in summer precipitation may increase fine fuel loading and thus increase fire frequency. Obviously, the effects of climate change on fire frequency are difficult to predict, in part because of the paucity of knowledge about future climate change, and also because of interactive effects of climate change, biological factors, and activities related to management and politics.

FUTURE RESEARCH POSSIBILITIES

Considerable research has investigated vegetation change in the southwestern United States. This research has generated many hypotheses (i.e. candidate explanations) regarding shifts in woodland/grassland boundaries, but few of these hypotheses have actually been tested. For example, soil types and characteristics associated with different geomorphic surfaces probably form an important constraint on vegetation distribution in the semi-arid southwest (e.g. McAuliffe 1994), but have yet to be investigated within the Madraen and higher elevation vegetation communities. Fundamental information about soil nutrient availability and spatial and temporal distribution, and processes affecting these phenomena, are generally lacking.

Resource partitioning is another hypothesis widely-invoked to explain apparent long-term stability of savannas and woodlands (e.g. Walter 1954, 1979, Knoop and Walker 1985, Sala et al. 1989, Brown and Archer 1990, Bush and Van Auken 1991). Seasonal patterns in precipitation distribution are thought to allow stable coexistence of woody plants and grasses: woody plants use moisture that percolates through surface layers when grasses are dormant, and grasses take advantage of growing-season precipitation (Neilson 1986, Archer 1989, Lauenroth et al. 1993). Although this hypothesis is intuitively palatable, it has yet to be explicitly tested. If resource partitioning does occur, then shifts in precipitation seasonality caused by atmospheric CO_2 enrichment may affect resource pools (i.e. soil moisture). Changes in soil moisture may in turn affect interactions between trees and grasses where they currently coexist, or may allow one or the other to establish where currently excluded by environmental constraints.

In addition, although research to date (Eggleston, unpubl. data) suggests that vertebrates and invertebrates are both seasonally important constraints on oak seedling survival, the spatial extent and importance of these mortality vectors has not been determined, let alone the particular species responsible for observed mortality.

The greatest gap in our knowledge about the Madraen oak woodland biome is the potential effects that global and regional climate change may have on vegetation interactions and community- and ecosystem-level processes. Currently, prediction of future changes in distribution and composition of oak woodlands is difficult, given the background of recurrent disturbances and the possible complexity and general paucity of knowledge about regionally-specific climate change (Mitchell et al. 1990). However, the determination of most-likely scenarios of climate change is relatively straightforward, and these may be tested using experimental research designs.

The use of field experiments in ecology is increasing, and Gurevitch and Collins (1994) make a compelling case for continuing this experimental approach. First, manipulative field-based experimental research will help disentangle important driving variables because of strong correlations between factors under investigation (Gurevitch and Collins 1994). Second, identification of underlying mechanisms of vegetation change will enable us to predict vegetation response to changes in driving variables (e.g. climate or land use) with a level of certainty useful to management. Most research conducted in southwestern ecosystems to date has lacked a rigorous experimental approach, which has limited its utility to managers. We join Gurevitch and Collins (1994) in calling for the implementation of appropriately designed experiments that contribute to the proper management of these ecosystems.

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Factors Affecting the Distribution, Pollination Ecology, and Evolution of *Agave chrysantha* Peebles and *A. palmeri* Engelm. (Agavaceae)

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Abstract.—Taxonomy, biogeography and pollination ecology of two closely related taxa of the Madrean Archipelago, *Agave chrysantha* Peebles and *A. palmeri Engelm.* are reviewed. Several questions remain regarding the reported obligate mutualism between *A. palmeri* and an endangered species of bat, *Leptonycteris curasorae*, and the role bats and other animals may play in the pollination of *A. chrysantha.* Preliminary evidence suggests that diurnal visitors play an important role in pollination of *A. chrysantha* and *A. palmeri*, and bats appear to have a more faculative role in pollination than previously thought. The seasonal, variable and migratory nature of *Leptonycteris* seems unlikely to support a tight mutualistic relationship with agaves. Plasticity in pollinator species may be most adaptive in agaves with large geographic ranges (*A. palmeri*) and variable habitats (*A. chrysantha*). "Bat-adapted" traits may be just as advantageous to insects and other animals in hot and arid climates where peak activity is near dawn and dusk.

INTRODUCTION

Agaves are perennial leaf succulents consisting of a basal rosette where water and carbohydrates are stored. Plants are monocarpic; they require 10-50 years to reach maturity, then initiate an inflorescence, flower and die. Although the genus *Agave* (Agavaceae) is an important vegetation component in the biotic communities of the Madrean Archipelago, reproductive, ecological and speciation processes are poorly understood. Taxonomic problems have long contributed to a large degree of confusion. During the early to mid-nineteenth century, agaves from the New World were imported to Europe as ornamental novelties. Early taxonomists in Europe attempting to name these cultivated species generally had no information regarding their origin, provided no preserved or type specimens, no illustrations, and used vegetative rather than reproductive characters to diagnose species. Leaf morphology was often grossly altered due to the unnatural conditions of cultivation in greenhouses of Europe, and as a result, most taxa described during this era are unrecognizable by their written descriptions alone (Gentry 1982). Although botanists became more familiar with the genus during the early 1900's, they rarely observed agaves in habitat and failed to realize the large degree of leaf variability that can exist both within and between populations. Floral characters were largely ignored, and the concentration on vegetative differences resulted in a large degree of taxonomic "splitting" at the species level (Gentry 1982). Other factors contributed to a poor understanding of agaves as well. Few botanists have collected specimens due to the presence of teeth, spines, caustic juices, and the difficulty in processing specimens. Consequently, few specimens of each taxon have been available for study, many of which were poorly prepared and lacked floral or other taxonomically significant characteristics. Numerous populations exist in rugged and inaccessible terrain which has resulted in limited distributional data. The long time span required by members of this genus to reach reproductive

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maturity makes *ex-situ* reproductive biology studies or rapid evaluation of offspring difficult (Gentry 1982). Thus, large gaps in knowledge exist with respect to ecology, reproductive biology, cytology and genetics.

Gentry's (1982) more recent and comprehensive monograph of *Agave* emphasized comparative morphology, particularly with regard to floral characters. Species comprehension was greatly enhanced by his understanding of morphological variability of populations and ecotypes, reproductive biology, introgression, hybridization and polyploidy. Both polyploidy and hybridization are common in *Agave* ($x = 30$), and appear to be important mechanisms in the evolution of the genus (Pinkava and Baker 1985). This trend towards reticulate evolution appears to be due to a lack of complete reproductive isolation between taxa recognized at the species level (Gentry 1967, Burgess 1979, 1985). The climatic fluctuations in the southwestern U.S. during the glacial-interglacial cycle of the Pleistocene may have resulted in repeated periods of range expansion and genetic interchange between species, followed by periods of range contraction and isolation in small, disjunct populations (Burgess 1985). This repeated contact may have been sufficient to prevent development of reproductive barriers.

The genus *Agave* is generally thought to have evolved in the mesic habitats of central Mexico (Gomez Pompa 1963), however, many species have successfully radiated northward into the more arid environments of northern Mexico and the southwestern United States. The Group Ditepalae within the genus *Agave* is composed of 13 taxa primarily centered in the Sierra Madre Occidental of Mexico, but two closely related members of this group, *A. chrysantha* Peebles and *A. palmeri* Engelm., extend into central and southern Arizona respectively, representing the northernmost distribution of the group. *Agave palmeri* occupies grama grasslands and oak woodlands of northern Mexico and southern portions of Arizona and New Mexico, whereas *Agave chrysantha* is found in desertscrub, chaparral, juniper woodland and the fringes of pine-oak woodland communities of central and southern Arizona. Both species may be found on granitic, volcanic and limestone mountain slopes. *Agave chrysantha* appears to be the nearest relative of *A. palmeri* based on floral and other morphological characteristics, and differs from *A. palmeri* by 1) its smaller flower size, 2) shallower tube, 3) clear yellow perianth (versus the pale greenish-yellow flowers with red to brownish tepal apices of *A. palmeri*), 4) more congested umbels, 5) shorter panicles, 6) broader and shorter lanceolate leaves with large teeth, and 7) undulate to repand leaf margins (Gentry 1982). *Agave chrysantha* has been recognized as a subspecies of *A. palmeri* (Little 1943) and as a distinct species (Gentry 1982). Gentry (1982) has suggested that *A. chrysantha* may be a geologically young species which has not yet reached a stabilized or isolated condition, possibly originating "through introgression with *A. palmeri* and *A. parryi*." Alternatively, *A. chrysantha* may represent the northern end of a cline of *A. palmeri* that has developed by primary or secondary intergradation with *A. palmeri*.

The pollination ecology of the Ditepalae is of interest as several recent studies have suggested that bats of the genus *Leptonycteris* are obligate pollinators of *A. palmeri* (Howell 1979, Schaffer and Schaffer 1979, Howell and Roth 1981). Howell and Roth (1981) proposed that reported declines in *Leptonycteris* populations could potentially severely impact sexual reproduction in paniculate agaves. This hypothesis was based on a decline in seed set of herbarium specimens over a 30 year period and low fruit and seed set (approximately 25% and 20% respectively) in *A. palmeri* populations where bats were absent. Fruit and seed set were high (81% and 70%) where bats were present. No data were presented documenting visitor or visitation rates. Sutherland (1982, 1987) has documented that mean fruit set for paniculate agaves is generally low (20-25%), however, fruit and seed set may be highly variable between branches. The high fruit set reported by Howell and Roth in bat-pollinated populations may be a result of inadequate sample size, while the "low" results may be more representative of normal fruit set. Cockrum and Petryszyn (1991) have questioned reported declines in *Leptonycteris* numbers based on the fact that few observers have understood the variability and seasonality of *Leptonycteris* movement in the northern part of its range (resulting in reports of absent, declining and low population numbers). Herbarium specimens cited by Howell and Roth were reviewed by Cockrum and Petryszyn who obtained different estimates of fruit and seed set. They also noted that specimens cited by Howell and Roth were from localities which were either near the edge or beyond the known range of *Leptonycteris*.

Gentry (1982) postulated that other members of the Ditepalae may have mutualistic associations with nectar-feeding bats due to their similar flower structure. He proposed that a "wave of nectar flow" exists from spring to winter, providing food for bats as they migrate south. Starting in the south with the March bloom of *A. colorata* in Sonora, this "nectar flow" moves north to Arizona for the summer with the flowering of *A. palmeri,* then extends south through the Sierra Madre Occidental via *A. shrevei* in southern Sonora, to *A. durangensis* in Chihuahua, and finally to *A. wocomahi* in Durango and Zacatecas which bloom into December. Arita (1991) has shown that the ranges of *L. curasoae* and *L. nivalis* significantly coincide with those of *A. angustifolia, A. salmiana,* and *A. tequilana,* although this relationship may be due to the fact that both bats and agaves occur in arid areas.

The distribution of the majority of Ditepalae members also coincides with the range of *Leptonycteris,* although *A. palmeri* is the only member with documented *Leptonycteris* pollination (Howell 1972, Howell and Roth 1981). Southern populations of *A. chrysantha* are potentially within the range of *Leptonycteris,* however, Baker and Cockrum (1966) have suggested that *Leptonycteris* probably never extended very far north of the Santa Catalina Mountains. Schaffer and Schaffer (1977) noted that a population of *A. palmeri* (? *A. chrysantha*) with bright yellow flowers on the north side of the Santa Catalina Mountains probably depended on large bees for pollination. Anther dehiscence and peak nectar production in *A. chrysantha* occurs at night, and flowers have a "ripening fruit" odor, all of which may attract bats or moths. However, flowers are yellow in color and have pollen and nectar available during the day to attract diurnal pollinators. Howell (1979) has suggested that bat-pollinated agaves are derived from insect-pollinated species, and that *A. chrysantha* is an intermediate form between primitive insect-pollinated and advanced bat-pollinated species. On the other hand, insect pollination may be secondarily derived in *A. chrysantha* from bat-pollinated Ditepalae (i.e., *A. palmeri*). Sutherland (1987) noted that *A. mckelveyana,* another paniculate form of *Agave,* also has nocturnal anther dehiscence and nectar production, but is primarily pollinated by insects. He postulated that agave floral characters are conservative and retain bat-adapted traits despite predominate pollination by insects.

Nectar production, nectar sugar concentration and pollen protein analysis may also provide important clues to pollinator importance. Nectar production in bat-pollinated species such as *A. palmeri* is nocturnal with peak production from 2000-2200 hours (Howell 1979). Pollen protein content of bat-pollinated agaves tends to be high (44% in *A. palmeri*) while nectar sugar concentration is relatively low (11-20%) (Howell 1972). Bee-pollinated species generally exhibit the opposite trend. Pollen protein content is generally low (8-16%) (Howell 1972), although nectar sugar concentrations are more variable (18-68%) (Schaffer and Schaffer 1977). Nectar production amount and pattern, nectar sugar concentration and pollen protein percentage are unknown in *A. chrysantha.*

Factors other than pollinators may be important with regard to fruit set and reproductive fitness in agaves. Sutherland (1982) found no significant difference in percent fruit set per inflorescence in *A. chrysantha* when pollinated naturally, pollinated naturally plus hand pollinated, or hand pollinated alone, suggesting that fruit set in agaves is not pollen or pollinator limited, but rather resource limited. Udovic (1981) obtained similar results in a study evaluating the effect of pollinators on fruit production in the semelparous species *Yucca whipplei* (Agavaceae). However, in a comprehensive study of fruit set in eight species of yucca, Addicott (1985) found that pollinator limitation was the factor that most often controlled fruit set. Genetic load may be a more important general factor in reproductive success than both pollen and resource limitation. Weins (1984) and Weins et al. (1987) have shown that preemergent reproductive success in outcrossing species is not linked to resource or pollen availablity, but rather to genetic load (any lethal mutation or allelic combination) as a result of meiotic recombination. In a recent review considering the roles of pollen limitation, resource limitation and genetic load in fruit and seed set, Burd (1994) found significant pollen limitation occurred in the majority of species evaluated, and this pollen limitation generally varied among times, sites or years. This suggests the pollination environment can be quite stochastic, resulting in frequent pollination limitation and limited female success at the level of individual flowers, entire plants or populations.

The purpose of this study was to investigate the pollination ecology of *A. chrysantha* and *A. palmeri,* and to determine the importance of various diurnal and nocturnal pollinators with regard to fruit and seed set.

METHODOLOGY

Study Sites

Research took place at four study sites in central and southern Arizona. *Agave chrysantha* study sites were located at the northern edge of its distribution in the Sierra Ancha Mountains above Parker Creek (Parker Mesa Site, Gila County, T5N R13E Sec. 24, elevation 1400 m) and near the southern edge of its range in the Santa Catalina Mountains above Peppersauce Canyon (Peppersauce Site, T10N R16E Sec. 21, elevation, 1450 m). Study sites for *A. palmeri* were located in the foothills of the Santa Rita Mountains (Santa Rita Site, Pima County, T19S R16E Sec. 10, elevation 1520 m) and the foothills of the Mustang Mountains (Mustang Site, Santa Cruz County, 31°43′13.6″ N latitude, 110°30′52" W longitude, elevation 1500 m). Research was conducted at the Parker Mesa Site during July 1993 and at the Santa Rita Site during August 1933. Studies were conducted at the Peppersauce and Mustang Sites during July and August 1994 respectively.

Flower and Pollinator Observations

Twenty flowers were chosen and labeled prior to dehiscensce. Time of pollen dehiscence, length of exerted style and condition of filaments, tepals and stigma were noted each day until stigmas wilted.

Observations of pollinators were conducted over 3-4 days at all study sites, except the Santa Rita site where pollinators were only observed one day due to stormy weather. Pollinators were determined by field observations of floral visitors who appeared to transfer pollen to receptive stigmas. Night vision goggles were used for nocturnal studies. Birds and bats were surveyed separately from insects with the observer situated approximately 10 m away from the inflorescence. Visitation rates of birds were measured by recording the number of visits to open flowers on an inflorescence for one hour shortly after dawn, during mid-day and approximately one hour prior to dusk. Bat visitation rates were determined by scanning a clumped group of agaves for approximately one hour after dusk, near midnight, and before dawn. Visitation rates of insects (primarily bees and moths) were determined by scan sample: the number of insects active on an umbel were counted for ten minutes every two hours during the day (approximately 0500-1900 hours) for diurnal visitors and three times during the night (approximately 2100, 2400 and 0430 hours) for nocturnal visitors. Insects were observed from a ladder approximately 1.5 m from the study umbel. Predominate flower stage(s) (predehiscent, dehiscent, post-dehiscent and pistillate) of each observed umbel was recorded. Identity of visitor, visitation behavior and environmental conditions were also noted. Insects were captured and mounted for later identification.

Pollen and Nectar Studies

Predehiscent flowers were observed during the night to determine time of dehiscence. Nectar production was measured on three replicates each of 20 predehiscent, dehiscent, postdehiscent and pistillate flowers every three hours from 2100 to 0600 (no nectar is produced during the day) with a tuberculin syringe and needle. Experimental flowers were located on umbels positioned in the middle section of the inflorescence and exclosed from pollinators with a fine nylon netting (Howell 1979). Standing nectar crop was measured at dusk and dawn on two replicates each of 20 predehiscent, dehiscent, postdehiscent and pistillate flowers. Nectar sugar concentration of standing nectar crop flowers was measured at dawn in the field with a hand-held refractometer.

Pollination Studies

Plants with inflorescences that were centrally located within a population were chosen at each site for pollination experiments. Test umbels were chosen from the middle section of inflorescences, and 15 plants each were randomly assigned to one of the following treatments: 1) control umbels available to both diurnal and nocturnal visitors, 2) umbels available to only diurnal visitors (umbels bagged at sunset and unbagged at sunrise), 3) umbels available to only nocturnal visitors (umbels bagged at sunrise and unbagged at sunset), and 4) umbels bagged, but liberally hand pollinated daily during stigma receptivity (3-4 days) with fresh pollen collected from different individuals within the population (Peppersauce and Mustang sites only). Umbels were covered with nylon net bags that excluded any animals greater than 1.5 mm in size. Umbels were bagged prior to stigma receptivity (generally after anther dehiscence), and bagging continued until all styles were wilted (4-5 days). Umbels of experimental and control plants from the Parker Mesa, Santa Rita and Peppersauce populations have been collected thus far, and percent fruit set was determined. Data were analyzed for each site by chi-square analysis.

RESULTS

Flower and Pollinator Observations

Agave flowers are protandrous, gradually changing from a male to female (pistillate) state over a 5-6 day period. On the first day of flowering (pre-dehiscent stage), the tepals open and the filaments and anthers are exerted. Flowers remain in this condition until the evening of Day 2 (dehiscent stage) when anthers dehisce. Time of dehiscence differs between taxa; anthers of *A. palmeri* open between 2000 and 2200, generally shortly after sunset, while *A. chrysantha* anthers dehisce later, between 2400 and 0200 of Day 3. Stigmas are tightly closed at dehiscence, although styles are beginning to elongate. *Agave chrysantha* styles are exerted 0-15 mm the morning of Day 3 (post-dehiscent stage), while styles in *A. palmeri* are exerted 15-35 mm above the tepals. The morning of Day 4 (early pistillate stage), the tripartite stigmas are usually closed, but are generally slightly moist and open by evening. Thus, flowers become receptive approximately 48 hours after dehiscence. Filaments are beginning to wilt at this time and styles are exerted 16-27 mm in *A. chrysantha* and 25-40 mm in *A. palmeri*. By the morning of Day 5 (pistillate stage) stigmas are open and sticky, and filaments are wilted by the end of the day. Styles are exerted from 21-30 mm and 25-48 mm in *A. chrysantha* and *A. palmeri,* respectively. Tepals have generally wilted by the morning of Day 6 (late pistillate stage), and stigmas may be widely parted and moist to dry and slightly wilted. Styles are completely wilted by Day 7.

Flower stage composition of umbels was noted to be different between *A. chrysantha* and *A. palmeri*. Flowers on *A. chrysantha* umbels tended to be predominately in only two stages throughout the flowering period of the umbel, although larger umbels might exhibit more flower stages. For example, an umbel might be composed mostly of buds and pre-dehiscent flowers, progressing the next day to pre-dehiscent and dehiscent stages, etc. However, *A. palmeri* umbels tended to have all flower stages present during the majority of time the umbel was blooming with a smaller numbers of flowers open in each stage.

Floral visitors included a diverse range of animals: honeybees (introduced), bumblebees, carpenter bees, hummingbirds, orioles, hawkmoths, butterflies, wasps, moths, and a variety of small solitary bees. Bats were not observed at any site despite over 15 total hours of periodic observations. Although visitors varied in composition and numbers between sites, honeybees *(Apis mellifera)* were the dominant visitors and consumers of pollen and nectar at all sites (Table 1). Bumblebees *(Bombus sonorus)* and carpenter bees *(Xylocopa californica arizonensis)* were generally the next most common visitors. Although present at the Peppersauce site, carpenter bees had low visitation rates as they tended to approach and then avoid the observed umbels, possibly bothered by the observer. Small moths and hawkmoths were the predominate nocturnal visitors, however, diurnal visitor frequency was greater than that of nocturnal visitors at all sites (Table 2). Peak visitation occurred at dawn and a smaller burst of activity took place prior to dusk. Both honeybees and bumblebees foraged most actively in the early morning, first actively gathering pollen, and once the majority of the day's crop was harvested, nectar was collected. Carpenter bee activity tended to peak later in the morning and continue through the afternoon. These results are similar to those obtained by Schaffer et al. (1979). Moths were most active shortly after dusk, however hawkmoths were active near dawn as well. Some evidence of aggression between foragers was observed. Hummingbirds seemed to be bothered by the presence of bumblebees at the Peppersauce site, and would pull away when bees approached. Carpenter bees were quite aggressive at the Mustang site, often chasing each other away from umbels. Hawkmoths and bumblebees were observed to knock one another off flowers during their interactions at dawn and dusk at the Santa Rita site.

Pollination was a very haphazard event, and only 36 potential pollination events were noted in over 30 hours of observation at all sites (bird and bat observation time excluded). The small size of the majority of visitors, allowed them to "rob" nectar by entering flowers above the tepals and avoiding the exerted, receptive stigmas. Honeybees were large exploiters of floral rewards who performed little pollination due to their small size and foraging habits. Honeybees tend to gather pollen from a single inflorescence (McGregor et al.

Table 1.—Between-site variation of major floral visitors of *A. chrysantha* and *A. palmeri* (visits/min/umbel).

A. chrysantha

Parker Mesa			Peppersauce		
Visitor	Visits/min	Total min observed	Visitor	Visits/min	Total min observed
Honeybee	0.34	480	Honeybee	1.38	690
Bumblebee	0.26	480	Moths	0.25	100
Hummingbird	0.13	360	Wasp	0.08	690
Moths	0.16	60	Carpenter bee	0.06	690
Hawkmoth	0.03	60	Bumblebee	0.04	690
Carpenter bee	0.02	480	Hummingbird	0.03	480
Scott's oriole	0.02	360	Housefly	0.02	690
Blk swallowtail	0.01	480	Sm blk bee	0.01	690
Bat	0.0	120	Hornet	0.01	690
			Bat	0.0	120

A. palmeri

Santa Rita			Mustang		
Visitor	Visits/min	Total min observed	Visitor	Visits/min	Total min observed
Honeybee	2.4	90	Honeybee	1.42	300
Bumblebee	0.92	90	Carpenter bee	0.52	300
Hawkmoth	0.05	10	Wasp	0.32	300
Moths	0.05	10	Sm blk bee	0.31	300
Sm bees	0.05	90	Hummingbird	0.12	240
Bat	0.0	120	Moths	0.18	90
			Small green bee	0.13	300
			Hawkmoth	0.10	90
			Sm bees	0.06	300
			Other wasps	0.03	300
			Brown wasp	0.02	300
			Blk wasp	0.01	300
			Bat	0.0	570

Table 2. —Between-site variation of diurnal and nocturnal visitors to *A. chrysantha* and *A. palmeri* (visits/min/umbel).

A. chrysantha

Parker Mesa			Peppersauce		
Visitor	Visits/min	Total min observed	Visitor	Visits/min	Total min observed
Diurnal	0.65	480	Diurnal	1.58	690
Nocturnal	0.20	60	Nocturnal	0.25	100
Birds	0.15	360	Birds	0.03	480
Bats	0.0	120	Bats	0.0	120

A. palmeri

Santa Rita			Mustang		
Visitor	Visits/min	Total min observed	Visitor	Visits/min	Total min observed
Diurnal	3.46	90	Diurnal	3.09	300
Nocturnal	1.00	60	Nocturnal	0.30	90
Birds	----	--	Birds	0.21	540
Bats	0.0	120	Bats	0.0	570

1959, Alcorn et al. 1961), so that if contact with receptive stigmas occurred, fertilization was not likely (agaves are primarily self-incompatible). Larger animals such as hummingbirds and hawkmoths were observed to hoover and avoid touching stigmas unless foraging in the middle of a moderate to large-sized umbel. Stigma contact generally occurred when insects landed awkwardly on umbels and touched stigmas, or while foraging on freshly dehiscent anthers with erect filaments, crawled over adjacent receptive stigmas. Bumblebees and carpenter bees were observed to most frequently come in contact with receptive stigmas (Table 3), their intermediate size making it more difficult for them to avoid exerted stigmas while foraging.

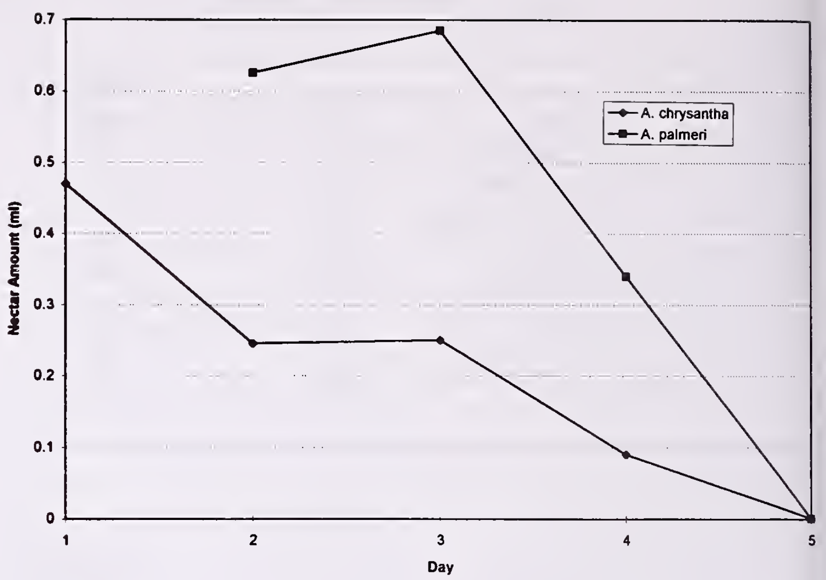

Figure 1.—Daily nectar production of *A. chrysantha* and *A. palmeri*.

Pollen and Nectar Studies

Mean daily nectar production of flowers is presented for *A. chrysantha* (Peppersauce site) and *A. palmeri* (Mustang site) in figure 1. Nectar production curves were similar, although nectar amounts were greater in *A. palmeri* due to the larger size of flowers. Nectar production was observed to decrease at a greater rate in *A. palmeri* after Day 3. As flowers moved from a male to female stage, nectar production decreased. Hourly nectar production differed somewhat between taxa (fig. 2). Nectar production in *A. chrysantha* began at dusk and nectar was produced at a fairly steady rate until 0300 when production slowly declined. *Agave palmeri* nectar production rose rapidly from dusk until 2400 when it peaked, then decreased steadily until dawn. This production curve was similar for all flower stages in both *A. chrysantha* and *A. palmeri* except for pistillate flowers (evening of Day 5-morning of Day 6) which produced a small amount of nectar from dusk until 2100 with negligible production afterwards.

Standing nectar crop production versus total hourly production and nectar sugar sugar concentration for Peppersauce and Mustang sites are presented in Table 4. Standing crop nectar

Table 3.—Observed stigma contact by floral visitors to *A. chrysantha* and *A. palmeri*.

			A. chrysantha		
	Parker Mesa			**Peppersauce**	
Visitor	**Stigma contacts**	**Total min observed**	**Visitor**	**Stigma contacts**	**Total min observed**
Blk Swallowtail	5	480	Bumblebee	3	690
Bumblebee	4	480	Honeybee	1	690
Carpenter bee	2	480	Housefly	1	690
Wasp	1	480			
			A. palmeri		
	Santa Rita			**Mustang**	
Visitor	**Stigma contacts**	**Total min observed**	**Visitor**	**Stigma contacts**	**Total min observed**
Hawkmoth	1	90	Carpenter bee	11	300
			Bumble bee	5	300
			Honeybee	2	300
			Sm bee	2	300
			Blk/white bee	1	300

amounts, although generally less than total daily production, were similar to total daily values. Thus, the majority of nectar produced was available for diurnal visitors at dawn. Variation in nectar production was greater in Days 4 and 5 as flowers aged and production decreased. Mean nectar sugar concentrations were similar in both taxa, and ranged from 13-21% in *A. chrysantha* and 13-25% in *A. palmeri.*

Visitation rate varied as a function of nectar production (Table 5). Umbels which were predominately pre-dehiscent/dehiscent and dehiscent/post-dehiscent had the highest visitation rates while pistillate umbels had low visitation rates.

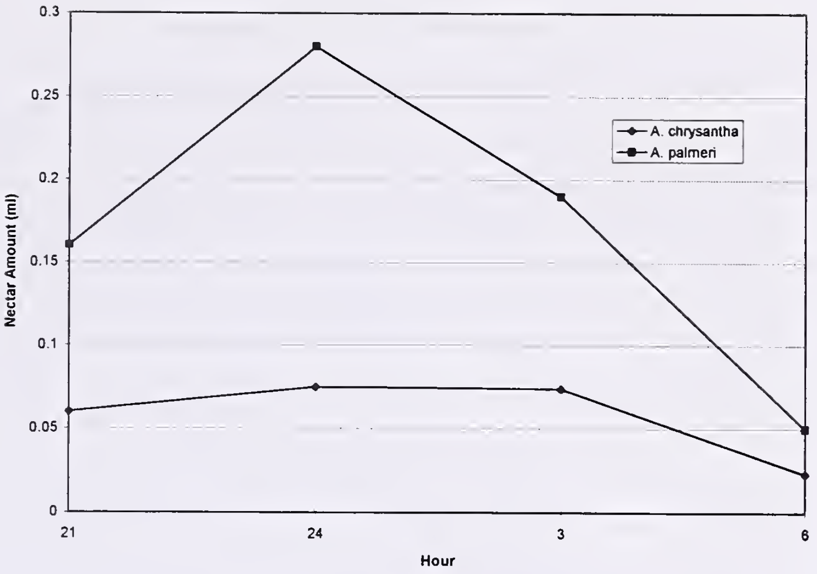

Figure 2.—Hourly nectar production of dehiscent to post dehiscent flowers in *A. chrysantha* and *A. palmeri.*

Table 4.—Standing nectar crop (ml), nectar sugar percentage and total daily nectar (ml) production of *A. chrysantha* (Peppersauce site) and *A. palmeri* (Mustang site). Data are mean values, numbers in parentheses are SE)

A. chrysantha

	Standing Crop			Nectar Sugar %	Total Daily Nectar
	Dusk	Dawn	Total		
Day 1	0.093	0.254	0.35	17.6	0.47
	(0.05)	(0.07)	(0.09)	(1.77)	(0.11)
Day 2	0.104	0.184	0.228	——	0.247
	(0.049)	(0.081)	(0.112)		(0.124)
Day 3	0.003	0.187	0.191	15.5	0.256
	(0.007)	(0.065)	(0.064)	(1.77)	(0.124)
Day 4	0.0	0.007	0.007	14.0	0.087
	——	(0.022)	(0.002)	(N = 1)	(0.088)
Day 5	0.0	0.0	0.0	——	0.001
					(0.002)

A. palmeri

	Standing Crop			Nectar Sugar %	Total Daily Nectar
	Dusk	Dawn	Total		
Day 1	——	——	——	——	——
Day 2	0.141	0.390	0.532	17.0	0.623
	(0.081)	(0.121)	(0.123)	(4.1)	(0.231)
Day 3	0.061	0.471	0.532	19.22	0.677
	(0.034)	(0.146)	(0.163)	(3.04)	(0.114)
Day 4	0.083	0.282	0.366	15.87	0.341
	(0.040)	(0.177)	(0.191)	(3.16)	(0.181)
Day 5	0.008	0.005	0.013	14.50	0.002
	(0.011)	(0.016)	(0.020)	(N = 3)	(0.007)

Pollination Studies

In preliminary studies at the Parker Mesa site, fruit set of *A. chrysantha* umbels exposed to only nocturnal pollinators was significantly lower (17.2%) than diurnally pollinated umbels (22.8%) $(0.001<P(X^2_{} = 19.02/1\ df))$ and controls (24.1%) $(0.001< P(X^2 = 43.1/1\ df))$ (fig. 3, Table 6). Night pollinated umbel fruit set in *A. chrysantha* at the Peppersauce site was also significantly lower (2.2%) than day pollinated umbels (16%) $(0.001<P\ (X^2 = 283.6/1\ df))$. Fruit set was 19% for controls (significantly higher than day-pollinated plants, $0.001<P(X^2= 19.15/1\ df))$ and 51% for hand pollinated plants (significantly higher than controls, $0.001 <P\ (X^2=319.61/1\ df))$. In *A. palmeri* (Santa Rita site), nocturnally pollinated umbels had significantly lower (10.3%) fruit set than day-pollinated treatments (14%) $(0.001<P(X^2_{} = 18.596/1\ df))$ and controls (16.5%) $(0.001<P(X^2 = 96.4/1\ df))$ (fig. 4, Table 6).

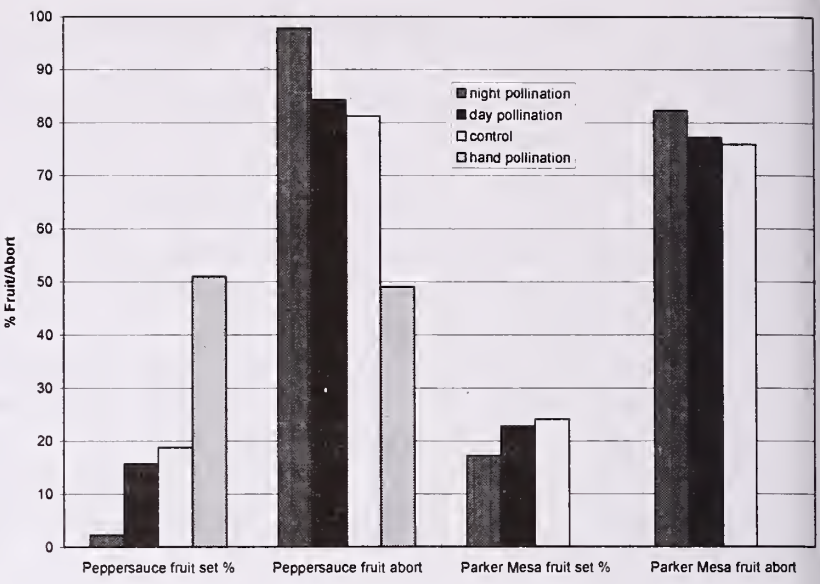

Figure 3.—Percent fruit set of *A. chrysantha* as determined by pollination treatment.

Mean total fruit set (entire inflorescence) of *A. chrysantha* at the Parker Mesa site was 25.9% in experimental plants (night and day pollinated plants) and 24% in controls, similar to previous findings of Sutherland (1982). However, fruit set was quite variable throughout the population (experimental plants 10.8%-50.9%, controls 12.1%-39.8%). Mean umbel number per inflorescence was 14.8 (range 11-20) in *A. chrysantha* with highest fruit set observed on umbel 6. Mean total fruit set in the experimental *A. palmeri* plants was somewhat lower (14.6%) than the control population (19%), and fruit set was also highly variable between individuals (4-40% in experimental plants, 5.3-42.7% in controls). Mean umbel number was 17.5 umbels/inflorescence (range 11-26) with the largest number of fruits occurring on umbel 10.

Table 5.—Mean daily nectar production (ml) vs. diurnal visitation (visits/min) in *A. chrysantha* (Peppersauce site) and *A. palmeri* (Mustang site).

A. chrysantha

Flower Stage	Nectar Amt	Visits/Min
Pre-dehiscent	0.47	4.7
Dehiscent	0.24	3.96
Post-Dehiscent	0.25	3.56
Pistillate	0.09	2.34
Late pistillate	0.001	0.13

*A. palmeri**

Flower Stage	Nectar Amt	Visits/Min
Pre-dehiscent/dehis.	0.623	4.5
Dehiscent	0.623	3.5
Post-dehiscent	0.677	—
Pistillate	0.341	1.27
Late pistillate	0.002	0.75

**Flower stage listed was the predominate stage, although flowers were present in previous and latter stages.*

Table 6.—Effect of pollination treatment on fruit set % in *A. chrysantha* and *A. palmeri*. (Data represents mean number of fruits/number of fruits + number of aborted fruits/umbel. Numbers in parentheses represent SE)

A. chrysantha

	Parker Mesa % Fruit Set		Peppersauce % Fruit Set	
Night pollinated	17.2	(18.6)	2.2	(3.49)
Day pollinated	22.8	(17.4)	15.7	(14.46)
Control	24.1	(15)	18.8	(16.62)
Hand Pollinated	—	—	51.0	(36.42)

A. palmeri

	Santa Rita % Fruit Set	
Night pollinated	10.3	(16.24)
Day pollinated	14.3	(18.67)
Control	16.6	(14.03)

DISCUSSION

Results of this study suggest that several differences exist between *A. chrysantha* and *A. palmeri* with regard to their reproductive biology. Time of pollen dehiscence, flower stage composition of umbels and peak nectar production were consistently different between taxa. When differences in floral color and phenology (yellow-flowered *A. chrysantha* blooms from late May-early August, *A. palmeri* flowers from late June-early September and flowers are cream-colored with reddish tepal apices) are also taken into account, separation at the species level appears appropriate despite the lack of complete reproductive isolation.

Pollinator observations suggest that diurnal insects appear to play an important role in pollination of *A. chrysantha* and *A. palmeri*, despite several characteristics of chiropterophily. Gregory (1963, 1964) and Waser (1978) have noted that plants with characteristics of a particular pollination syndrome may often depend on other animals for the majority of pollination. Although a large number of animals visiting flowers were "thieves," pollination was predominately achieved by diurnal insects (particularly native bumblebees and carpenter bees) by "accidently" making contact with receptive stigmas while foraging. The "mess and soil" pattern of pollination (Faegri and van der Pijl 1979) appears to be the primary method by which pollen is transferred to stigmas in the populations observed, and this rather primitive method of pollination can be achieved by a variety of animals which may or may not include bats.

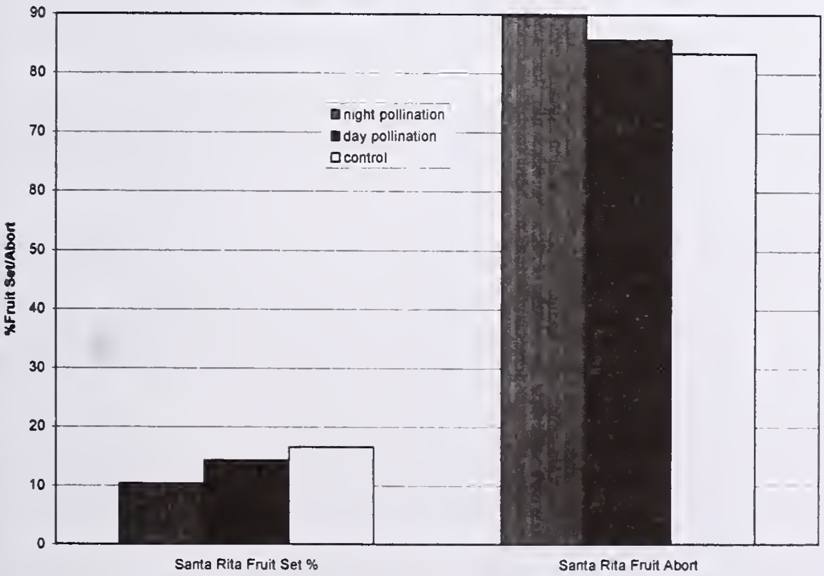

Figure 4.—Percent fruit set of *A. palmeri* as determined by pollination treatment.

The arrangement of floral stages within umbels appears to impact pollination as well. Pollination was most frequently observed when insects, attracted to flowers with freshly dehisced pollen or large amounts of nectar, would rather haphazardly touch adjacent flowers with receptive stigmas. Consequently, as flowers aged and floral rewards decreased, visitation rates decreased and pollination events were less likely. Umbel size and position on the inflorescence may also effect fruit set. Umbels located in the middle of the inflorescence were the largest in size, and had the highest fruit set. The higher number of flowers and floral stages at any one time in large umbels presumably increases pollination success. Flowering of individual agaves within a population is asynchronous, so that umbels positioned in the middle of the inflorescence of an early or late blooming plant may have a better chance of receiving pollen from another individual than those umbels on the bottom or top of an inflorescence.

Diurnal pollinators appear to contribute significantly to pollination and subsequent fruit set in *A. chrysantha* and *A. palmeri*. Control and day pollinated umbel fruit set percentages were near 20% and are similar to results of natural fruit set (Sutherland 1982). Outcrossing, hermaphroditic plants commonly have low fruit set (Sutherland and Delph 1984), and observed pollination rates of 20% suggest adequate pollination occurred. The similarity of fruit set in control and day-pollinated umbels imply that nocturnal pollinators are not critical for sufficient fruit set. Night pollinators contributed little to fruit set (2.2%) in the Peppersauce population, and approximate reported self pollination fruit set rates (1.58%) (Sutherland 1982). Although the presence of bats may increase fruit set of nocturnally pollinated flowers, their presence does not appear to be vital for adequate fruit set to occur. Further studies are needed to determine whether populations pollinated by bats have significantly higher fruit and seed set than populations where bats are not present. If agaves are resource limited as Sutherland (1982) suggests, then mean fruit set in any population would not be expected to be significantly higher than 20-25%. Hand pollination was very effective in increasing fruit set above control and treatment percentages, indicating some pollinator limitation existed. Further studies are required to evaluate the percent seed set per fruit.

Data from this study indicates that pollinator populations vary between sites and years. An intermediate or facultative pollination syndrome may be more adaptive in species that occur in diverse habitats *(A. chrysantha*) or have large geographic ranges *(A. palmeri),* allowing plants to utilize a variety of pollinators that may vary both temporally and spatially. Bats often do not arrive to known roosts in southeastern Arizona until mid-August (S. Schmidt, pers. comm.), however, *A. palmeri* in the vicinity begins flowering in late June-early July. The variable, seasonal and somewhat unreliable movements of *Leptonycteris* (Cockrum and Petryszyn 1991, pers. comm., V. Dalton) seem unlikely to support a tight mutualistic system. Recent studies have shown that the long-accepted example of obligate mutualism between *Yucca* and the yucca moth *(Tegeticula)* appears to be faculative as well (Dodd and Linhart 1994). Fruit set results of this study suggest that a more faculative relationship exists with *A. palmeri,* and the "bat-adapted" traits that *A. chrysantha* and *A. palmeri* exhibit may be just as advantageous to insects and other animals in hot and arid climates where peak activity is near dawn and dusk.

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Conservation of Madrean Archipelago and Regional Forest Development Projects in Mexico

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Abstract.—The Madrean Archipelago is a priority for conservation of biodiversity in Northwestern Mexico. Also, the Chihuahua and Durango Forestry Development Project was proposed to manage the forest of those two Mexican states to modify current deforestation rates. An environmental baseline study was performed to provide baseline data for the protection of the biodiversity in the region and to comply with Mexican environmental law and the World Bank requirements.

Biological data is biased to accessible sites and limited to a few taxonomic groups (several families of vascular plants and terrestrial vertebrates). Consequently, to optimize the use of available data, a GIS modeling approach was used to identify species-rich areas. Modeling was performed by means of multivariate statistics (correspondence analysis and generalized linear models). The GIS was used to environmentally characterize the collection sites and to display the spatial patterns of species-rich areas.

The results delineated a set of priority areas for conservation. Within these areas, special forestry management considerations were recommended for more detailed environmental impact assessments required by law. The modeling approach was useful to derive legally defensible inferences to reduce environmental conflicts between conservation and forest development, despite the limitations of biological inventories.

INTRODUCTION

Preservation of biological diversity has been acknowledged as an imperative task for sustainable development. Thus, governments all over the world and multinational developments banks are setting up policies aimed at integrating conservation priorities and regional development. Environmental assessments (EAs) are planning studies to evaluate the effect of development projects. Typically, EAs are short duration studies, performed with scarce funds and limited data (Bojórquez-Tapia *et al.* 1994). Moreover, EAs of large regional development projects have been criticized in the following grounds: (1) EAs have not been properly integrated into the planning process, (2) data are insufficient to derive useful conclusions, (3) and results are not suitable for planning because of their small scale and lack of accuracy.

The Madrean Archipelago is a critical region for biodiversity conservation. In Mexico, the Madrean Archipelago extends along the Sierra Madre Occidental in the states of Chihuahua and Durango. Nonetheless, the Forestry Development Project of Chihuahua and Durango has been perceived as a major threat to biological diversity.

The purpose of this paper is to present the results of an investigation on biodiversity distribution patterns for Chihuahua and Durango. This research was carried out as part of the EA of the Chihuahua and Durango Regional Forestry Development Project. The objective of the forestry development project was to introduce modern management practices and to expand village and

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commercial forest-based industries in the Sierra Madre Occidental. It was expected that with the new forestry practices current deforestation rates in the Sierra Madre Occidental would be curtailed.

A major problem related to the absence of adequate, current, and usable data on the locations of the most biologically important areas. Therefore, a predictive approach was used in this study to map the biologically important areas. The approach was a modification of the gap analysis technique (Scott *et al.* 1987) to adjust for the constraints and biases of biological data in Mexico (Bojórquez-Tapia *et al.* 1994). In essence, the method consisted of a modeling exercise, carried out by means of computer databases, geographical information systems (GIS), and multivariate statistics.

Through GIS modeling, the data constraints of EAs were overcome. Furthermore, the resulting maps provide a useful baseline for regional land-use planning and protection of biological diversity.

THE FORESTRY DEVELOPMENT PROJECT

The Chihuahua and Durango Forestry Development Project originated in 1989. This year, Mexico solicited a $45.5 million loan to the World Bank to complement the financing of a $91.1 million five-year project. The project was expected to affect about 15% of the 9.3 million ha of forest land in the two states (which represents about 35% of remaining forest land in Mexico).

Major problems of regional forestry development were lack of product classification systems and modern technology, combined with a deficient enforcement of forestry policies. These conditions resulted in extensive logging, mainly through high-grading, in the region. Hence, the Project rationale was that current environmental deforestation trends would be restrained by the introduction of better forestry practices into local communities and small private producers.

Funding was directed to financing road work, new sawmills and equipment, although about 10% of the capital was aimed at environmental protection, technical training, supervision, and administration. To achieve the goal of introducing better forestry practices, about 90,000 credits would be given to people from local communities (20% of total population in the forests in the two states).

Both the Mexican forestry authorities and the World Bank maintained that the project was feasible form the technical, social, economic and environmental viewpoints. On the other hand, non-governmental organizations in both Mexico and the United States of America asserted that the impacts of this project on the environment, especially on biodiversity, could be extremely adverse. They claimed that protective measures were inadequate to provide a reasonable response to potential effects, because of the insufficient coordination, planning and monitoring capabilities of Mexican authorities.

Although the World Bank loan was eventually canceled, the Project is being carried out by Mexican forestry authorities. The viewpoint of Mexican authorities is that the environmental risks are outweighed by the long and short-term benefits likely to be realized by the implementation of the Forestry Development Project.

STUDY AREA

The study area is located within the states of Chihuahua and Durango, along the Sierra Madre Occidental (fig. 1). This region is characterized by a variety of environmental conditions. The Sierra is rough and altitude ranges from 250 to 3,150 m a.s.l. The drainage pattern of the Sierra is complex; the principal rivers -Yaqui, Mayo, Fuerte, and Sinaloa- drain to the Pacific Ocean, though one -the Conchos- flows north to the Rio Bravo or Rio Grande.

According to the Koeppen's classification, the Sierra Madre Occidental presents Bs and Cw climate types in ridges, and Aw along canyons (INEGI 1982). Mean annual precipitation ranges from 800 to 1,200 mm. Though rainfall is bimodal (summer and winter); 60-80% of the rainfall occurs from June to September. The spring drought period is more intense and longer than the fall one. Mean annual temperature ranges from 24-26°C, in the lowest locations, to 6-8°C, at the highest altitudes; maximum and minimum annual temperatures are 40°C and -15°C, respectively.

The study area presents the following vegetation types (INEGI 1992, Rzedowski 1978):

- Madrean coniferous forest.- It is located in the highest and coldest zones in the Sierra Madre, especially in northern aspects at 2,200 m a.s.l., although it can be found at higher elevations in southern aspects. The dominant species are *Pseudosuga menziesii, P. ayacahuite, P. arizonica, P. strobiformis, Abies concolor, A.*

durangensis, P. tremuloides, A. acuminata. Relict and isolated populations of *Picea chihuahuana,* an endangered species, are located in northern aspects in restricted zones, such as Cerro Mohinora, and Cascada de Baseseachic.

- **Pine forest.**- The pine forest distributes at elevation from 1,500 to 3,000 m a.s.l. Dominant species include *P. reflexa, P. arizonica, P. lumbotzi, P. ayacahuite,* and *P. ponderosa.* Microhabitats are important for the dominance of a particular species; for example, *P. reflexa* is dominant in the most xeric aspects, while *P. ayacahuite* prevails on more mesic slopes in canyons.
- **Pine-oak forest.**- The similar ecological requirements of pines and oaks, their entangled successional relationships, and the diversity of microhabitats produce a mosaic of pines and oaks. Oak forest components often can be found above the lower limit of the pine forest, especially in xeric aspects. On disturbed sites, oak s are more abundant than pines. Common species are *Quercus emoryi, Q. oblongifolia, Q. grisea, Q. santaclarensis, Q. durifolia, Q. arizonica, Q. albocincta, Q. coccolobifolia, Q. crassifolia, Q. hypoleucoides, Q. pennivenia, Q. sideroxyla, P. cembroides, P. emoryi, P. oocarpa, P engelmannii, P. leiophylla, Cuppresus arizonica,* and *Juniperus deppeana.*

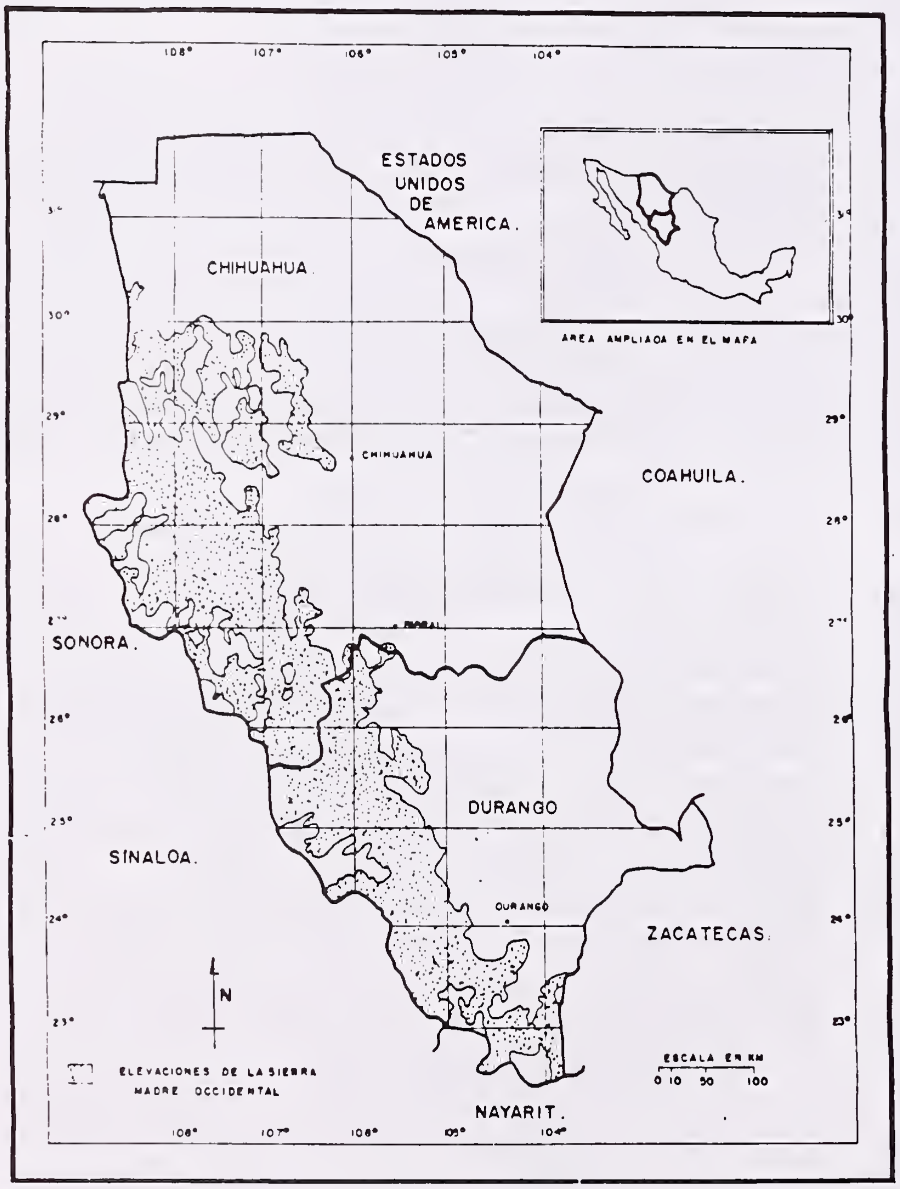

Figure 1.—Study area.

- **Oak woodland.**- Deciduous oaks dominate between 1,000 and 2,000 m a.s.l., in slopes and plateaus. The most abundant oak species are *Q. chihuahuensis, Q. tuberculata, Q. sipuraca, Q. santaclarensis,* and *Q. fulva.* Dominant understory species are bunchy grasses, such as *Bouteloa, Eragrostis, Muhlenbergia,* and *Schizachyrium.*
- **Grassland.**- Grasslands locate in plateaus and valleys of moderately deep soils, between 200 and 2,000 m a.s.l. Important species are *Bouteloa* spp., *Muhlenbergia* spp., *Bacharis* spp., *Schizachrium* spp., and *Hilaria* spp. In disturbed areas by fire, overgrazing, overcutting, of abandoned agricultural lands, *Aristida* spp. are common.
- **Desert scrub.**- This vegetation type is widespread in Northwestern Mexico. In the study area, it extends along the Pacific Coastal Plain, the lowlands of Sonora, and the highlands in Chihuahua. In the highlands, the desert scrub can be found as high as 3,000 m a.s.l. It is composed by shrubs with small leaves or folioles. Typical species are *Larrea tridentata, Yucca carnerosana, Fouqueria splendens, Opuntia* spp., *Celtis* spp., *Prosopis,* and *Acacia.*
- **Tropical deciduous forest.**- This vegetation type is typical of subhumid hot climates. It extends along the lowest elevations until 29°N, due to the protection against northern winds of the Sierra Madre. Most of the individuals (75%-100%) loose their leaves after the summer rains and for long periods (6-8 months). The dominant trees lack of spines and the tallest are 15 m. The dominant species are: *Lysiloma microphylla, L. watsoni, Ceiba acuminata, Bombax palmeri, Cochlospermum vitifolium, Lamiocereus* spp., *Caesalpinia atomaria, Tababoua palmeri, Conzattia sericera, Bursera* spp., *Guazuma ulmifolia,* and *Ipomea arborescens.* Representative understory species are: *Hintonia latiflora, Schopfia parvifolia, Sebastiana pringlei, Agonandra racemosa, Wimmeria mexicana, Willardia mexicana,* and *Erythrina flabelliformis.*

MATERIALS AND METHODS

Our methods combined GIS layers, a biological computer database, and multivariate statistics. The equipment included five IBM compatible microcomputers, and two digitizing tables (Kurta IS/ONE and Numonics 2200). The GIS consisted of the programs AU2 (ICFA 1987), Roots (Corson-Rikert 1990), and CI/SIG (CI 1992).

Our database was compiled species information obtained from comprehensive literature and scientific collection revisions. Species data were gathered from the literature, and biological collections. The data consisted of species names and collection sites. Each collection site was georeferenced in 1:250,000 topographic maps before it was transferred to the GIS.

The following 1:1,000,000 maps (INEGI 1982) were digitized into the GIS: soils, geology, vegetation and land-use, topography, mean annual precipitation, and mean annual temperature. With respect to the vegetation and land-use map, this map was reclassified to reduce the number of categories; thus, the categories in the new layer were the following: Mixed coniferous forest, pine forest, pine-oak forest, oak woodland, grassland, desert scrub, tropical deciduous forest, and agriculture and ranching. A one km$_2$ cell size was used for each raster layer. An additional layer was the binary map of collection sites.

The digitized maps were overlaid on the layer of collection sites to environmentally characterize these sites. Results from the overlays were transferred to presence-absence matrices of species and environmental variables. From these matrices, corresponding contingency tables were prepared for the subsequent modeling.

Modeling was carried out by means of ordinations, through correspondence analysis of species and environmental variables or CASEV (Montaña and Greigh-Smith 1990) and generalized linear models. Programs ORDEN version 1.4 by E. Ezcurra, and GLIM version 3.77 (London Royal Statistical Society 1985) were used for all statistical analyses.

CASEV was used to detect the relations between ecological factors and species distributions. The relationships between axes and environmental variables were evaluated by visual examination to identify species assemblages. A frequency matrix was prepared for each species assemblage. Thus, a matrix cell showed the number of records that corresponded to that specific combination of the orthogonal environmental variables that explained the species distribution patterns. Non existent combinations of values between the orthogonal environmental variables were eliminated.

A log-linear model was fitted to each frequency matrix (Atkin *et al.* 1990). Models were assessed according to their coefficient of determination ($r^2 > 0.25$) and significance ($p < 0.001$. for linear terms; $p < 0.05$ for quadratic terms). The value combinations that predicted the highest frequencies were mapped in the GIS. We draw a final map by overlaying all the predicted distributions and the vegetation and land-use layer.

RESULTS

The biological database included many records, although site description for about one half of the records was insufficient to determine their latitude and longitude (Table 1). With respect to the number of families, species, and records included in the database, birds encompassed most of the data, followed by mammals, reptiles, and amphibians. The majority of the georeferenced records corresponded to mammals, while amphibians represented a small percentage of the data (Table 1).

Table 1.—Number of species and records compiled in the data base from Chihuahua and Durango.

Taxa	Families		Species		Records		Geo-referenced records	
	(#)	(%)	(#)	(%)	(#)	(%)	(#)	(%)
Amphibians	6	7	11	2	114	3	79	5
Reptiles	10	12	44	10	510	15	231	15
Birds	49	59	327	71	1,516	45	428	27
Mammals	18	22	79	17	1,244	37	838	53
Total	83	100	461	100	3,384	100	1,576	100

The following matrices were obtained: presence absence (species x environmental variables), amphibians (114 x 6), reptiles (510 x 6), birds (1,516 x 6), and mammals (871 x 6); contingency tables (species x categories of environmental variables), amphibians (10 x 26), reptiles (38 x 30), birds (296 x 26), and mammals (116 x 29).

Twenty species assemblages with similar ecological requirements were obtained from the CASEV (Table 2). The variables that best explained the highest variance were elevation, mean annual temperature, mean annual precipitation, and vegetation and land-use (Table 2). Since elevation and mean annual temperature were highly correlated ($r^2 = -0.8$), the former was discarded from further analyses. Vegetation type and land-use was not included in the GLIM to simplify the models. However, it was used as an additional layer in the GIS to increase the accuracy of the predicted areas.

The general linear model consisted of five terms:

$$y=e^{a+bt+cp+dt_2+ep_2+fpt}$$

Where y is the predicted species frequency, t is mean annual temperature, and p is mean annual precipitation. The importance of each term varied between models (Table 3).

Significant fits of GLIM were possible for 13 from the original 20 species assemblages (Table 4). These models were transfered to the GIS to display their spatial distribution, and were combined with the observed spatial distributions of the

Table 2. —Species assemblages generated by correspondance analysis for terrestrial vertebrates of Chihuahua and Durango (MC=mixed coniferous forest; P=pine forest; PO=pine-oak forest; O=oak woodland; TD=tropical deciduous forest; DS=desert scrub; A=agriculture and cattle ranching).

Species Assemblage	Temperature Range (°C)	Precipitation Range (cm)	Elevation range (m a.s.l.)	Vegetation type	Area (km²)	Area (%)
			Amphibians			
1	8-20	400-1,200	1.000-3,000	MC,PO	3,128	1.0
2	22-24	700-1,500	0- 600	TD	1,174	0.5
			Reptiles			
1	8-20	200- 500	0- 600	P,A	392	0.1
2	18-20	500-1,500	1,000-1,500	PO,O,MC	1,270	0.4
3	20-22	500- 700	1,000-1,500	NA	887	0.3
4	20-22	500- 600	500-1,000	TD	1,777	0.5
			Birds			
1	16-18	500- 600	2,000-3,000	MX,P	392	
2	8-16	600-1,500	2,000-3,000	TD		
3	16-18	600-1,500	2,000-3,000	O,PO		
4	18-22	600-1,500	600-2,000	O,PO,MC		
5	22-28	500-1,500	600-2,000	NA		
			Mammals			
1	8-16	700- 800	2,000-3,000	O,PO,MC	5,574	1.8
2	16-20	700- 800	1,000-2,000	O,PO	2,360	0.8
3	20-22	600- 800	1,000-2,000	O,TD	772	0.3
4	22-28	600- 700	0-1,000	TD	2,856	0.9
5	16-20	600- 700	1.000-2,000	O	66	0.0
6	8-16	600- 700	2.000-3,000	NA	5,137	1.7
7	20-22	500- 600	1,000-2,000	A	4,621	1.5
8	18-20	500- 600	1.000-2,000	DS, P	672	0.2
9	8-18	500- 600	2,000-3,000	P	7,593	2.5

seven species assemblages that did not significantly fit a linear model (fig. 2).

Predicted and observed distributions of species assemblages covered approximately 10% of the area of influence (fig. 2). Based on the spatial patterns, we delineated 12 areas critical for conservation (fig. 2). Some of these areas layed outside the project region, but all were placed within the area of influence of the project. For the forestry project, we considered areas 5, 6, 8, 9, 10, 11, and 12 as critical. Total predicted areas for each of the taxonomic Classes were the following: mammals, 2,965,100 ha; birds, 413,600 ha; reptiles, 432,600 ha; and amphibians, 486,200 ha.

DISCUSSION

Successful biodiversity conservation compels the use of a large-scale landscape strategy to merge nature reserves and sensible management of the semi-natural landscape matrix. While nature reserves are crucial for conservation, the semi-natural matrix renders a critical role in conservation by increasing the effectiveness of reserve areas (Franklin 1993).

Table 3.—Generalized lineal models (GLIM) for terrestrial vertebrates in Chihuahua and Durango. The order of the variables in the model indicates their importance (1 = mean annual temperature; 2 = mean annual precipitation; and 3 = interaction between 1 and 2).

Group	Model	Degrees of freedom	r^2
	Amphibians		
1	1 + 2	4	0.45
	Reptiles		
1	1 + 2	3	0.52
2	1 + 2	4	0.43
3	2 + 1	4	0.36
	Birds		
1	1 + 2 + 3	4	0.29
2	1 + 3 + 2	4	0.25
	Mammals		
1	1 + 2 +3	5	0.62
2	1 + 2	4	0.35
3	2 + 1	4	0.36
5	1 + 2	4	0.34
6	1 + 2	4	0.57
8	2 + 1 + 3	4	0.36
9	1 + 2 + 3	7	0.72

A landscape approach also facilitates the resolution of the current conflict between logging and forest preservation in the Sierra Madre Occidental. Much of the conflict is over the location of critical sites for conservation (for example, old-growth stands and species-rich hot spots) and the presence of priority species (Burns *et al.* 1994). Clearly, a knowledge on species distributions and on ecosystem processes is obligatory for a successful implementation of a landscape strategy.

Gap analysis is a technique designed to identify priority areas for conservation by comparing the location of existing nature preserves with the location of species-rich areas (Scott *et al.* 1987, 1988). The gap analysis approach combines the emerging concepts in conservation biology with up-to-date advances in data management and analysis.

However, utilization of gap analysis is severely limited because of the quality and quantity of the available information in Mexico. As in other regions in the country (Bojórquez-Tapia *et al.* 1994), biological data of Chihuahua and Durango are biased to a few families of vascular plants and terrestrial vertebrates, and to accessible sites (eg. along major roads or close to cities). Similarly, most of the thematic maps are small scale and outdated, especially the themes on species distribution and on vegetation and land-use. Consequently, the design of a landscape level approach for the Sierra Madre depends on portraying species richness and species distribution patterns.

No adequate theory exists for predicting areas of species richness (Austin 1991). Thus, approaches to minimizing the effects of forestry development on sensitive wildlife are generally derived from experience (Irwing and Wigley 1993). Nonetheless, inferences for regional land-use planning cannot be restricted to those originated from experience. On the contrary, effective regional land-use planning has to satisfy two conditions:

(1) results have to be obtained from accurate methods, and
(2) inferences have to be legally defensible (Steiner 1983).

The method used for depicting species distribution patterns in Chihuahua and Durango was based upon readily available information. The baseline database included the readily available biological data and many collection sites (Table 1). Twelve high biodiversity areas were identified

Figure 2.— Predicted distribution areas of terrestrial vertebrates and critical regions for conservation (numbered squares) in Chihuahua and Durango (white = study area; black = predicted distributions of terrestrial vertebrates; gray = no data).

through ordination analysis and GIS modeling (fig. 2).

Albeit the models are yet to be validated, we assume that the predicted species-rich areas are accurate, based upon previous experiences with the application of empirical models elsewhere (Austin *et al.* 1984, Bojórquez-Tapia *et al.* in press, Ezcurra *et al.* 1987, Margules and Stein 1989, Miller *et al.* 1989, .Scott *et al.* 1993). The species-rich areas included sites that have not been explored in past biological surveys. Consequently, while the use of available data was optimized, these results represent an improvement in the ability to identify ecologically sensitive areas.

From the legal viewpoint, our study can be considered as an unbiased mapping exercise to outline priority areas for biodiversity conservation. The twelve high biodiversity areas correspond to regions where nature reserves should be established. Also, by overlying a map of proposed forestry operations on the species assemblages distribution map, areas where conflicts between forestry and conservation are more likely to occur can be delineated.

According to environmental legislation, forestry practices that blend conservation with sustained forest development should be devised for the conflicting areas. As a first step, a detail survey should be done before the implementation of any forestry practices; detailed surveys should include a biological inventory, a ground truth vegetation map, and locate landscape corridors connecting areas of high species richness. Subsequent research and adaptive-feedback monitoring should refine the strategies and reduce risks of extinction and impacts caused by forestry development.

CONCLUSIONS

The Forestry Development Project of Chihuahua and Durango has been perceived as a major threat to biological diversity. Given the limitations in data and knowledge, a predictive approach was carried out to delineate potential species-rich areas.

The results included 12 areas where special forestry management considerations should be set up. Such considerations must be the base of detailed EAs of specific forestry practices.

This research illustrates how a predictive approach -through multivariate models and GIS- can be used to delineate conservation priorities in regional land-use planning. Furthermore, the usefulness of the modeling approach is demonstrated by the optimization of available biological information to derive defensible inferences from rigorous methods.

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Persistence of Uncommon Cryopedic Plants in the Chiricahua Mountains Spruce Forest Island

W.H. Moir[1]

Abstract.—There are small populations of boreal plants persisting in spruce forests. Twenty years after they were first noted by the author, plants such as *Vaccinium myrtillus, Lonicera utahensis, L. involucrata, Sorbus scopulina,* and *Rubus parviflorus* survived the warm decade of the 1980s. The spruce forests are not well structured into herb and shrub layers as they are elsewhere in Arizona and New Mexico. Instead these understory plants of cryic soil temperature regimes are found where there is little competition from other plants and where compensatory microsite factors exist. In 1993 most populations were at about their levels in 1974 or increasing. Climate change in these mountains does not seem to be a threat of population decline.

INTRODUCTION

Plants growing near the extreme of their physiological tolerances can be sensitive to small changes in climate (Woodward 1987, Colhoun 1979). If a climatic change, when expressed locally, exceeds an ecophysiological threshold, plants with short response times can become locally extinct. Plants of insular environmentsare vulnerable if their genetic variability is small and favorable microenvironments for surviving adverse climates are not available.

The northern hemispheric climate of the 1980s has been exceptionally warm, and a similar warm period during the 1980s, though less pronounced, occurred in the southern Rocky Mountains (Karl et al. 1990; fig. 1). This warm period was reflected in weather records of some of the mountains along the U.S./Mexico border. In March, 1993, I and and several plant pathologists visited the Chisos Mountains, Texas, to examine a forest monitoring plot established in 1978 where Douglas-fir (*Pseudotsuga menziesii*) was growing very near its environmental limit of moisture and temperature (Moir et al. 1993). In addition to unusually high temperatures, a severe drought had occurred here in the 1980s. We speculated that because of adverse climate the Douglas-fir population might reveal high mortality or other symptoms of stress. We remeasured the monitoring plot and found that all the Douglas-fir seedlings and saplings were of extremely low vigor and had suffered near-lethal defoliation(s) from unknown cause(s). It was tempting to conclude that under climatic extremes of that decade the heat and drought stressed trees became vulnerable to insect predation or disease (Colhoun 1979, Franklin et al. 1987), events which in fact took place although the exact causes remain unresolved.

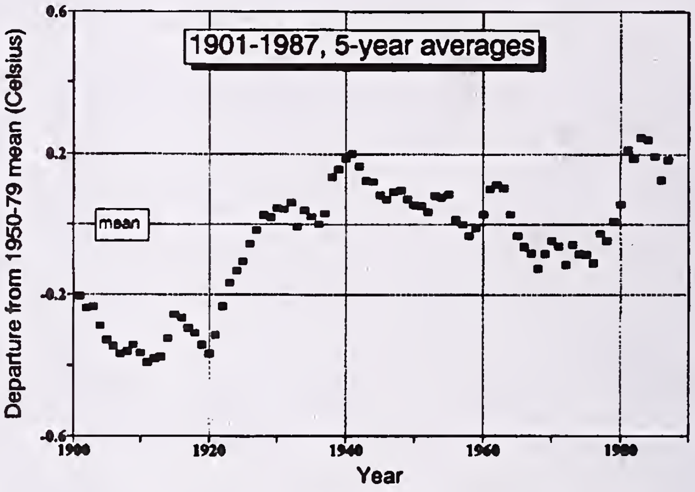

Figure 1.—Running 5-year averages of departures from Northern Hemisphere mean annual temperatures (from Karl et al. 1990).

Could similar happenings have taken place in other mountains of the U.S.-Mexico border? Could plants of Engelmann spruce forests in the Chiricahua Mountains, adapted to cold environments mostly above 2680 m (8800 ft) elevation, be

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harbingers through mortality or loss of vigor of a warming climate? The forests belong to the Cork-bark-fir-Engelmann spruce-White fir series whose average soil temperatures are at the warm end of the cryic soil temperature regime (around 3-6 °C mean annual soil temperature at 50 cm depth; Moir 1993, Carleton et al. 1991).

In 1974 I observed some uncommon or rare plant populations in the spruce (*Picea engelmannii*) forests as part of a habitat type study (Moir and Ludwig 1979), but most of the plants were not in the sample plots (Table 1). The understory plants in the plots were mostly those that were common in mixed conifer forests where frigid rather than cryic soil temperature regimes exist (Carleton et al. 1991, appendix B in Muldavin et al. 1990). Why were we not finding the usual cryopedic plants in the sample plots, which were chosen to represent typical characteristics of the spruce forests here (Moir and Ludwig 1979)? To try to answer this question, I explored the spruce forests to find just where these plants occurred. Apparently, one reason we did not sample them more frequently was that the plants were at low population levels, in extreme cases less than 10 individuals and in many cases less than 3-4 subpopulations were located. Another reason was that the plants grew in special microsites, rather than the more typical and extensive sites where the spruce forests occurred.

Table 1.—Spruce forest plots, Chiricahua Mountains, Arizona, sampled for habitat type classification (Muldavin et al. 1990).

Plot	Cima Cabin	Fly Peak	Round Park	Raspberry Ridge
yea	1974	1982	1982	1983
elev	2773	2880	2880	2804
TREES and SIZE		stems/ha		
Picea engelmannii				
dbh<5cm	134	1709	27	961
dbh 5-22.5cm	53	187	80	294
dbh>22.5cm	187	107	107	134
Pseudotsuga menziesii				
dbh<5cm	347	27	53	2056
dbh 5-22.5cm	0	53	0	107
dbh>22.5cm	27	80	107	214
Abies concolor				
dbh<5cm	347	53	1202	134
dbh 5-22.5cm	0	0	0	27
dbh>22.5cm	27	27	80	0
Pinus strobiformis				
dbh<5cm	0	134	0	721
dbh 5-22.5cm	0	0	0	107
dbh>22.5cm	0	0	0	27
Populus tremuloides				
dbh 5-22.5cm	27	454	187	0
dbh>22.5cm	0	214	27	0
UNDERSTORY		% canopy coverage		
Acer glabrum	10	0.01	35	0.01
Physocarpus monogynus				0.1
Holodiscus dumosus				0.1
Vaccinium myrtillus				2
Bromus ciliatus	1		0.01	
B. porteri				0.01
Festuca sororia	4			
Chimaphila umbellata				0.01
Erigeron eximius			0.1	
Goodyera oblongifolia	0.01		0.01	
Ligustricum porteri	0.01	0.01	0.1	
Lonicera arizonica	0.01			0.1
Pteridium aquilinum	0.01		3	0.01
Pyrola chlorantha			0.01	
Senecio bigelovii	0.01		0.1	
Smilacina spp.	0.01		0.01	0.1
Vicia americana		0.01		0.01
Viola canadensis	0.1	0.01	0.1	
HERBACEOUS understory	5.2	0.01	3.6	0.3

In September 1993 I returned to most of these locations to see if any of the populations had declined. I was especially interested to see if the events observed in the Chisos Mountains, namely climatically induced stress followed by low vigor or heightened mortality, had also taken placed among vulnerable plants in the Chiricahua Mountains.

HYPOTHESIS

Cryopedic plant populations of spruce forests in the Chiricahua Mountains declined during an adverse warming period in the 1980s.

METHODS

Plants censused in 1974 and 1993 were *Goodyera oblongifolia, Sorbus dumosus, Vaccinium myrtillus, Chimaphila umbellata, Lonicera utahensis, Pyrola chlorantha, Rubus parviflorus, Veratrum californicum, Erigeron scopulinus,* and *Lonicera involucrata.*

The 1974 census was conducted in September by searching for the above plants along the Crest Trail and at other trailside locations where *Picea engelmannii* forests occurred. When found, notes were made of location, abundance, and vigor. A population consisted of individuals at a particular location. Abundance was measured by counting individuals or ramets. I made no attempt to discern between genetically distinct individuals and ramets. Vigor was a subjective assessment of shoot robustness, growth rates, and symptoms of disease, herbivory, or parasitism.

In addition I examined aspects of weather records from two Chiricahua Mountain stations. The Portal 4SW station is in Cave Creek canyon, subject to cold night airflow, and the Chiricahua National Monument station is in Madrean oak woodland. Neither reflects an Englemann spruce climate, although they might reveal significant trends. I graphed yearly precipitation from 1967 to 1992 and maximum monthly temperatures during the growing season from April through September from 1967-1993 inclusive. Running 5-year averages were computed to visually reveal possible trends of temperature or precipitation during this 26 year period.

RESULTS

Here are the reports for the two surveys:

- *Goodyera oblongifolia* - 1974: Found at 2 locations along Crest Trail and in one plot, with a few (4-7) shoots at each site. No flowering shoots. 1993: no change. An additional clone (4 shoots) was found near Goobber Spring in 1994 (see postscript below).
- *Sorbus dumosus* - 1974: one tree above Cima Cabin; in 1993 that individual not relocated, but 3 additional small trees were found along the Crest Trail near Raspberry Peak.
- *Vaccinium myrtillus* - 1974: occasional small populations grew in extremely cobbly soils along the Crest Trail and on similar soil on north-facing slopes along the Greenhouse and Monte Vista Lookout trails; in 1993 these populations remained intact. The populations were segregated from *Holodiscus dumosus* and *Physocarpus monogynus* which also occurred on these cobbly soils. The Vaccinium shoots were sparse, had few leaves (about 4-6 per shoot), and were not filling in the site with high canopy cover as usually occurs in spruce-fir/vaccinium environments (fig. 2, Muldavin et al. 1990).
- *Chimaphila umbellata* - 1974: one individual with about 20 ramets was found along the Crest Trail. In 1993 this individual had increased to about 80 ramets and occupied a larger area; 9 additional populations varying from 3-30 ramets were found along the Crest Trail, which were probably missed in the 1974 census. No flowers or fruiting stalks in either census.
- *Lonicera utahensis* - 1974: nine individuals were scattered and uncommon along the Crest Trail; 1993 - only three individuals were relocated, however a population of between 10-20 individuals was found near the junction with the Monte Vista LO trail. This population was clearly overlooked in 1974. No flowers or fruits were seen in either census.
- *Pyrola chlorantha* - 1974: one location with a few shoots; in 1993 I found four shoots (possibly ramets of 1 individual) at the same site. I am unsure if the exact location was the same as it was in 1973.
- *Rubus parviflorus* - 1974: rare along the Crest Trail but frequent along the Greenhouse Trail. 1993: one population of 8 shoots grew along the Crest Trail near the 1974 location; 3 extensive populations (30 shoots) were growing along the Greenhouse Trail. There were no flowers or fruits in either census.
- *Veratrum californicum* - common along Cave Creek in vicinity of Cima Cabin in both 1974 and 1993, some individuals flowering. Also at Goobber and Anita Springs. Shoots in both censuses were robust and preempted wet sites to the exclusion of other species.
- *Erigeron scopulinus*, a plant of particular interest because of its rarity (Nesom and Roth 1981) - 1974: 3 individuals on rhyolite rock near Raspberry Peak; 1993: no change, and no additional individuals upon further search. No flowering stalks at either date. Identificatuon was based upon distinctive vegetative characters of this compactly matted plant and where the plants were growing.
- *Lonicera involucrata* - 1974: 4 individuals grew streamside along the Greenhouse Trail above Wynn Falls; 1993: 7 individuals were tallied along the same reach.

Figure 2.—Vaccinium myrtillus on cobbly soils in spruce forests, Chiricahua Mountains, Arizona, September 1994.

DISCUSSION

There was no evident diminution in populations of any of the species during the 20 years. Some plants increased. Although the sampling methods precluded statistical comparisons between survey dates, the generally similar responses by all species are suggestive. If a period of climate warming had taken place, why would plants arguably of cold soils be increasing? A climatic lag (Davis 1989) is possible for long-lived perennials, but would not account for population increases. I suggest some possibilities, and perhaps there are others.

It is possible that sample biases account for the apparent increases in plant populations; in the second census I was more efficient in finding additional populations and individuals. However, the hypothesis may be true for some species, untrue of others, and again the sampling was too subjective to distinguish.

The assumption of climate warming may be untrue in the Chiricahua Mountains. Examination of weather data indicates that the Chiricahua Mountains were not subject to adverse climates during the 27-year interval from 1967 to 1993. The Chiricahua Mountains have sufficient geomass to modify a regional climate. Figures 3-4 show patterns of temperature and precipitation from the two weather stations. There is no evidence of a 1980s warm interval during the growing season. There was a trend of increasing precipitation during the 1980s which could have favored population growth of plants in the spruce forests (Stephenson 1990).

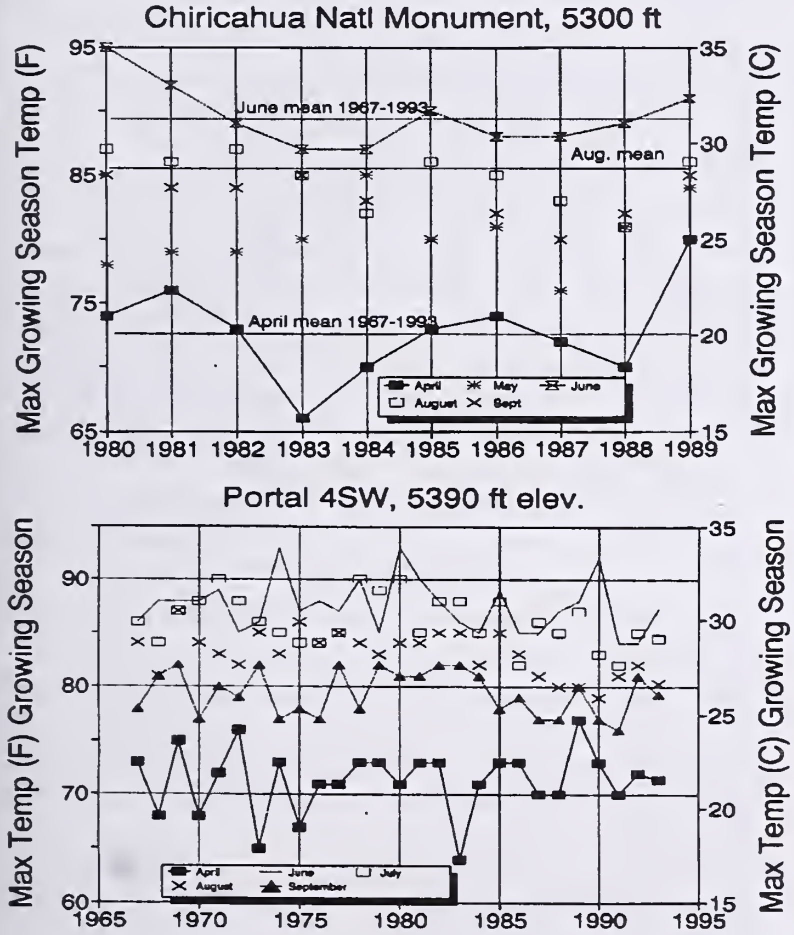

Figure 3.—Growing season temperature variations at two weather stations in the Chiricahua Mountains, Arizona. The graphs reveal that there was no warm decade of the 1980s. Other measures of temperature from these stations lead to the same conclusion.

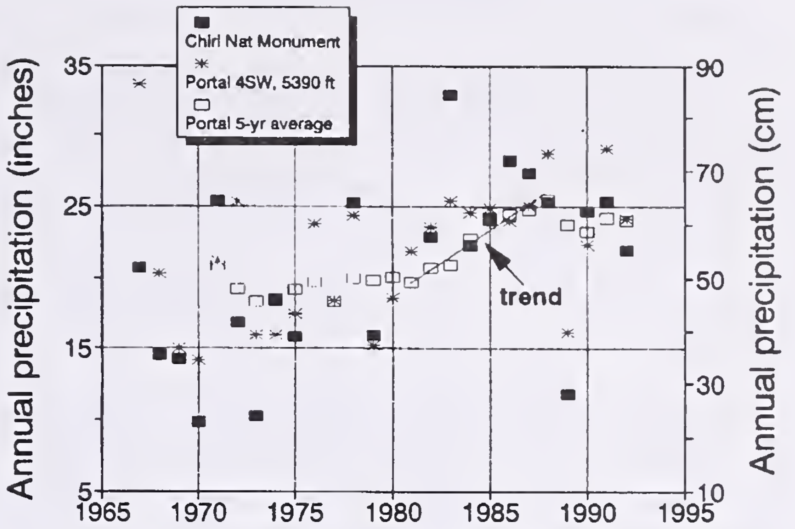

Figure 4.—Mean annual precipitation at two weather stations in the Chiricahua Mountains, Arizona. The period, 1981-1988, was wetter than average, with yearly precipitation totals mostly above the trend line.

The hypothesis may be false and makes no sense if the premise is untrue. In this "island" environment it is not necessarily true that plants maintain the same genetics as they do on "continents" (i.e., more contiguous forest locations throughout the Southwest). Some ecotypes may be adapted to warmer soils (i.e., a frigid soil temperature regime). Others, like *Veratrum* and *Lonicera involucrata* may simply need wet soils, and temperature fluctuations are immaterial. Another, *Erigeron scopulinus*, is a plant of rhyolite cracks and crevices, not necessarily a cryic soil temperature regime. In the aggregate, therefore, the various species corroborate nothing, since each responds to different microsite conditions.

Vaccinium myrtillus inhabits extremely cobbly soils that may buffer it against adverse soil moisture or temperature extremes. Its greatest threat appears to be competitive displacement by *Physocarpus* and *Holodiscus dumosus* of similar soils. Seldom were vacciniums found on sites occupied by these taller shrubs. These shrubs are generally of warmer mixed conifer forests and clearly seem able to displace *Vaccinium* if stress from any cause further lowered its vigor. This may in fact be occurring, not because of any short climate trend, but possibly driven by a more general warming since the end of the Little Ice Age about 100 years ago.

CONCLUSION

I found little sign that climatic variability during the last 30 years adversely affected rare or uncommon plants of the spruce forests in the Chiricahua Mountains. Would these plants - *Vaccinium* especially - provide an adverse climate signal, using a more rigorous monitoring technique, if climate warming intensified? I am unsure that even if a population decline is measured, it can be interpreted without additional information. Many of the species discussed here can persist vegetatively, expanding or contracting in response to a complexity of microsite variables. Small, insular populations are vulnerable to a wide possibility of events leading to local extinction. Environmental or demographic stochasticity might be hard to distinguish, [1]Research Ecologist, USDA Forest Service Rocky Mountain Forest and Range Experiment Station, Ft Collins, Coloradoand correlative observations would need experimental treatments to test for causative factors of population changes.

Nevertheless, these plants have persisted in the Chiricahuas from the time boreal forests were extensive in the Southwest (Betancourt et al 1990). Their future may not be so certain.

POSTSCRIPT AFTER THE 1994 FIRES

The Rattlesnake burn took its toll of these plant populations. On September 17, 1994 I revisited their locations along the Crest Trail with side trips to Boogger and Anita Springs and along a short portion of the Monte Vista Lookout Trail. *Erigeron scopulinus* was gone, along with lichens, mosses, and other saxicolous plants of rhyolite cliffs and ledges that got roasted. The fire was so hot at sites where *Chimaphila umbellata* grew that I doubt any survived. The same holds for *Rubus parviflorus*. The *Sorbus dumosus* trees that I knew are gone. Two populations of *Vaccinium myrtillus* survived where scorching ground fires missed, and I saw *Lonicera utahensis* in similar places. The site where *Pyrola chlorantha* occurred had burned hot enough to doubtless kill the plant and/or its fungal symbionts. *Goodyera oblongifolia* was alive and well in the Goobber Springs area, but nowhere else in its former sites did I find it.

The Rattlesnake burn is an example of how vegetation changes are not gradual but sudden. The spruce forests of the Chiricahua Mountains continue to harbor relictual boreal plants, but after the fire their tenure is more precarious. Further search in remaining, unburned forests of this island summits will doubtless turn up plants that I missed.

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Characteristics and Consequences of Invasion by Sweet Resin Bush into the Arid Southwestern United States

Elizabeth A. Pierson and Joseph R. McAuliffe[1]

Abstract.—*Euryops multifidus* (sweet resin bush), a shrubby composite native to South Africa, was introduced to the arid southwestern United States in 1935 by the USDA Soil Conservation Service. The spread of this shrub represents one of the most serious threats to the ecological integrity and economic value of several ecosystems in the semiarid Southwest. In southern Arizona, this shrub readily invades vegetationally intact, semi-arid grasslands and eventually forms virtually uninterrupted monocultures from which native grasses, shrubs, and succulents are almost completely excluded. Study of plant responses at the advancing front of the areas occupied by sweet resin bush demonstrated that death of native species is linked to the spread of this exotic shrub. These dramatic vegetation alterations are persistent and lead to a variety of additional detrimental changes, including marked increases in soil erosion.

We have identified the climatic, vegetation, elevation, and soil characteristics of sites that are susceptible to invasion by *E. multifidus*. In southern Arizona sweet resin bush can occur in vegetation ranging from Sonoran Desert at low elevation (ca. 850-1060 m) to grasslands, chaparral, and woodland at higher elevation (ca. 1300^+ m). In grassland, this shrub can invade a wide variety of different soil types, ranging from loamy calcic soils typically occupied by stands of black grama *(Bouteloua eriopoda)* to heavy clay soils occupied by tobosa *(Hilaria mutica)* and curly mesquite *(H. belangeri)*. A significant amount of public and private southwestern rangeland is within the range of this invasive species. Our results demonstrate the catastrophic consequences of invasion by sweet resin bush in the arid southwestern United States.

INTRODUCTION

Invasion of natural plant communities by introduced plants constitutes one of the most serious threats to natural ecosystems worldwide. The resulting transformations can permanently decrease native diversity, and can produce permanent, self-perpetuating changes in ecosystem properties including hydrology, biogeochemical-cycling, and disturbance regimes (especially fire). There are few ecosystems in the world that have not been affected by invasions of exotic terrestrial plants, and purposeful or accidental introduction combined with urbanization and land usage have been a major causal factor in these invasions.

At a global scale, grasslands are among the most vulnerable ecosystems to extensive vegetation change due to plant invasions. According to Mack (1989), in less than 300 years (and in most cases, little more than 100 years) much of the temperate grassland outside Eurasia (a collective area of 2.0×10^6 km^2) has been irreparably transformed by human settlement and the concomitant introduction of alien plants. In contrast to temperate grasslands, semi-arid grasslands have been viewed as less vulnerable to invasion. The perception is based on the notion that because of the

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greater environmental limitations placed on existence in arid and semi-arid climates, few species are assumed capable of invading and the few that are capable are unlikely to bring about extensive vegetation change. The paucity of information available on the consequences of plant invasions in semi-arid grasslands has perpetuated the notion that these grasslands are less vulnerable to invasion.

For the arid southwestern United States, this notion may prove to be dangerously inaccurate. The biseasonal rainfall and subtropical temperatures characteristic of the Sonoran Desert and adjacent semi-arid grassland make them vulnerable to invasive species tolerant of both Mediterranean and neotropical climate regimes (Burgess, et al. 1991). Species of exotic plants tolerant of both climatic regimes have already become naturalized in the semi-arid vegetation of the Southwest; many were deliberately introduced by the United States Soil Conservation Service (SCS) for their climate tolerance (Table 1). The consequences of these invasions are just beginning to be recognized and further vegetation change due to invasion is likely to be only a matter of time.

Examination of the characteristics of successful invading species and the consequences of their spread for the invaded ecosystem provides an excellent opportunity to study the structure and function of the native biological community and assess the vulnerability of these communities to further invasion. In this paper we focus on *Euryops multifidus* (Asteraceae), commonly known as sweet resin bush (fig. 1). This woody subshrub was introduced into the arid southwestern United States from South Africa in 1935 by the SCS. The ecosystem-level changes that have occurred as a result of the range expansion of this species from experimental introductions by the SCS are among the most dramatic examples of the consequences of plant invasions in the arid Southwest. Interestingly, relatively little has been written previously about this serious ecological problem. In this paper, we summarize what is presently known about the A) taxonomy and B) ecology of *E. multifidus*; C) describe the history of introduction of sweet resin bush and other exotic species by the SCS to the southwestern United States, D) describe some of the changes in the structure and function of vegetation communities that have been invaded by sweet resin bush, E) describe the potential mechanisms that can account for these changes, and F) delineate the geographic area in North America at risk of future invasion by this invasive species.

Table 1.—Examples of exotic plant species that have become widely established in semi-arid and arid vegetation in Arizona as a result of deliberate introduction for erosion control and range improvement prior to 1942. The table gives the family, genus, and species names, country of origin, and source of introduction. An asterisk (*) indicates those species that were either imported and introduced for the first time by the USDA Soil Conservation Service (SCS) or widely distributed by the SCS, having been initially introduced by other means.

Plant names	Origin Source
Asteraceae *Euryops multifidus*	South Africa*
Asteraceae *Pentzia incana*	South Africa*
Chenopodiaceae *Atriplex semibaccata*	Australia*
Fabaceae *Melilotus indicus*	Eurasia*
Fabaceae *Melilotus officinalis*	Eurasia*
Geraniaceae *Erodium cicutarium*	Europe*
Poaceae *Agropyron cristatum*	Turkey*
Poaceae *Andropogon ischaem*	Turkey*
Poaceae *Avena fatua*	Europe
Poaceae *Bromus rubens*	Europe
Poaceae *Cynodon dactylon*	Old world*
Poaceae *Eragrostis curvula*	South Africa*
Poaceae *Eragrostis lehmanniana*	South Africa *
Poaceae *Pennisetum ciliare*	South Africa*
Poaceae *Schismus barbatus*	Old World*

Figure 1.—*Euryops multifidus* (Asteraceae), also known as sweet resin bush, is a perennial subshrub. It has showy, yellow inflorescences which bloom in Arizona from December to March.

TAXONOMY, PHYTOGEOGRAPHY, AND PHYTOCHEMISTRY OF *EURYOPS MULTIFIDUS*

Euryops multifidus belongs to the tribe Senecioneae (Asteraceae), which includes the prominent genera *Senecio, Othonna,* and *Euryops* (Nordenstam, 1968). Representatives of the tribe are most common in South Africa. There are 97 species of *Euryops,* all of which occur natively only on the African continent; 96 of them occur only in South Africa. *Euryops multifidus* has a western Cape distribution in South Africa, ranging from the Malmesbury Flats in the south to Lake Namaqualand in the north (range includes the Cape Province, The Orange Free State, Basutoland, and Namaqualand States). It occurs in transitional communities between arid fynbos and karriod vegetation, in rhenosterveld and in succulent karroo. It often occurs on rocky outcrops between sea level and 1500 m in elevation (Nordenstam, 1969). The distribution of *E. multifidus* strongly overlaps that of *E. tenuissimus.* Interestingly, the latter species has been introduced as an ornamental in the arid southwestern United States, but has not yet become invasive.

The common name "resin bush" has been applied to all species of the genus *Euryops* (Smith, 1966). The common name is a literal translation of the Dutch name Harpuis bosch, "hars" (resin) "puisje" (a small pimple), referring to the resinous secretion exuded from the stem and branches in the form of small pimply drops on most *Euryops* species. Apparently the resin which accumulates under the bushes of most species was noted in colonial South Africa for its alleged medicinal value and was easily collected (Smith, 1966). Several of the species are known locally by distinctive names. The names applied specifically to *E. multifidus* include Soetharpuis ("soet" meaning "sweet"), Skaapbossie (meaning "sheep bush"), and Kapokbossie (meaning "chicken pox bush") (Smith, 1966; Nordenstam, 1968).

All members of the Senecioneae tribe are known for their distinctive phytochemistry compared to other Asteraceae and this has been used to taxonomically distinguish the genera of the tribe and species within each genera (Hegnaur, 1977). Known phytochemicals common to the three prominent genera of the tribe are diterpene derivatives, sesquiterpene lactones, furanoelemophilones, and acetophenones. The production of sesquiterpene lactones particularly is believed to be involved in defense against herbivores and parasites since most of them are intensely bitter and several are toxic (Hegnaur, 1977). Almost all members of the genus *Euryops* produce and secrete resin. The nature of the distinctive phytochemistry of the entire tribe suggests that many of the chemicals produced serve a role in defense against herbivores and parasites, as chemical inhibitors involved in allelopathy, or both.

ECOLOGY OF *EURYOPS MULTIFIDUS* IN ITS NATIVE RANGE

Euryops multifidus is listed in *A Catalogue of Problem Plants in Southern Africa* (Wells, et al., 1966), as a ruderal, agrestal, and pastoral weed. The undesirable characteristics of this weed include a) its ability to replace "preferred vegetation" b) its unpalatability and c) its occurrence as a contaminant of seed (Wells, et al., 1966). Sweet resin bush, like most members of the genus, has showy, yellow flowers which bloom during the winter and early spring. The 3-4 mm long, 1-2 mm wide achenes are covered by a wooly indumentum of 3-7 mm long white or brown hairs and are easily transported on clothing or fur. Three to seven achenes per inflorescence are commonly produced (fig. 2).

Information on the range ecology of *E. multifidus* in South Africa, particularly its palatability, is both sparse and contradictory. The problem stems from its description in *The Flowering Plants of South Africa* (Pole-Evans, 1928), one of the most prominent early floras of South Africa. Here, *E. multifidus* is described as being highly palatable to sheep, yet invasive of over-grazed and over-stocked land. Another more recent source

Figure 2.—The fruits of sweet resin bush, 3-4 mm long, 1-2 mm wide achenes, are covered by a wooly indumentum and are easily transported on clothing or fur. Three to seven fruits per inflorescence are commonly produced.

(Wells, et al., 1966) describes the palatability of sweet resin bush as uncertain. The early reference by Pole-Evans may have contributed to the selection of *E. multifidus* by the SCS in the 1930's for introduction to the southwest on the basis of its forage value. The unresolved question of the plant's palatability in its native range is further complicated by the distinctive phytochemistry of the genus described previously.

HISTORY OF INTRODUCTION OF SWEET RESIN BUSH BY THE SCS IN THE SOUTHWESTERN UNITED STATES

According to SCS Annual Reports, *Euryops multifidus* was among the first species collected by Regional Director F. J. Crider in 1934 for introduction to the arid Southwest. The main requisites for the species selected by the SCS for introduction into Arizona and New Mexico, were a) general climatic adaptation especially drought resistance, b) suitability for erosion control and other economic uses, and c) ease of propagation" (Crider, 1935). It should not be surprising given these criteria that *E. multifidus* and other species introduced by the SCS have become invasive and now constitute serious threats to native vegetation (Table 1). Each of the species was selected from vegetation native to semiarid regions such as western Asia, South Africa, and Australia. *Euryops multifidus* was selected for introduction into the arid southwest because it was believed to be extremely drought resistant; have good forage value, especially for sheep; and to propagate readily from seed" (Crider, 1935).

Each species selected by the SCS for introduction to the arid southwest was observed and increased for distribution in the Tucson Regional Conservation Nursery and then distributed to Area Nurseries in Safford, Arizona, and Shiprock and Albuquerque, New Mexico. Test plantings of exotics on public and private lands outside the nurseries were carried out by each area nursery. The Civilian Conservation Corps (CCC) was ultimately provided with stock from the nurseries and this was used in range restoration projects throughout the arid Southwest. Based on the recommendations of the SCS, seeds and young plants were also made available to anyone wishing to use them for range improvement. Unfortunately, the SCS kept few records describing the exact locations, dates, and fates of test plantings, and those that were kept have been lost as the SCS Plant Introduction Offices were closed or moved. One site of introduction at Frye Mesa, Arizona has been identified from the caption of a 1935 SCS photograph of a test planting. Few other specific records of test plantings and revegetation projects have been identified, although SCS Annual Reports indicate that they occurred.

In order to determine the current distribution of *E. multifidus* in the arid Southwest, we have compiled a list of sightings recorded in local floras and on specimens from herbarium collections in Arizona, California, New Mexico and Texas. We have found no records of the presence of sweet resin bush outside of Arizona. We have recently visited every documented report of sweet resin bush to determine whether it is still present, the extent of vegetation change that has taken place, and, if possible, the source of the introduction. We have determined that the current distribution of sweet resin bush is localized around four epicenters where sweet resin bush was apparently deliberately introduced in the late 1930's: Frye Mesa, Marijilda Canyon, Upper Verde Valley, and Sabino Canyon (fig. 3). Below we describe what is known about the introduction of sweet resin bush at each of these locations.

Frye Mesa

Sweet resin bush was introduced in 1935 onto Frye Mesa, 18.1 km southwest of Thatcher, Arizona, as part of an SCS experimental planting program (fig. 4). Sweet resin bush has spread from the abandoned 27 x 27 m fenced enclosure and has become established on the mesa top, on depositional slopes and along washes below the mesa, and at the base of the mesa. It occurs in vegetation ranging from the creosote bush-dominated flats at the base of the mesa (elev. 1060) to semi-arid grassland and surrounding chaparral and woodland on the mesa top (elev. 1300^{+} m). At the foot of the mesa, *E. multifidus* occurs on relatively deep, loamy, and calcic soils that are occupied by black grama *(Bouteloua eriopoda)* and a variety of native shrubs. On terraces of relatively young alluvium along washes, it has displaced stands of mesquite *(Prosopis velutina)* and catclaw acacia *(Acacia greggii)*. On the mesa top, it occurs on extremely clayey soils that support grasslands dominated by curly mesquite *(H. belangeri)*.

Vegetation dominated by *E. multifidus* on the mesa top is centered approximately on the abandoned planting site and is spreading on the mesa top from the point of introduction primarily as an advancing front (i.e., enlarging circle), radiating out in all directions from the point of introduction but advancing more quickly downslope and along drainages. This pattern of spread has produced an almost uninterrupted monoculture of *E. multifidus* over one quarter of the mesa top (ca. 1.3 km^2 of the ca. 4 km^2 area covered by semi-arid grassland). Interspersed within the semi-arid grassland vegetation on the mesa top there exists a mosaic of disjunct patches of vegetation dominated by *E. multifidus* ranging in size from 2000 m2 to less than 1 m^2. These patches serve as invasion foci (Mack, 1985) expanding in the same way as the main population and eventually coalescing with other patches or merging with the main population. The result is a patchwork of vegetation that is clearly visible from the valley floor at most seasons because of the contrasting phenology of the dominant grassland species and *E. multifidus*. Sweet resin bush is a brilliant green throughout the much of the year with showy yellow flowers from late December to March, when much grassland vegetation is dormant. The situation is reversed in summer.

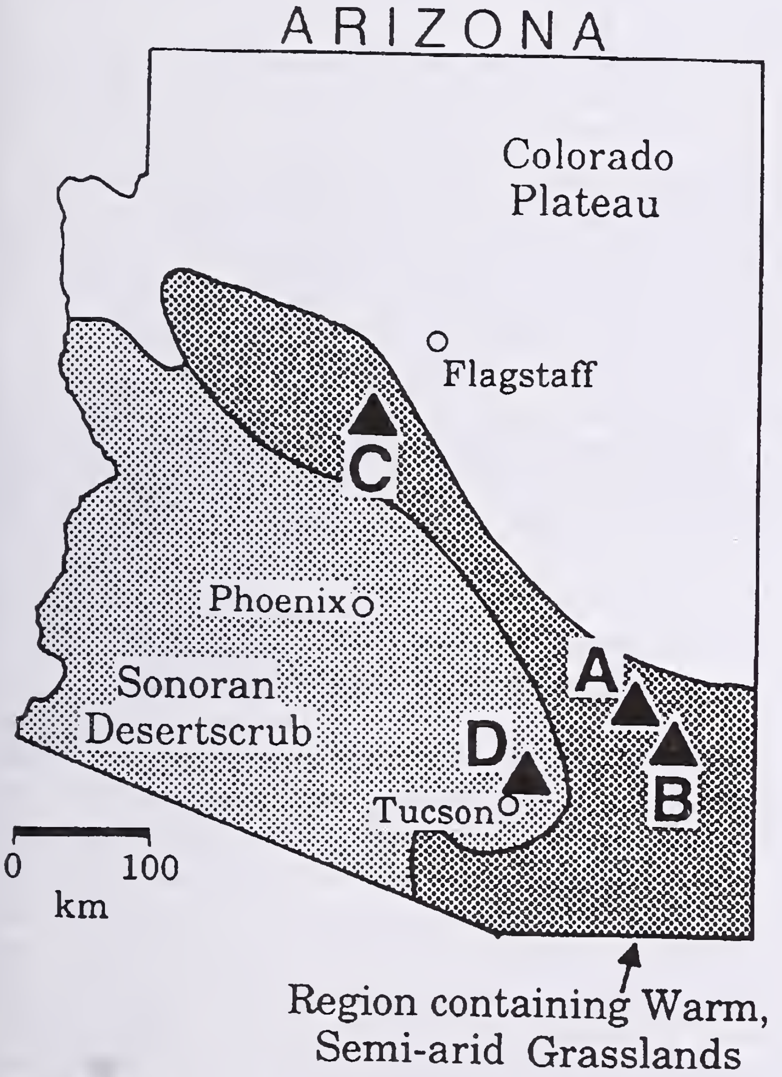

Figure 3.—The current distribution of sweet resin bush is localized around four epicenters in Arizona where this exotic was deliberately introduced. The locations of these epicenters are represented by solid triangles on this map of Arizona: *A.* Frye Mesa, *B.* Marijilda Canyon, *C.* Upper Verde Valley, and *D.* Sabino Canyon. At risk of future invasion are the warm, semi-arid grassland and Sonoran desertscrub vegetation of Arizona. The geographic range of these vegetation types is indicated on the map.

Figure 4.—Repeat photographs of the Soil Conservation Service (SCS) test planting at Frye Mesa, Arizona: *top, taken in 1935 by the SCS; and bottom, taken in 1991 by R. M. Turner. Sweet resin bush was introduced into the 27 x 27 m exclosure pictured in the 1935 photograph. Almost 60 years later, sweet resin bush forms an almost uninterupted monoculture over one quarter of the mesa top.*

Marijilda Canyon

E. multifidus was apparently introduced along FSR 57 approximately 2.4 kilometers from its intersection with Swift Trail Road (State Route 366), although no record of this introduction was found in the SCS documentation available in Tucson, Arizona. Circumstantial evidence for the role of the SCS include the presence of a Civil Conservation Corp (CCC) work camp in Marijilda Canyon during the period from 1934 to 1942 when *E. multifidus* was being used for revegetation work. CCC labor was used frequently to set up test plots and to revegetate eroded sites with plants recommended and provided by the SCS. The co-occurrence of *Pentzia incana* (a South African composite which was also introduced by the SCS for revegetation during this period) and the presence of small spreader dams (used by the CCC for erosion control) are also strong indications that *E. multifidus* was introduced by the SCS using CCC labor at this site.

E. multifidus occurs in two adjacent, yet currently distinct patches, one approximately 100 x 200 m and the other approximately 60 x 60 m in size. The populations occur along the gentle slope next to the roadway and extend into the adjacent Marijilda Wash. Individuals can be found in Marijilda Wash and along its banks as much as one quarter mile downstream from the introduction site. Both areas have relatively clayey soils and support a mixed species grassland in which sideoats grama *(Bouteloua curtipendula)* is the dominant species.

Upper Verde Valley

E. multifidus was also apparently introduced southeast of Cottonwood, Arizona along Camino Real near its junction with FSR 359. Similar to the Marijilda Canyon site, we have found no record of this introduction in the SCS documentation available in Tucson, Arizona, however sufficient circumstantial evidence exists to suggest this was also an SCS site where *E. multifidus* was planted for erosion control. The population occurs on a 1% slope and perpendicular to this slope are a series of berms built for erosion control. *E. multifidus* appears to have been planted in association with berm construction in an effort to control erosion.

The native vegetation appears to have been heavily disturbed and is currently dominated by *Gutierrezia sarothrae, Prosopis velutina,* and *Bromus rubens,* although it probably previously supported a grassland dominated by tobosa *(Hilaria mutica). E. multifidus* occurs on both sides of Camino Real. It appears to have been introduced only on the uphill side of the road and currently occupies an area of approximately 250 x 175 m. Downslope and north of the road *E. multifidus* occurs in a series of disjunct patches in approximately the same size area; however, individuals can be found as far as 300 m downslope from the edge of the patch.

Sabino Canyon

At Sabino Canyon in the Coronado National Forest in Tucson, Arizona, *E. multifidus* was apparently introduced at the Lowell Ranger Station. It is unknown whether this introduction was part of a SCS test planting or whether it escaped from a garden at the Ranger Station. Sweet resin bush has become naturalized on the grounds surrounding the Station and has spread into surrounding Sonoran Desert vegetation along washes and roadways.

CONSEQUENCES OF INVASION BY *EURYOPS MULTIFIDUS* IN THE SOUTHWEST

We sampled the vegetation in the four sites discussed above where sweet resin bush was introduced and has become invasive (fig.3). The sites represent an elevational and climatic continuum. The two sites at the upper elevational end experience greater effective precipitation and are characterized by vegetationally intact semiarid grassland (Frye Mesa, elevation 1300 m; Marijilda Canyon, elevation 1220 m). The intermediate site is a former semiarid grassland converted to a shrub-dominated community by a century of intense grazing (Upper Verde Valley, elevation 1065 m). The remaining site, characterized by Sonoran desertscrub, occurs on the lower, drier end of the continuum (Sabino Canyon, elevation 850 m).

Vegetation Change Resulting From Invasion By Sweet Resin Bush

At each of the four sites, we sampled vegetation within areas lacking sweet resin bush and adjacent areas invaded by sweet resin bush in order to characterize differences in the number and coverage of species occurring in each type of vegetation. At each site, the areas used in these comparisons were matched for slope, aspect, and soils. At Marijilda Canyon, Upper Verde Valley, and Sabino Canyon the coverage in each vegetation type was estimated in a total of fifty, 0.25 m^2 square plots spaced at 1 m intervals along two parallel, 25 m transects. At Frye Mesa, where the area invaded by sweet resin bush is much more extensive, the plots were spaced at 6 m intervals along two parallel, 150 m transects. The coverage of grasses and forbs was estimated from basal area, the coverage of shrubs and succulents was estimated from canopy area, and the coverage of bare soil was estimated to be the area of the plot not covered by plant basal area or rocks. Coverage is expressed as a percentage of the plot area and was recorded in six classes (0-5, 5-12, 12-25, 25-50, 50-75, 75-100 %).

Additionally, at Frye Mesa, we quantified the effect of sweet resin bush on the vigor of the small tree *Prosopis velutina* which is not excluded by *E. multifidus*, but exhibits significantly greater mortality of major branches in areas dominated by *E. multifidus* than in intact grassland. Stem mortality was expressed as the percentage of the total canopy composed of persistent, dead branches and was recorded in one of six mortality classes (0-5, 5-25, 25-50, 50-75, 75-95, 95-100%). We estimated the stem mortality for all trees in 5, 1000 m^2 circular plots spaced 40 m apart.

Frye Mesa and Marijilda Canyon, Semi-arid Grasslands

Invasion by sweet resin bush has produced dramatic and apparently persistent changes in the structure and function of the semi-arid grasslands sites we sampled. Sweet resin bush has spread extensively, forming near monocultures within both of these semi-arid grassland sites. All native grasses and most woody perennials including the prevalent subshrubs *Calliandra eriophylla, Eriogonum wrightii,* and *Gutierrezia sarothrae* are completely excluded from areas now dominated by sweet resin bush (Figs. 5A, 5B). The decrease in the species richness of perennial plants on areas occupied by sweet resin bush is dramatic (19 versus 2 species at Frye Mesa and 23 versus 6 species at Marijilda Canyon). Most striking is the elimination of *Gutierrezia sarothrae,* a weedy native which increases rapidly with disturbance. The small tree *Prosopis velutina* is not excluded by *E. multifidus,* but at Frye Mesa exhibits significantly greater mortality of major branches in areas dominated by *E. multifidus* than in intact grassland (59 versus 15% of major branches, respectively). The only woody perennial that is apparently unaffected by sweet resin bush is the subshrub *Krameria parvifolia* , which is equally prevalent and vigorous in intact and invaded areas at Marijilda Canyon (fig. 5B). Interestingly, *K. parvifolia* is a facultative root parasite (MacDougal and Cannon, 1910). The significance of this exception is discussed in the next section.

In both grassland sites, elimination of native species, especially grasses, leads to significant and dramatic increase in exposure of bare soil (Figs. 5A, 5B) and increased soil erosion. In the intact grassland vegetation, interdigitating bunches of native perennial grasses, particularly *Hilaria belangeri* , form soil dikes which capture and hold soil. Where the sweet resin bush has replaced the native species, not only is more bare soil exposed, but the soil is more easily removed. Exposed roots and soil pedestals around the bases of the remaining native grasses caused by soil erosion are clearly evident in the transition zone and in vegetation dominated by sweet resin bush. This situation is ironic since one of the goals of the SCS Plant Introduction Program was to introduce species which would reduce soil erosion.

Upper Verde Valley, Altered Semi-arid Grassland

In the upper Verde Valley, where the grasslands have been altered by heavy grazing, the native perennial grasses *(Hilaria mutica, H. belangeri,* and *Panicum obtusum)* have been excluded and replaced by woody plants *(Gutierrezia sarothrae* and *Prosopis velutina).* Inspite of this transition to vegetation dominated by indigenous disturbance tolerators, we found that the coverage and diversity of these species are significantly reduced in the presence of sweet resin bush (Fig 5C). Coverage of the annual forb *Plantago insularis* was also found to be dramatically different in invaded and uninvaded vegetation during the spring of 1993. In the uninvaded vegetation, this annual formed a nearly continuous carpet in 100% of the plots sampled (average density 3700 plants/m^2, average biomass 48 g/m^2), whereas in vegetation dominated by sweet resin bush, *P. insularis* occurred in 90% of the plots sampled (average density 1100 plants/m^2, average biomass 12 g/m^2).

In this altered grassland, more than 50% of the soil surface is bare even in the absence of sweet resin bush (as compared to less than 10% in vegetationally intact grassland). However, the exposure of bare soil does not increase further following sweet resin bush establishment (fig. 5C).

Sabino Canyon, Sonoran Desertscrub

In contrast to the grassland sites, the species richness of the desertscrub vegetation is not significantly reduced in the presence of *E. multifidus*

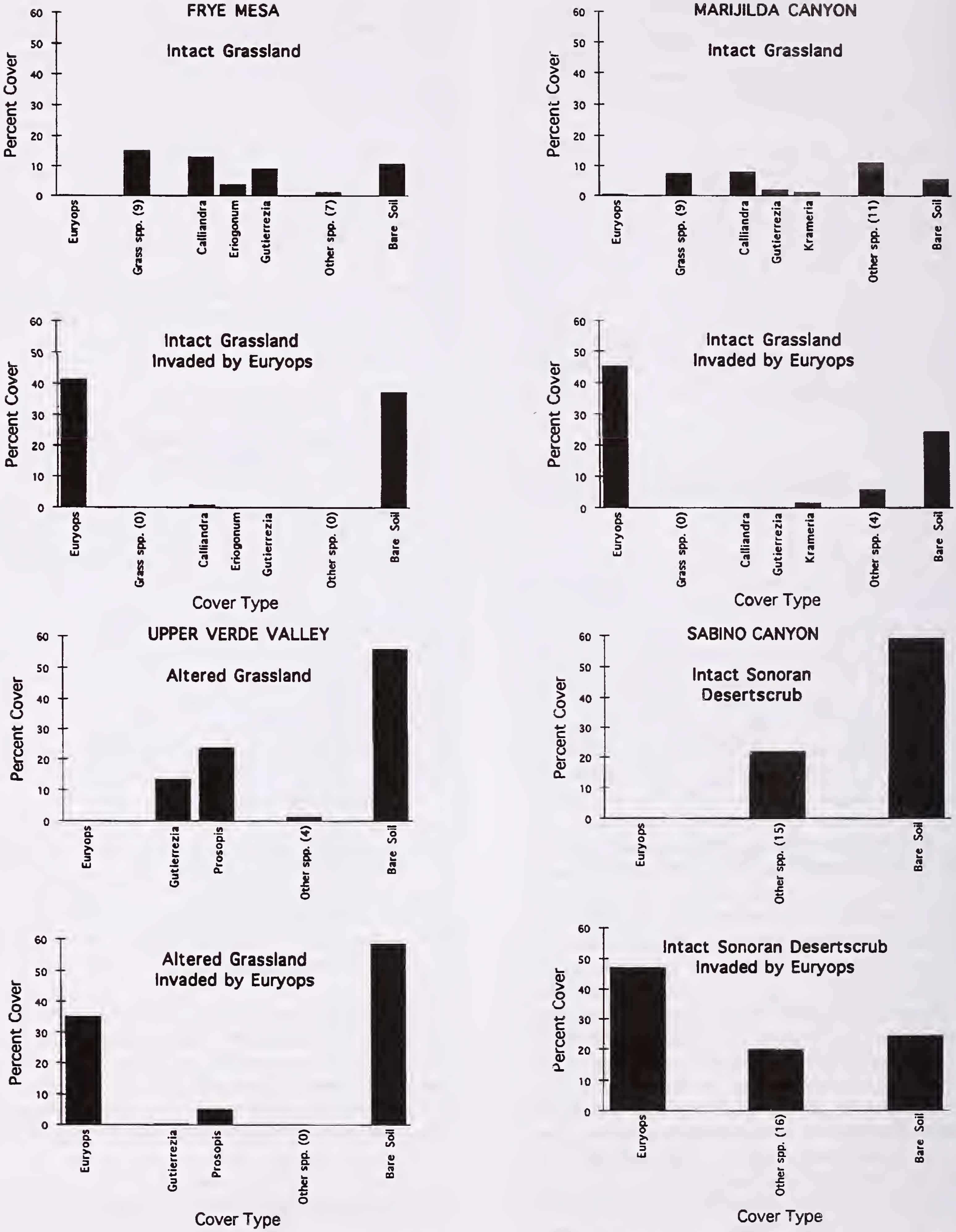

Figure 5.—Mean percent cover of *Euryops multifidus* and native species in vegetationally intact and adjacent invaded areas. Coverage is given for perennial grasses, prominent woody species, and all other perennial species combined at: *upper left, Frye Mesa, upper right, Marijilda Canyon, lower left, Upper Verde Valley, lower right, Sabino Canyon. Coverage of bare soil, the area of the plot not covered by plant basal area or rocks, is also given.*

(fig. 5D). However, some common perennial subshrubs *(Encelia farinosa* and *Porophyllum gracile)* were significantly less frequent in vegetation invaded by *E. multifidus* (fig. 5D). At this site, sweet resin bush seems to be invading bare ground, rather than displacing the existing members of the community (notice the reduction in coverage of bare soil where sweet resin bush has invaded, fig. 5D). Although the coverage of *E. multifidus* at this site is comparable to the coverage found in semi-arid grassland vegetation, a significant number of plots contained large, recently dead individuals of *E. multifidus.* The inability of sweet resin bush to replace the native species and the high turnover in the exotic population suggests this site occurs near the lower, drier limits of the range of this plant.

ABRUPT TRANSITION FROM NATIVE VEGETATION TO VEGETATION DOMINATED BY *EURYOPS MULTIFIDUS*

One of the most striking features of the grasslands that have been invaded by sweet resin bush is the sharpness of the transition between native vegetation and vegetation dominated by *E. multifidus.* We characterized this transition at Frye Mesa by sampling vegetation along transects from intact grassland to areas dominated by sweet resin bush. The transects, 25 m in length, were oriented such that the 10 m point was located at the edge of the area dominated by sweet resin bush, the start of the transect (0 m) within desert grassland vegetation, and the end (25 m) within the area invaded by sweet resin bush. In this way, vegetation sampling from 0 to 25 m along the transect characterized the spatial transition from desert grassland to zones dominated by *E. multifidus.* The canopy coverage of vegetation was measured as described above.

Our vegetation sampling demonstrates that the transition from native vegetation to *E. multifidus* monoculture is extremely abrupt and is characterized by the death and loss of dominant native grasses and shrubs, concomitant with an increase in sweet resin bush (fig. 6). An extreme consequence of the loss of perennial grass cover is an increase in the exposure of bare soil. Within 6 m along transects from desert grassland to vegetation invaded by *E. multifidus* the mean coverage of *E. multifidus* and of bare ground increased from 0 to 36% and 9.5 to 25%, respectively; in the same space the mean coverage of the dominant bunchgrass species, *Hilaria belangeri,* dropped from 12% to less than 4% and the frequency of dead clumps of this grass increased (fig. 6). The coverage of the small shrubs *Gutierrezia sarothrae* and *Calliandra eriophylla* also declined as the coverage of sweet resin bush increased. Isolated patches of sweet resin bush representing more recent foci of establishment and occurring up to hundreds of meters away from the central population exhibit the same sharp transition from monoculture to grassland.

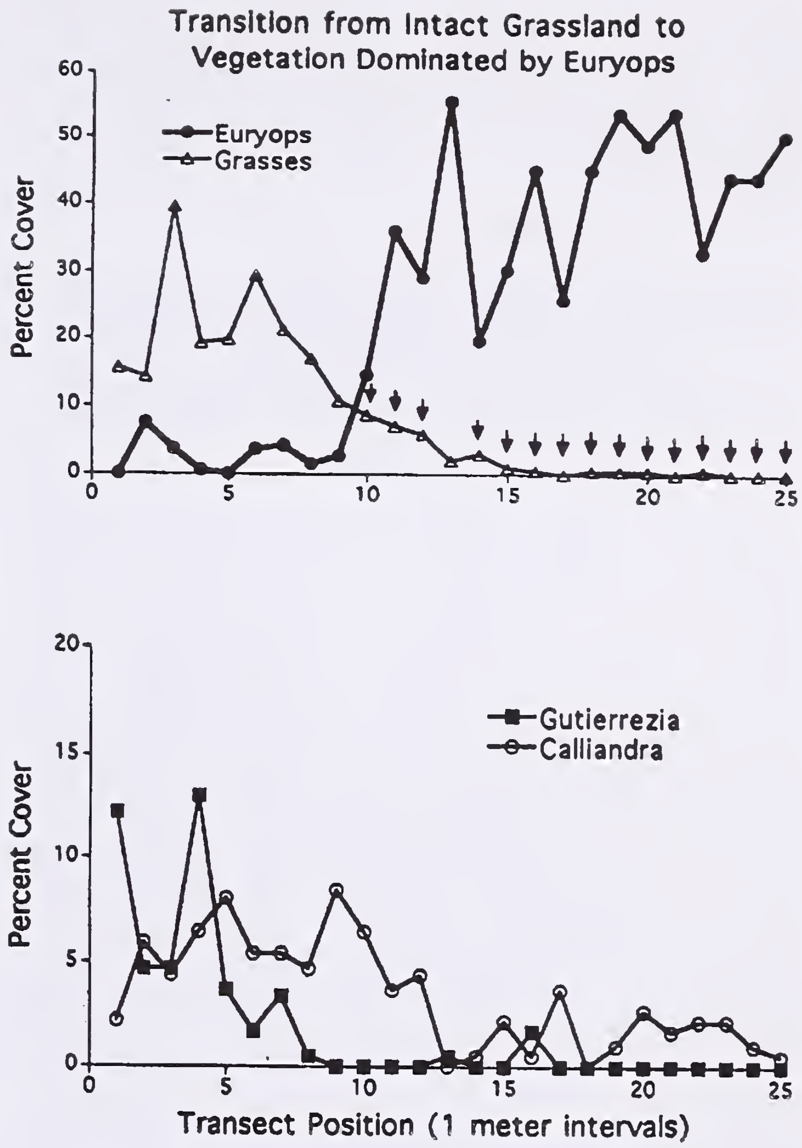

Figure 6.—Mean percent cover of *E. multifidus*, native perennial grasses, and the prominent subshrubs *Gutierrezia sarothrae and Calliandra eriophylla* along five, 25 m transects from grassland to sweet resin bush dominated vegetation. The transects were oriented such that the 10 m point was located at the edge of the area dominated by sweet resin bush, the origin within grassland vegetation, and the 25 m endpoint within the area invaded by sweet resin bush. The *Small Arrows* indicate the presence of dead remains of perennial grasses.

The sharpness of the transition is due in part to limited recruitment of sweet resin bush away from mature individuals. Although the achenes can be dispersed by attachment to fur or clothing or by water, most accumulate near the base of the adults where they germinate. The increase in bare soil at the base of adult plants may also aid the seedlings of sweet resin bush in becoming established there. Whether recruitment away from the patch is limited by seed dispersal or the availability of suitable sites (i.e., areas with exposed soil) is unknown.

POTENTIAL MECHANISMS TO EXPLAIN THE CHANGES IN STRUCTURE AND FUNCTION OF VEGETATION COMMUNITIES INVADED BY *EURYOPS MULTIFIDUS*

We have demonstrated that sweet resin bush is capable of changing the structure of semi-arid grassland communities by forming sharply defined areas characterized by the elimination of almost all native species and the concomitant exposure of soil to erosion. The substantial mortality of native species in the transition zone suggests that this dieback is the result of the proximity of the older *E. multifidus* individuals. These changes may result from either direct interaction between exotic and native (such as interference or exploitation competition) or indirect interaction (such as the alteration of an ecosystem level property by the exotic which in turn affects the native vegetation). We are currently testing hypotheses consistent with the possibility of both direct and indirect interactions between exotics and natives although much of our research is as yet preliminary.

The nearly complete exclusion of native flora by *E. multifidus* and the formation of a zone of bare soil and dead plants at the advancing front of even small populations of sweet resin bush suggested that interference competition may be the primary mechanism of interaction.With a simple germination experiment, we tested the hypothesis that this interaction may be due to persistent allelopathic soil alteration. We collected soil from intact grasslands and areas dominated by *E. multifidus*. Quick-germinating radish seeds were sown in both of these soils as well as in a mixture of each soil with 20% (by volume) finely ground, activated charcoal. The activated charcoal was added to adsorb any potential allelopathic compounds. A total of 96 seeds per treatment were sown, 4 seeds per 5 x 5 x 7 cm pot, in a completely randomized design. Surprisingly, we found no difference in germination (nearly 100% in all treatments) and no difference in seedling height among soil treatments (data not shown). Both of the charcoal amended treatments had slightly increased seedling mortality due to charcoal particles adhering to and damaging cotyledons. Given the extensive mortality of native species that occurs in proximity to established sweet resin bush plants, we believe that this simple experiment was adequate to identify persistent soil alterations if they did exist. We now feel that persistent allelopathic soil alteration is not the primary mechanism by which sweet resin bush excludes native grassland species. However, there may be other types of interference between sweet resin bush and native species such as the root interactions that occur between *Larrea tridenta* and *Ambrosia dumosa* as described by Mahall and Callaway (1991).

Other field observations suggest that competitive exploitation of resources, especially water, may be an important competitive mechanism. The bright green appearance of sweet resin bush much of the year, especially during the winter when many of the dominant native perennials are dormant, suggests that sweet resin bush is capable of efficiently acquiring and potentially exploiting most of the available moisture within its proximity up to two months before native species become active. We hypothesize that this exploitation of water is the mechanism responsible for partial dieback (rather than complete elimination) of some woody plants such as *Prosopis velutina*. The only woody plant that thrives in both intact grassland and monocultures of sweet resin bush is *Krameria parvifolia* (fig. 5B) at Marijilda Canyon. This shrub is a facultative root parasite which is capable of obtaining water from the xylem of other plants (MacDougal and Cannon, 1910). Since *Krameria parvifolia* can potentially obtain water parasitically from the roots of *E. multifidus*, it may be immune to the depletion of soil water by *E. multifidus*. We will be investigating further the potential competition between sweet resin bush and native grassland species for soil moisture in our future research.

A third category of mechanisms we are investigating involves indirect interactions between sweet resin bush and the native vegetation. In future research, we will test the hypothesis that changes in ecosystem level properties such as accelerated erosion or the elimination of members of the community that make up different trophic levels (e.g., rhizosphere microorganisms) may in turn accelerate the death of the native plant species.

Although our investigations of the potential mechanisms to explain the success of sweet resin bush in the Southwest are preliminary, they suggest that pre-adaptation of sweet resin bush to the climate of the arid Southwest has played a significant role in its success.

GEOGRAPHIC AREA IN NORTH AMERICA AT RISK OF FUTURE INVASION BY EURYOPS MULTIFIDUS

In southern Arizona, semi-arid grasslands occupy an elevational range between 900 and 1520 m. The three grassland sites where sweet resin bush has become invasive range from 1060 to 1460 m elevation. Sweet resin bush becomes dominant on many kinds of soil including 1) those with thick clay-enriched horizons (Haplargids, Paleargids, Argiustolls), 2) deep, loamy calcic soils (Calciorthids), and 3) young, sandy to gravelly soils of recently formed alluvial terraces (Torrifluvents and Camborthids). These account for most of the soils of semi-arid grasslands in southern Arizona. Consequently, we believe that most of the semi-arid grasslands of southern Arizona are at risk (fig. 3). The considerably colder winter conditions of the temperate, semi-arid grasslands of the Colorado Plateau in northeastern Arizona are probably too severe for *E. multifidus*.

The occurrence of sweet resin bush in Sonoran desertscrub at Sabino Canyon suggests that some areas supporting this vegetation type may also be at risk (fig. 3). However, at Sabino Canyon, *E. multifidus* did not entirely exclude the native vegetation. The abundance of dead *E. multifidus* following a recent dry year suggests that habitats supporting desertscrub may be at the drier limit of the potential range of *E. multifidus*. Detailed future analyses of the distribution of *E. multifidus* with respect to climate in South Africa may provide a more detailed and predictive estimate of potential range of spread in North America.

DISCUSSION

Between 1935 and 1942 the SCS introduced a number of exotic species in the arid southwestern United States for the purpose of range improvement and erosion control (Table 1). The introduction of many of these species has subsequently been encouraged by public and private groups, the end result being that many of the exotics introduced in the early days of the SCS have become some of the Southwest's most serious ecological problems. The most notorious examples are the drought-tolerant African grasses: bufflegrass (*Pennisetum ciliare*) and the lovegrasses (*Eragrostis lehmanniana* and *E. curvula*). All three of these species have been introduced extensively in heavily grazed pastureland and, like sweet resin bush, are capable of maintaining virtual monocultures by competitively excluding native species where they have been introduced. In one of the few studies which has attempted to document the consequences of invasion by these exotic grasses, Bock et al. (1986) demonstrated that the native semi-arid grassland community in their southeastern Arizona study site had a significantly greater variety and abundance of indigenous grasses, herbs, shrubs, grasshoppers, rodents and birds than the areas dominated by African lovegrasses. Our preliminary observations suggest that monocultures of sweet resin bush may be equally biologically sterile with regard to mammalian, avian, and insect species (data not shown).

The consequences to the native ecosystem of invasion by exotic plants can extend beyond the loss of native diversity, resulting in ecosystem level changes that perpetuate further reductions in native diversity. For example, many of the exotic grasses which have established in the Southwest, especially bufflegrass and red brome (*Bromus rubens*), tolerate burning better than most natives. Because they can alter the structure of vegetation communities by producing continuous canopies of grass and can produce substantially more biomass than the natives during favorable years, they seem to promote fires that have a more adverse affect on the long-lived native vegetation than the exotics. We do not know whether sweet resin bush has altered disturbance regimes in the vegetation communities it has invaded, but effects on hydrologic and biogeochemical-cycling regimes are likely to have occurred. Further, we have observed substantially enhanced erosion rates where sweet resin bush has invaded semi-arid grassland. This ecosystem level change is likely to have permanently altered sites that have been invaded by sweet resin bush, even if the exotic is removed.

The growing list of exotics which have become naturalized in the Sonoran Desert and semi-arid grassland vegetation of the southwestern United States suggests that these vegetation types are indeed highly vulnerable to invasion by exotic plants, particularly to those pre-adapted to the local climate and grazing regimes. The dramatic consequences of invasion that have been documented for the few exotic species studied suggest that these vegetation types are not only vulnerable, but have little resilience to invasion once exotics become established and ecosystem changes are initiated.

We suggest that the ecological danger posed by sweet resin bush in the Southwest is significant. We believe that by examining further the characteristics of successful invaders and the consequences of their spread, we can continue to learn more about the structure and function of the native vegetation communities and their vulnerability to invasion. We suggest future research on sweet resin bush be focused on a) the life history characteristics of sweet resin bush and the mechanisms by which native species are excluded, b) the rate and mode of spread in different vegetation communities where it has been introduced c) the ecology of interactions between sweet resin bush and other species in its native range, d) quantification of native ecosystem level changes as a consequence of invasion by sweet resin bush (including soil erosion and the biodiversity of microorganisms in the soil), and e) assessment of the necessity and feasibility of an eradication program based on our knowledge of the ecological consequences of invasion by sweet resin bush.

We hope this discussion of the dramatic consequences that have occurred as a result of invasion by sweet resin bush and the other exotics mentioned above demonstrates the severity of this ecological problem and illustrates the importance of implementing management practices that minimize the future consequences of invasion by exotic species.

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One Hundred Years of Vicissitude: Terrestrial Bird and Mammal Distribution Changes in the American Southwest, 1890 - 1990

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Abstract.—Distribution changes over the past 100 years are summarized for a number of species of terrestrial mammals and birds in Arizona and New Mexico. At least 39 species appear to have been extirpated or suffered range restrictions, while 55 others have experienced range expansions. Even when exotics are excluded, the biodiversity of endotherms is now greater than in 1890. As expected, the ranks of the "losers" contain a disproportionate number of large predators and grassland-associated animals. By way of contrast, the majority of the "winners" were forest and/or scrubland-adapted species. More germane to this study was the fact that more than 70 percent of the "winners" were species which have their primary biotic affinity south of the U.S.-Mexico border. Few Rocky Mountain, Great Basin, or Great Plains species increased in distribution. Possible reasons for these phenomena are discussed including the potential effect of increasing winter temperature minima on plant distributions and the availability of invertebrates.

Much well-deserved concern has recently been expressed regarding an increase in the number of endangered species and a loss in biodiversity. Each year sees additional animals proposed for state or federal listing as "threatened" or "endangered" species. But, although much effort is expended to determine the actual status of these animals, the stated reasons for their decline are often vague and subjective. Rarely, and only recently, have overall changes in the status of an animal's habitat and its associated biota been properly evaluated and appreciated. To achieve a better perspective of the possible influence of an overall environmental change, we examined the distributional status of terrestrial mammals and birds in the states of Arizona and New Mexico during the past 100 years.

THE STUDY AREA

The states of New Mexico and Arizona in the American Southwest provide an ideal study area for a long term analysis of the effects of climatic change on endothermic animals. The region's southern position astride the Continental Divide, and its great range in elevations from less than 30 m where the Colorado River enters Mexico to more than 4,000 m atop Wheeler Peak in the Sangre de Cristo Mountains, provide climates ranging, from subtropical to arctic-boreal. Also, depending on location, mean annual precipitation can be as low as 75 mm to greater than 780 mm. The result is that almost every biome found in North America — alpine tundra, boreal conifer forest, temperate deciduous forest, evergreen woodland, chaparral, grassland and desert — can be found somewhere in these two states. Moreover, the Southwest's othography provides both mountain and valley corridors extending northward into the Rocky Mountains and Great Basin as well as southward into Mexico. Thus, birds, and many mammals, can, in a single day, travel

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from an environment in which freezing temperatures may occur at any time of the year to those which rarely experiences a 24-hour freeze.

The American Southwest's biotic diversity is also due to its special evolutionary history. Most of the region was not covered by ice sheets during the Pleistocene Epoch. Although the alternating drying and cooling that accompanied glacial advances and retreats had an immense effect on Southwest environments, the region's great topographic relief, manifested in such features as the Grand Canyon and Mogollon Rim, coupled with it southern latitudes, served to provide warm-temperate refugia for a number of endemic Pleistocene plants and animals. These features, coupled with the erratic but overall drying and warming trend that accompanied the onset of Holocene times about 11,500 years ago, have resulted in the Southwest being the location of isolated Pleistocene forests on mountain-tops, relict mild-winter conifers and water-dependent deciduous forests beneath the Mogollon Rim, and a tension zone of diminishing areas of grasslands and evergreen woodlands between 1000 and 2000 m elevation. The most recent phenomenon has been the development and advance of the four North American deserts, parts of all of which occur in the Southwest (see e.g., Van Devender et al. 1987). The result today is a great mixing of old and new plant and animal species that have segregated out into a mosaic of Tertiary, Nearctic and Neotropical habitats (Lowe and Brown 1982).

This biodiversity, coupled with the region's general aridity, has made the Southwest a focal point of study for a variety of environmental disciplines. During the last 100 years the Southwest has provided a unique field laboratory for zoologists, botanists, ecologists, archeologists and paleontologists. Not only has the region's abundant fossil record been much investigated (see e.g., Harris 1985), much of the pioneering and ongoing work on fossil pollen analysis, tree-ring chronology and other techniques to measure climatic change have been focused in or near the Southwest. Especially germane to this effort is the work of Hastings and Turner (1965) and their successors who have demonstrated important landscape changes over the past 100 years through the use of repeat-photography. The result is that few if any regions of North America have a more complete fossil and recent history of faunal and vegetative changes. That these changes have been dramatic and have been shown to have continued into modern times, both facilitates and lends impetus to the work at hand.

Another factor contributing to our understanding of the Southwest's biota was its relatively late settlement by Western Man. Acquired by the United Stated from Mexico in the mid-19th Century, New Mexico Territory had remained virtually uninhabited by either Spaniards or Mexicans. This circumstance enabled American scientists to report on the region's landscapes and biota prior to large scale ranching and agricultural development (see e.g., Davis 1982). Moreover, this late settlement, combined with the region's rugged topography and general aridity, prolonged the settlement process. Even as late as 1880, few settlements existed outside of the river valleys and the environs of mining camps. The late entry of Arizona and New Mexico into the Union in 1912 also allowed for the inclusion of sizable tracts of land within National forests and parks before they were irreversibly impacted by a long history of unregulated grazing, land clearing and other ecologically disruptive influences.

Last, but not least, the American Southwest was visited by a number of competent naturalists around the turn of the Century. People like Elliot Coues, E.A. Mearns, Herbert Brown, H.S. Swarth, Vernon Bailey and Florence Merriam Bailey made systematic attempts to inventory the birds and mammals of Arizona and New Mexico and reported on their habitat affinities and status (e.g., Swarth 1914). Other investigators conducted studies on the distributions of particular species of birds and mammals as well as the natural history of specific locales (e.g., Merriam 1890). These studies have continued to the present day, allowing for a progression of comprehensive treatments on the region's mammals and birds (e.g., Coues 1867, Mearns 1907, Ligon 1927, Bailey 1928, Bailey 1931, Hall 1946, Ligon 1961, Phillips et al. 1964, Findley et al. 1975, Hubbard 1978, Monson and Phillips 1981, Hoffmeister 1986). Also relevant to this study is the fact that 100 years of climatological data are now available for a number of New Mexico and Arizona stations (see e.g., Karl et al. 1989, Sellers et al. 1985).

STUDY METHODS AND LIMITATIONS

Using as base references the basic works on avian and mammalian distribution noted above, state endangered animal summaries (Arizona Game and Fish Department 1988, New Mexico Department of Game and Fish 1992), specific journal articles (e.g. Hock 1952, Hubbard 1977, Lomolino et al. 1989) and our own work (e.g.

Brown 1973 and 1989, Davis and Dunford 1987, Davis and Brown 1989, Davis and Callahan 1992), we listed those species of terrestrial mammals and birds which appear to have increased or decreased their Southwest distributions during historic times. For comparative purposes we have also listed terrestrial species of exotics which are deemed to have established self-sustaining populations. To determine if the distribution of animals in certain habitats had changed more than in other habitats, each species was assigned the biotic community or communities with which it is primarily associated. These lists were then commented on and added to by John Hubbard, Gale Monson and Barry Spicer. Dr. Hubbard and Mr. Monson are recognized authorities on the status of birds in New Mexico and Arizona, and Dr. Hubbard and Mr. Spicer have been involved in the preparation of status reports on rare and endangered species for their respective state agencies. Their enthusiastic assistance was a major contribution to this study.

Bird names follow Hubbard (1978) and Monson and Phillips (1981). Mammal names follow Jones, et. al. (1992). The biotic community affiliations are those discussed in Brown (1982, 1994) and mapped by Brown and Lowe (1980, 1990).

Our lists only include those species of terrestrial birds and mammals known to have bred in the Southwest states of Arizona and New Mexico since 1890. Subspecies are not included. This limited geographical perspective is due both to a lack of comparable historical data for the Mexican states of Baja California, Sonora and Chihuaha and to the fact that we have less experience with conditions in these states as well as those in California, Nevada and Texas. Regrettably, comparable historical data and experience are also lacking for the Southwest's herptile and invertebrate faunas. Such information could have contributed greatly to the breadth of our analysis.

The massive changes that have occurred in the Southwest's riparian and other wetland habitats also precludes a comparable analysis of the region's aquatic and wetland faunas. However, it is important to point out that the dire status of the Southwest's native fishes and their extensive displacement and replacement by "exotics" has been well documented (see e.g. Minckley and Deacon 1991). It goes without saying that endothermic animals such as the River Otter (*Lutra canadensis*) and Beaver (*Castor canadensis*) have experienced similar displacements. Nonetheless, it should also be noted that a number of wetland birds including the Bald Eagle (*Halieatus leucocephalus*), Clapper Rail (*Rallus longirostris*), Mexican Duck (*Anas diazi*), Black-bellied Whistling Duck (*Dendrocygna autumnalis*) and Cattle Egret (*Bubulcus ibis*) now enjoy a greater distribution in these two states than they did in 1900.

There are, of course, a number of problems inherent in any comparative analysis of patterns of past and present animal distributions. Perhaps the foremost of these is that any knowledge of the actual previous (and present) distribution of a species is imperfect and open to interpretaiton. The age-old question of whether a new locale for a species represents a range extension or merely a lack or failure of previous sampling efforts will never be answered in every case to everyone's satisfaction. The distributions of some species, especially those at the edge of their range, are especially dynamic and the occurrence of these species in Arizona or New Mexico is inherently sporadic (e.g. the Ghost-faced Bat (*Mormoops megalophylla*) and Rose-throated Becard (*Pachyramphus aglaiae*) in Arizona. These species are either omitted from our analysis or indicated with a question mark. Moreover, the status and distribution of some species such as the Long-nosed Bat (*Leptonycteris curasoae = sanborni*) is a matter of some debate (see e.g., Howell and Roth 1981, Cockrum 1991). For purposes of this analysis, we have excluded those species which are known to irregularly occur in the American Southwest or whose past and present distributional status is considered questionable by biologists involved in their study. Since this is a study of the dynamics of distribution, we have considered only changes in the distribution of species, not an increase or decrease in population sizes.

RESULTS

Nine species have been were extirpated in Arizona and New Mexico (Table 1). Not surprisingly, three of these are large carnivores which were systematically hunted as livestock predators. One other, the black-footed ferret, may have been lost as a result of prairie dog control efforts, although the animal's demise due to one or more introduced pathogens is a distinct possibility. Two large game animals, the elk and bison, formerly present and subsequently extirpated, have since been reintroduced, the former with marked success. The remaining three extirpated species are grassland-associated birds.

Thirty-four species are still present but appear to have experienced range reductions since 1890 while 55 species now seem to enjoy an expanded distribution (Tables 2 and 3). Although human-assisted introductions and the occurrence of artificial feeding and watering sites can explain some of the increases in distribution, the reasons for most are unclear and cannot be explained by direct human intervention. Conversely, introduced diseases, competition with exotic animals and grazing by livestock have been implicated as reasons for many of the species now having decreased distributions.

Only 19 exotics (13 mammals and six birds) appear to have become established in Arizona and New Mexico by 1890 (Table 4). The two camels have since been eliminated and the status of several other species (e.g., Swine, Chukar Partridge and Black Rat) may be tenuous. A surprising result of the analysis was that even when exotic animals are excluded and extirpated species included, more animals appear to have experienced range expansions (55) than declines (43). As far as terrestrial birds and mammals are concerned, biodiversity is now greater in the American Southwest than it was in 1890.

Tables 5 and 6 summarize the formation-types, biotic community affinities and centers of biogeographic distributions of 39 mammals and birds which appear to now have reduced distributions in the American Southwest. The majority (59%) of these are grassland-affiliated species. Nearly all of the biogeographic provinces are represented, with nearly as many species having their centers of distribution to the north or northeast (49%) as to the south or southeast (51%).

Formation-class affinities and biogeographic centers for the 55 species of mammals and birds breeding in the American Southwest and which have experienced range expansions are presented in Tables 7 and 8. Twenty-nine, or more than half (53%), of these "winners" are forest and woodland species. Another seven (13%) are associated with chaparral or other scrublands, only seven are grassland-associated species and, oddly enough, only three (5%) are desert species. The most surprising statistic, however, is the number of species having their biogeographic center of distribution to the south of the American Southwest (Table 8). More than half of the "winners" have their nearest ecological center in either Mexico's Sierra Madre (27%) or the forests and scrublands of Sonora and Sinaloa (29%). None of the "winners" are headquarted in the Great Basin and only two mammals and two birds can be considered as Rocky Mountain species.

The above distributional changes strongly suggest recent changes in both landscape character and climate. Indeed, a change in vegetation from open grasslands and woodlands to more closed communities of forest and scrubland has been well documented for Arizona by Hastings and Turner (1965) and in New Mexico by Dick-Peddie (1993). While climatic change has been going on in the Southwest since the advent of the Holocene (see e.g., Houghton et al. 1990, Davis and Shafer 1992), the amount of this occurring within a time frame of only 100 years is difficult to assess. Climatic data since 1890 show no appreciable trends in either summer or winter precipitation amounts in Arizona (Sellers et al. 1987) and changes in minimum temperatures are often masked by the effects of urban warming (Kirby and Sellers 1987, Sellers 1990). Nonetheless, regional climatic data which has been corrected for the effects of urban warming shows a significant increase in winter, summer and annual temperature minima since ca. 1960 for the "Southern Deserts" which encompasses southern New Mexico and Arizona (Karl et al. 1989). No such trend in apparent for the "Great Basin" and "Southern Rockies" regions. Clearly, further investigation into the possible effects of short-term climatic change are warranted. It may be instructive to moniter and evaluate short-term (50 to 100 year) changes in the distributions of select species of terrestrial ectotherms (invertebrates and herptiles) to determine what role, if any, climate change might also be playing on their distributions in the American Southwest.

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Table 1.—Nine species of terrestrial mammals and birds breeding in the American Southwest in 1890 and which were extirpated prior to 1990.

Species	Primary Biotic Affinities in the Southwest
	MAMMALS
Ursus arctos, Grizzly Bear[1]	Rocky Mountain Subalpine Forests and Grasslands downward to Madrean Evergreen Woodland and Interior Chaparral
Canis lupus, Gray Wolf[1]	Rocky Mountain Montane Forests downward through Plains Grassland and Madrean Evergreen Woodland to Chihuahuan Semidesert Grassland
Mustela nigripes, Black-footed Ferret[2, 3]	Great Basin Grassland
Panthera onca, Jaguar[1]	Madrean Evergreen Woodland and Riparian communities upward to Rocky Mountain Conifer Forest
Cervus elaphus, Elk[4]	Rocky Mountain Conifer Forest and Meadow Grassland
Bos bison, American Bison[4]	Plains Grasslands in West Texas and New Mexico
	BIRDS
Falco femoralis, Aplomado Falcon	Chihuahuan Semidesert Grassland
Centrocercus urophasianus, Sage Grouse[5]	Great Basin Desertscrub with Wet Meadows
Pediocetes phasianellus, Sharp-tailed Grouse[5]	Intermountain Grassland interspersed with Scrub

[1] Purposefully extirpated through direct human intervention.
[2] Inadvertently extirpated through direct human intervention.
[3] Shown to be susceptible to diseases transmitted by introduced animals.
[4] Successfully reintroduced after 1912.
[5] Populations shown to be susceptible to livestock grazing and changes in land use.

Table 2.—Thirty-four species of terrestrial mammals and birds breeding in the American Southwest and experiencing range reductions since 1890.

Species	Primary Biotic Affinities in the Southwest
	MAMMALS
Lepus alleni, Antelope Jackrabbit	Sonoran Savanna Grassland, Sonoran Desertscrub, Chihuahuan Semidesert Grassland
?*Spermophilus tridecemliniatus*, Thirteen-lined Ground Squirrel	Plains and Great Basin Grasslands
Cynomys ludovicianus, Black-tailed Prairie Dog[1]	Plains and Chihuahuan Semidesert Grasslands
Cynomys gunnisoni, Gunnison's Prairie Dog[1]	Great Basin Grassland
?*Tamius minimus*, Least Chipmunk	Rocky Mountain Subalpine and Montane Conifer Forests and Montane Meadows
?*Crategeomys castanops*, Yellow-faced Pocket Gopher	Plains Grassland
Microtus pennsylvanicus, Meadow Vole[2]	Rocky Mountain and Great Basin Meadows and Marshlands
?*Sigmodon arizonae*, Arizona Cotton Rat	Grassy areas within Sonoran Desertscrub and various Riparian Biomes
Zapus hudsonius, Meadow Jumping Mouse[2]	Rocky Mountain Subalpine and Montane Meadows; Marshlands
Vulpes velox, Kit Fox, Swift Fox[1,3]	Sonoran, Mohave and Chihuahuan Desertscrubs;Plains Grassland
Ursus americanus, Black Bear[1]	Rocky Mountain Subalpine and Montane Conifer Forests
Odocoileus virginianus, White-tailed Deer	Madrean Evergreen Woodland, Chihuahuan Semidesert Grassland and Riparian Forest within Interior Chaparral and other Biomes
Antilocapra americana, Pronghorn	Plains and Chihuahuan Semidesert Grasslands; Sonoran Desertscrub (Lower Colorado River Valley subdivision)
Ovis canadensis, Bighorn Sheep[3]	Sonoran and Mohave Desertscrub; Chihuahuan Semidesert Grassland; various Great Basin and Rocky Mountain Biomes
	BIRDS
Buteo regalis, Ferruginous Hawk	Great Basin Grassland
Buteo nitidus, Gray Hawk	Sonoran and adjacent warm-temperate Riparian Woodlands of Mesquite and Cottonwood trees
Caracara cheriway, Caracara	Sonoran Desertscrub
Meleagris gallopavo, Wild Turkey[3,4]	Madrean and Rocky Mountain Conifer Forests, Riparian Deciduous Forest
Tympanuchus pallidicinctus, Lesser Prairie-chicken[5]	Plains Grassland
Lagopus leucurus, White-tailed Ptarmigan[5]	Rocky Mountain Alpine Tundra and Shrubland
Callipepla squamata, Scaled Quail	Chihuahuan Semidesert Grassland
Colinus virginianus, Bobwhite[5]	Plains Grassland; Sonora Savanna Grassland
Cyrtonyx montezumae, Montezuma Quail[5]	Madrean Evergreen Woodland Savanna
Columbina passerina, Ground Dove	Weedy fields within Chihuahuan Semidesert Grassland and Sonoran Desertscrub
Melanerpes erythrocephalus, Red-headed Woodpecker[5]	Riparian Deciduous Forest and telephone poles and trees within Plains Grassland
Glaucidium brasilianum, Ferruginous Pygmy Owl	Sonoran Desertscrub (Arizona upland subdivision)
Tyrannus tyrannus, Eastern Kingbird	Riparian Deciduous Forest and other Wooded Habitats within Plains Grassland
Empidonax fulvifrons, Buff-breasted Flycatcher	Madrean Evergreen Woodland and Chaparral
?*Vireo vicinior*, Gray Vireo	Great Basin Conifer Woodland, Interior Chaparral
?*Passerina ciris*, Painted Bunting	Riparian Deciduous Woodlands
Ammodramus savannarum, Grasshopper Sparrow	Plains Grassland, Chihuahuan Semidesert Grassland
Aimophila carpalis, Rufous-winged Sparrow	Sonoran Savanna Grassland
Aimophila botterii, Botteri's Sparrow	Chihuahuan Semidesert Grassland
Coccothraustes vespertinus, EveningGrosbeak	Rocky Mountain Subalpine Conifer Forest

[1] Some isolated populations extirpated through direct human intervention.
[2] Largely a wetland species in the Southwest.
[3] Shown to be susceptible to diseases transmitted by introduced animals.
[4] Also successfully introduced to non-native habitats.
[5] Populations shown to be susceptible to livestock grazing and/or browsing.

Table 3.—Fifty-five species of terrestrial mammals and birds that appear to have increased their breeding distribution in the American Southwest since 1890.

Species	Primary Biotic Affinities in the Southwest
	MAMMALS
Didelphis virginiana, Virginia Opossum	Various warm temperate Biomes in Southwestern Arizona
?*Mormoops megalophylla*, Ghost-faced Bat	Riparian communities within Madrean Evergreen in Southwest Texas
Idionycteris phyllotis, Allen's Big-eared Bat	Various warm and cold temperate Biomes
Nyctinomops femorosaccus, Pocketed Free-tailed Bat	Sonoran Desertscrub and adjacent warm temperate Biomes
Dasypus novemcinctus, Nine-banded Armadillo	Warm temperate Riparian communities along the Pecos River in West Texas
Sciurus aberti, Albert's Squirrel[2]	Madrean and Rocky Mountain Montane Conifer Forests
Baiomys taylori, Northern Pygmy Mouse	Plains and Chihuahuan Semidesert Grasslands
?*Sigmodon hispidus*, Hispid Cotton Rat	Chihuahuan Semidesert Grassland and various Riparian communities
?*Sigmodon fulviventer*, Tawny-bellied Cotton Rat[3]	Madrean Evergreen Woodland and Chihuahuan Semidesert Grassland
Sigmodon ochrognathus, Yellow-nosed Cotton Rat	Madrean Evergreen Woodland Savanna and Montane Meadow Grassland
Microtus mexicanus, Mexican Vole	Meadow and Grassland areas within Madrean, Rocky Mountain and Great Basin Montane Biomes
Canis latrans, Coyote	All, or nearly all, Biomes
?*Vulpes vulpes*, Red Fox	Rocky Mountain Alpine Tundra and Subalpine Conifer Forest; may now be extending its range into Plains and Great Basin Grasslands and other Biomes
Nasua narica, White-nosed Coati	Madrean Evergreen Woodland
Conepatus mesoleucus, Common Hog-nosed Skunk	Various warm temperate Biomes
Tayassu tajacu, Collared Peccary	Sonoran Desertscrub and adjacent warm temperate Biomes
Cervus elaphus, Elk[4]	Rocky Mountain Montane Forest and adjacent Meadows
Bos bison, Bison[4]	Plains and Great Basin Grasslands within and outside of historical range
Odocoileus hemionus, Mule Deer	Nearly all Biomes having sufficient cover and not occupied by O. virginianus
	BIRDS
Coragyps atratus, Black Vulture	Sonoran Desertscrub
Ictinia mississippiensis, Mississippi Kite	Riparian Deciduous Forest within Sonoran Desertscrub
Elanus leucurus, White-tailed Kite	Riparian Deciduous Forest within Chihuahuan Semidesert Grassland
Parabuteo unicinctus, Harris Hawk	Sonoran Desertscrub (Arizona upland division); Mohave Desertscrub; Mesquite and other dense vegetation within Chihuahuan Desertscrub
Scardafella inca, Inca Dove	Urban areas within Sonoran Desertscrub
Zenaida asiatica, White-winged Dove	Sonoran Desertscrub and adjacent warm-temperate Biomes including residential areas
Caprilmulgus ridgwayi, Buff-collared Nightjar	Riparian communities within Chihuahuan Semidesert Grassland and Sonoran Desertscrub
?*Chaetura pelagica*, Chimney Swift	Urban and residential areas
?*Calothorax lucifer*, Lucifer Hummingbird[1]	Riparian communities within Madrean Evergreen Woodland Savanna
Calypte anna, Anna Hummingbird[1]	Urban areas within Sonoran Desertscrub
?*Amazilia berylina*, Berylline Hummingbird[1]	Riparian communities within Madrean Evergreen Woodland
Amazilia violiceps, Violet-crowned Hummingbird[1]	Riparian communities within Madrean Evergreen Woodland
Trogon elegans, Coppery-tailed Trogon	Riparian communities within Madrean Evergreen Woodland
Euptilotus neoxenus, Eared Trogan	Riparian communities within Madrean Evergreen Woodland
Dendrocopos pubescens, Downy Woodpecker	Deciduous trees within Rocky Mountain Subalpine and Montane Forests; Riparian Deciduous Forest
Tyrannus crassirostris, Thick-billed Kingbird	Riparian Deciduous Forests within Chihuahuan Semidesert Grassland and Sonoran Desertscrub
Tyrannus melancholicus, Tropical Kingbird	Riparian deciduous woodlands within Chihuahuan Semidesert Grassland and Sonoran Desertscrub
Cyanocitta cristata, Blue Jay	Riparian deciduous trees and residential areas
Parus atricapillus, Black-capped Chickadee	Rocky Mountain Subalpine and Montane Conifer Forests; cold temperate Riparian Deciduous Forest
Toxostoma bendirei, Bendire Thrasher	Sonoran Desertscrub, Chihuahuan Desertscrub, Chihuahuan Semidesert Grassland
Sialia sialis, Eastern Bluebird	Riparian Deciduous Woodland, Madrean Evergreen Woodland

Heliminthophila luciae, Lucy Warbler	Mesquite communities within Sonoran Desertscrub and various warm temperate Riparian Biomes
Cardellina rubrifrons, Red-faced Warbler	Madrean Evergreen Forest and Woodland
Cardinalis cardinalis, Cardinal	Riparian communities within Sonoran Desertscrub (Arizona upland subdivision)
Cardinalis sinuatus, Pyrrhuloxia	Denser communities within Sonoran and Chihuahuan Desertscrub
Piranga bidentata, Flame-colored Tanager	Riparian communities within Madrean Evergreen Woodland
Icterus spurius, Orchard Oriole	Riparian Deciduous Woodlands and residential areas in Southeast New Mexico
Icterus cucullatus, Hooded Oriole	Tropical and warm temperate Riparian Deciduous Forests within Sonoran, Chihuahuan and Mohave Biomes
Quiscalus mexicana, Great-tailed Grackle	Urban and cultivated lands within Sonoran Desertscrub and various warm temperate and cold temperate Biomes
Quiscalus quiscula, Common Grackle	Urban and cultivated lands within various cold temperate Biomes
Molothrus ater, Brown-headed Cowbird	Ranch yards, irrigated areas and Riparian areas from tropical to cold temperate Biomes
Molothrus aeneus, Bronzed Cowbird	Ranch yards, irrigated areas and Riparian communities within Chihuahuan semidesert Grassland and Sonoran Desertscrub
Passerina cyanea, Indigo Bunting	Riparian Woodlands within Sonoran Desertscrub as well as various warm and cold temperate Biomes
Passerina versicolor, Varied Bunting	Woody Riparian thickets within Sonoran Desertscrub and various warm-temperate Biomes
Aimophila cassinii, Cassin Sparrow	Chihuahuan Semidesert Grassland
Aimophila quinquestriata, Five-striped Sparrow	Chihuahuan Semidesert Grassland

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[1] Range expansion possibly influenced by the provision of feeding stations.
[2] Some, but not all, range expansions are due to introductions.
[3] Despite what appears to be a general increase in distribution, at least one race (*S. f. goldmani*) of this species is believed to have been extirpated in the Southwest.
[4] Populations of this species have continued to increase in distribution since being reintroduced (and in some cases introduced) after 1912.

Table 4.—Exotic species of terrestrial mammals and birds which became established in the American Southwest between 1890 and 1990.

Species	Primary Biotic Affinities in the Southwest
	MAMMALS
Scirus niger, Eastern Fox Squirrel	Riparian Deciduous Forests, Orchards and residential Parks within Chihuahuan and Sonoran Biomes
Rattus rattus, Black Rat[1]	In and around human habitations within Chihuahuan Semidesert Grassland, Chihuahuan Desertscrub and Sonoran Desertscrub
Rattus norvegicus, Norway Rat	In and around human habitations within a variety of Biomes
Mus musculus, House Mouse	In and around human habitations; Chihuahuan Semidesert Grassland, Plains Grassland and Riparian communities within several biomes
Camelops spp., Dromedary and Bactrian Camels	Mohave and Sonoran desertscrubs
Equus asinus, Feral Ass	Sonoran and Mohave desertscrubs; Chihuahuan SemidesertGrassland, Great Basin Desertscrub and Great Basin Conifer Woodland
Equus caballus, Feral Horse	Chihuahuan Semidesert Grassland, Sonoran Desertscrub, Interior Chaparral, Great Basin Conifer Woodland and possible other Biomes
Ammotragus lervia, Barbary Sheep[1]	Rugged areas within Plains, Chihuahuan and Great Basin
Oryx gazella, Gemsbok	Chihuahuan Semidesert Grassland and Chihuahuan Desertscrub
Capra hircus, Goat[1]	Sonoran Desertscrub, Chihuahuan Semidesert Grassland, Interior Chaparral
Capra ibex, Ibex	Interior Chaparral, Chihuahuan Semidesert Grassland, Great Basin Scrubland and possibly other Biomes
Sus scrofa, Feral Pig	Madrean Evergreen Woodland
	BIRDS
Alectoris chukar, Chukar	Great Basin Desertscrub and Grassland
Phasianus colchicus, Pheasant	Agricultural areas within various warm temperate and cold temperate Biomes
Lophortyx californicus, California Quail	Riparian Scrubland within Plains Grassland
Columba livia, Rock Dove	In and around human habitations within various Biomes
Sturnus vulgaris, Starling	In and around human habitations within various Biomes
Passer domesticus, House Sparrow	In and around human habitations within various Biomes

[1] Present status unknown; may now be absent from the Southwest.
[2] Extirpated from the Southwest through direct human intervention by 1900.
[3] Extirpated from native Plains Grassland in the Southwest prior to 1890.

Table 5.—Formation-type affinities of 39 terrestrial mammals and birds that have been extirpated or experienced range reductions in the American Southwest since 1890.[1]

Alpine Tundra	**Forests and Woodlands**	**Scrublands**
Lagopus leucurus	*Tamius minimus*	*Epidonax fulvifrons*
	Odocioleus virginianus	*Glaucidium* brasileanum
	Buteo nitidus	
	Meleagris gallopavo[2,3]	
	Melanerpes erythrocephalus	
	Tyrannus tyrannus	
	?Vireo vicinior	
	?Passerina ciris	
	Coccthraustes vespertinus	
Grasslands (includes Meadows and Savanna)	**Desertlands**	**Residential Areas and Farmlands**
Lepus alleni	*Vulpes velox*[2]	*Columbina passerina*
Spermophilus tridecemliniatus	*Ovis canadensis*[2]	
Cynomys ludovicianus[2]	*Caracara cherwayi*	
Cynomys gunnisoni[2]		
Crategeomys castanops		
Microtus pennsylvanicus		
Sigmodon arizonae		
Zapus hudsonius		
Mustela nigripes[2]		
Antilocapra americana		
Cervus elaphus[3]		
Bos bison[3]		
Buteo regalis		
Falco femoralis		
Tympanuchus pallidicinctus		
Centrocercus *urophasianus*		
Pediocetes phasianellus		
Callipepla squamata		
Colinus virginianus		
Cyrtonyx montezumae		
Ammodramus savannarum		
*Aimophila*carpalis		
*Aimophila*botterii		

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[1] Large predators excepted.
[2] Shown to be susceptible to diseases transmitted by introduced animals.
[3] Now successfully introduced to both former and non-native habitats.

Table 6.—Principal biotic affinities and direction of biogeographic center for 39 species of terrestrial mammals and birds that have been extirpated or experienced range reductions in the American Southwest since 1890.[1]

Great Basin (N, NW)	Rocky Mountain (N, NE)	Plains (NE, E)
Cynomys gunnisoni	*Tamias minimus*	*Spermophilus* tridecemliniatus
Mustela nigripes[2]	*Microtus pennsylvanicus*	*Cynomys ludovicianus*[2]
Centrocercus urophasianus	*Zapus hudsonius*	*Crategeomys* castanops
Pediocetes phaasianellus	*Lagopus leucurus*	*Bos bison*[4]
Buteo regalis	*Coccothraustes vespertinus*	*Tympanuchus pallidicinctus*
Vireo vicinior		*Colinus virginianus*[3]
		Ammodramus savannarum
Southeastern (E)	**Tamaulipan (E, SE)**	**Chihuahuan (SE, S)**
Odocoileus virginianus[3]	*Falco femoralis*	*Callipepla squamata*
Meleagris gallopavo		*Aimophila botterii*
Melanerpes erythrocephalus		
Tyrannus tyrannus		
Passerina ciris		
Madrean (S)	**Sonoran/Sinaloan (S, SW)**	**Widely Distributed Within Southwest**
Odocoileus virginianus[3]	*Lepus alleni*	*Vulpes velox*[2]
Meleagris *gallopavo*[2,3,4]	*Sigmodon arizonae*	*Ovis canadensis*
Cyrtonyx montezumae	*Buteo nitidus*	
Empidonax fulvifrons	*Caracara cheriway*	
	Colinus virginianus[3]	
	Columbina passerina	
	Glaucidium brasilianum	
	Aimophila carpalis	

[1] Large predators excepted.
[2] Shown to be susceptible to diseases transmitted by introduced animals.
[3] Southwest populations having more than one primary biotic affinity.
[4] Successfully introduced to former and non-native habitats after 1890.

Table 7.—Primary Formation-type affinity of 55 terrestrial mammals and birds breeding in the American Southwest and that have experienced range expansions since 1890.

Alpine Tundra	Forests and Woodlands	Scrublands
None	*Didelphis virginianus*	*Tayassu tajacu*
	?Mormoops megalophylla	*Odocoileus hemionus*
	Idionycteris phyllotis	*Parabuteo unicinctus*
	Dasypus novemcinctus	*Zenaida asiatica*
	Sciurus aberti[2]	*Heliminthophilia luciae*
	Sigmodon fulviventer[3]	*Cardinialis cardinalis*
	Sigmodon ochrognathus	*Cardinalis sinuatus*
	Nasua narica	
	Conepatus mesoleucus	
	Cervus elaphus[4]	
	Ictinia mississippiensis	
	Caprilmulgus ridgwayi	
	?Calothorax lucifer[1]	
	?Amazilia beryllina[1]	
	Amazilia violiceps	
	Trogon elegans	
	Euptilotus neoxenus	
	Dendrocopos pubescens	
	Tyrannus crassirostris	
	Tyrannus melancholicus	
	Cyanocitta cristata	
	Parus atricapillus	
	Sialia sialis	
	Cardellina rubrifrons	
	Piranga bidentata	
	Icterus spurius	
	Icterus culcullatus	
	Passerina cyanea	
	Passerina versicolor	
Grasslands (includes Meadows and Savannas)	**Desertlands**	**Residential Areas and Farmlands**
Baiomys taylori	*Nyctinomops femorosaccus*	Scardafella inca
Sigmodon hispidus	*Coragyps atratus*	*Chaetura pelagica*
Microtus mexicanus	*Toxostoma bendirei*[1]	*Calypte anna*
Bos bison[4]		*Quiscalus quiscula*
Elanus leucurus		*Molothrus ater*
Aimophila cassinii		*Molothrus aeneus*
Aimophila quinquestriata		
Two or More Formation Types		
Canis latrans		
Vulpes vulpes		

[1] Range expansion possibly influenced by the provision of feeding stations.
[2] Some, but not all range expansions are due to introductions.
[3] Despite what appears to be a general increase in distribution, one race of this species, *S. f. goldmani*, is believed to have become extinct.
[4] Populations of this species have continued to increase in distribution since being reintroduced or transplanted after 1912.

Table 8.—Principal biotic affinities and direction of biogeographic center for 55 species of terrestrial mammals and birds that have expanded their range in the American Southwest since 1890.

Great Basin (N, NW)	**Rocky Mountain (N, NE)**	**Plains (NE, E)**
None	*Vulpes vulpes*	*Bos bison*
	Cervus elaphus	
	Dendrocopos pubescens[1]	
	Parus atricapillus[1]	
Southeastern (E)	**Tamaulipan (E, SE)**	**Chihuahuan (SE, S)**
Didelphis virginiana[1]	*Dasypus novemcinctus*	*Baiomys taylori*
Ictinia mississippiensis		?*Sigmodon hispidus*
?*Chaetura pelagica*		*Sigmodon fulviventer*
Cyanocitta cristata		*Aimophila cassinii*
Sialia sialis		
Icterus spurius		
Quiscalus quiscula		
Passerina cyanea		
Madrean (S)	**Sonoran/Sinaloan (S, SW)**	**Californian (W)**
?*Mormoops megalophylla*	*Didelphis virginiana*[1]	*Elanus leucurus*
Idionycteris phyllotis	*Nyctinomops femorosaccus*	*Calypte anna*
Sciurus aberti	*Tayassu tajacu*	
Sigmodon ochrognathus	*Coragyps atratus*	
Microtus mexicanus	*Parabuteo unicinctus*	
Nasua narica	*Scardafella inca*	
Conepatus mesoleucus	*Zenaida asiatica*	
Calothorax lucifer	*Caprilmulgus ridgwayi*	
?*Amazilia beryllina*	*Tyrannus crassirostris*	
Amazilia violiceps	*Tyrannus melancholicus*	
Trogon elegans	*Toxostoma bendirei*	
Euptilotus neoxenus	*Heliminthophila luciae*	
Cardellina rubifrons	*Cardinalis cardinalis*	
Piranga bidentata	*Quiscalus mexicana*	
Aimophila quinquestriata	*Molothrus aeneus*	
	Passerina versicolor	
Centered or Widely Distributed Within the Southwest		
Canis latrans		
Odocoileus hemionus		
Cardinalis sinuatus		
Icterus cucullatus		
Molothrus ater		

[1] Advancing in more than one direction.

The Decline of Bighorn Sheep in the Santa Catalina Mountains, Arizona

Paul R. Krausman, William W. Shaw, Richard C. Etchberger, and Lisa K. Harris[1]

Abstract.—Desert bighorn sheep (*Ovis canadensis mexicana*) are an important component of the biodiversity in the Pusch Ridge Wilderness (PRW), Santa Catalina Mountains, Arizona. The population has decreased from approximately <20 in 1926 to in 1994 and their distribution is limited to < 50 km^2 in the PRW. The population decline has been attributed to human activities including the development of roads and trails, housing and resorts, hiking, dogs, and fire suppression. Fire suppression effectively has altered vegetation so parts of the PRW are not suitable for bighorn sheep. Human encroachment into the remaining areas has been too severe for the population to increase. Disease, predation, and hunting may have contributed to the recent decline but their influence has not been evaluated. Prior to any reintroduction efforts, managers should understand the factors that have caused the decline. The public is supportive of management options including those that restrict the use of areas and prohibit dogs from bighorn sheep habitat. However, human intrusion into bighorn habitat may be too severe for recovery efforts to be successful.

Since the 1920s desert bighorn sheep in PRW have declined from >200 to <20 (fig. 1). Likely cause for the decline are directly related to human activity (i.e., construction of roads, trails, hunting, hiking, fire suppression). Unfortunately, as the population declined the efforts to maintain a viable population were not successful. Our objectives were to summarize the decline of desert bighorn sheep in PRW, review the research that has been conducted related to bighorn in PRW. This study was funded by the School of Renewable Natural Resources, University of Arizona, Tucson. J. C. deVos, Jr. and K. A. Kelly reviewed earlier drafts of the manuscript.

THE PUSCH RIDGE WILDERNESS

The PRW (fig. 1) was established 24 February 1978 through the Endangered American Wilderness Act. One of the major goals of the 22,837 ha wilderness was to protect habitat for desert bighorn sheep (Anon. 1978). The PRW formed the southwest portion of the Santa Catalina Mountains located in the Coronado National Forest, Arizona. The Santa Catalina Mountains are roughly triangular in shape with an east-west base of about 32 km and the apex 32 km north of the base (Krausman et al. 1979). Elevations ranged from >2,745 m at Mount Lemmon to 854 m at the southwestern base of the range (Whittaker and Niering 1965).

The Santa Catalina Mountains are unique among Arizona and New Mexico mountain ranges because they possess a full sequence of plant communities from subalpine fir (*Abies lasiocarpa*) forests to Sonoran Desert. Vegetation patterns of other ranges in southeastern Arizona are similar (Blumer 1909, Martin and Fletcher 1943, Nichol 1952, Wallmo 1955, Lowe 1961) to the Santa Catalinas but differ because the forest types are reduced or absent and/or Sonoran Desert communities are limited or absent (Whittaker and Niering 1964). Vegetation of the Santa Catalina Mountains brings together mountain coniferous forests, Mexican oak (*Quercus oblongifolia*) and pine (*Pinus* spp.)-oak communities of southern affinities, desert grasslands with affinities to the east and Sonoran Desert with affinities to the west and south (Whittaker and Niering 1965).

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Figure 1.—Estimates of desert bighorn s heep in the Santa Catalina Mountains, Arizona. Data are from the United States Forest Service and Arizona Game and fish Department files.

The PRW consists of steep, highly erosive areas with large, deep canyons that support riparian vegetation. Hogbacks rise from the desert floor to higher elevations forming vertical rock faces and spectacular geologic formations. Vegetation varies from desert grassland at the lower elevations to ponderosa pine (*Pinus ponderosa*) and mixed conifers at higher elevations (Krausman et al. 1979). Whittaker and Niering (1964, 1965) provide a physical and vegetation analysis of the Santa Catalina Mountains. The PRW is further described by deVos (1983), Gionfriddo and Krausman (1986), Etchberger et al. (1989, 1990), and Mazaika et al. (1992).

PREVIOUS STUDIES

Krausman et al. (1979) recommended that the "... future well-being of this population will require management and planning based on a sound understanding of basic biological parameters of the herd and of human intrusions into it's habitat." Krausman et al. (1979) recommended that information on density, distribution, lambing, habitat, fire, recreation, and human impacts as they relate to desert bighorn sheep were needed for efficient management. Each of these arenas has been addressed to a limited degree and research has been conducted in 2 major areas: habitat and biology, and human influences.

Biological Studies

Krausman et al. (1979) reviewed the literature and status of bighorn sheep in PRW and recommended that more information was needed to understand the ecological relationships between sheep and their habitat and between humans and bighorn sheep in PRW. The first study was conducted by deVos (1983) to collect data to be used as a basis for management decisions. He radio collared 11 bighorn sheep (5M, 6F) and made recommendations based on 374 locations of sheep from November 1981 through June 1983. deVos (1983) reported 6 important results.

1. Over 70% of bighorn sheep locations were in oak associations.
2. Approximately 80% of bighorn sheep locations occurred within 700 m of a burned area. "The differences between the use of burned area and the random values was highly significant (P ≥ 0.99) deVos 1983:26."
3. Bighorn sheep preferred areas > 700 m from trails.
4. Bighorn and Pusch peaks and west of Montrose Canyon and south of Buster Springs are lambing and nursing areas.
5. Home-range size varied from 7.1 to 34.4 km^2.
6. The population estimate was from 45 to 75 sheep. Unpublished data reported by deVos (1983:29) indicated the best estimator available revealed a population of 60. "It is important that any future research be directed and sufficiently funded to provide an accurate population estimate."

Based on these data deVos (1983) recommended 5 areas for continued research that would ".... alleviate much of the jeopardy to this herd."

1. Obtain better lambing data and refine population estimates.
2. Monitor recreation and the response of sheep to humans.
3. Discourage human development adjacent to bighorn sheep habitat.
4. Allow fires to burn in sheep habitat.
5. Controlled burns should be planned to enhance sheep habitat.

During the study by deVos (1983), Gionfriddo and Krausman (1986) began a study examining summer habitat use by bighorn sheep on PRW. The land adjacent to the PRW was being developed for housing and the study was to establish information on bighorn sheep habitat use prior to encroachment by humans. Gionfriddo and Krausman (1986) described summer (May-Sep) habitat use in 1982 and 1983 based on 234 observations of sheep groups containing 1,010 individuals.

Sheep selected the nonprecipitous open oak woodland in 47% of the observations and 85% were on sites located at the base of large rocky cliffs. Areas ≤150 m from cliff bases accounted for <1% of the aerial surface on the study areas but 40% of all sheep groups observed were using these sites. These areas were tree-invaded semidesert grassland at the lower fringe of evergreen oak distribution with 15.5% thermal cover.

Sheep habitat in summer in PRW was characterized by 59-79% slopes, western aspects, elevations between 1,098 and 1,341 m, upper slopes of drainages, tops of ridges and mountains, and areas ≤20 m from escape terrain.

These findings are characteristic of sheep habitat in southwestern Arizona. However, Gionfriddo and Krausman (1986:334) stated that "Responses of bighorn sheep to slope steepness, elevation, and topographic position may be related to other factors such as visibility, forage availability, and proximity to escape terrain rather than to steepness, elevation or topographic position ..." Because fires in PRW have been suppressed in the past 70 years, Gionfriddo and Krausman (1986:335) recommended a program of habitat rehabilitation through prescribed burning. Because human recreation was occurring they also suggested a well enforced set of recreational use restrictions to improve the chances of long-term survival of mountain sheep in PRW. Another recommendation was for "... close monitoring of the population's responses to management actions and to the nearby suburban development ..."

Etchberger et al. (1989) conducted a study in the Santa Catalina Mountains in 1987-1988 to contrast habitat used by desert bighorn sheep (44 km^2) with habitat that had been abandoned (206 km^2). "Habitat currently used by mountain sheep in PRW has greater distance to human disturbance, greater visibility, more side oats grama (*Bouteloua curtipendala*), red brome (*Bromus rubens*), brittle bush (*Encelia farinosa*), and forbs, but less ground cover, bush muhly (*Muhlenbergia porterii*), and turpentine bush (*Haplopappus laricifolius*) than abandoned habitat (Etchberger et al. 1989:905)."

Differences between currently used and abandoned habitat were not found for variables commonly considered important to bighorn sheep: steep, rugged terrain with considerable topographic relief (Risenhoover and Bailey 1985, Gionfriddo and Krausman 1986, Wakelyn 1987). In PRW other factors influenced sheep distribution: human disturbances in and adjacent to PRW and fire suppression. Fire suppression in abandoned habitat that has encouraged vegetation that obstructs visibility has been detrimental to bighorn sheep. Fire suppression reduces the amount of high-visibility habitat used by mountain sheep (Risenhoover 1981, Wakelyn 1987). Risenhoover and Bailey (1985) documented a strong preference by bighorn sheep for grassy, open areas with high visibility (Etchberger et al. 1989:906). Fires have been suppressed in the PRW until the early 1980s and although approximately 3,000 ha have burned since 1958 <2% burned >125 ha at one time.

Habitat fragmentation due to human disturbance threatens the survival of large mammalian populations because they require large spaces and specific habitat features (i.e., visibility) (Wilcox and Murphy 1985). Etchberger et al. (1989) recommended that fires should be used to maintain high visibility habitat and human encroachment should be monitored closely. In a later study Etchberger et al. (1990) examined the influence of a fire on sheep habitat in PRW and documented the beneficial aspects of fire. According to Etchberger et al. (1990:56) fire reduced visibility-obstructing vegetation and enhanced desirable species. These results are supported from long term evaluation of fire in PRW (P. R. Krausman and G. Long, unpubl. data).

Researchers also examined other aspects that may limit bighorn sheep in PRW. Mazaika et al. (1992) estimated seasonal forage availability and quality for bighorn sheep. The results suggested that bighorn sheep "... were not limited by forage quantity or quality ... (Mazaika et al. 1992:372)." Mazaika et al. (1992) concluded that habitat management for bighorn sheep in PRW should concentrate on factors other than the availability or quality of forage (i.e., fire management to enhance visibility).

Throughout these studies ≥3 consistent issues are raised in relation to bighorn sheep management in PRW.

1. Habitat features for bighorn sheep are similar to other habitat features for bighorn sheep in the Southwest.
2. Fire suppression is reducing visibility for bighorn sheep and effectively reducing PRW as bighorn sheep habitat.
3. Human disturbance and activities, including housing developments and recreation on forest lands, are eliminating habitat available for bighorn sheep in PRW.

Sociological Studies

Sociological studies were recommended by Krausman et al. (1979) and were initiated shortly thereafter. Purdy and Shaw (1981) examined the recreational uses and users of bighorn habitat in PRW. They described human use patterns of 2 groups: lower canyon visitors and backcountry visitors. Most humans were lower canyon visitors and <10% of all users entered the backcountry. The later group posed a greater threat to bighorn sheep due to their increased activities and longer duration of visits. Although backcountry users did not believe their activities were detrimental to bighorn sheep they did favor recreational use restrictions if necessary for the welfare of the sheep population. This is further reflected by the value of bighorn sheep to recreationists in PRW. Purdy and Shaw (1981) found <1% of 844 responses from backcountry users observed bighorn sheep. Most of those who observed sheep (60%) believed the "... sightings were the highlight of all past recreational experiences in PRW (Purdy and Shaw 1981)."

This attitude is supported by later studies of King et al. (1986, 1988). The total value of a resource is the sum of use and existence values. Use values include consumptive, nonconsumptive, and future use values. Existence values are motivated by altruism and is not derived from direct use of the resource (Randall and Stall 1983).King et al. (1986, 1988) estimated the total and existence values of bighorn sheep in PRW to residents of the Tucson urban area, and estimated the effects of socioeconomic and other preference related variables on the total and existence values of the herd. King et al. (1986, 1988) concluded that "when the sample values ae [are] projected to the population of metropolitan Tucson, total value falls within the range of 2.1 and 3.9 million dollars per year and existence values within the range of 1.3 to 2.4 million dollars per year." As with other authors, King et al. (1986, 1988) emphasized that increasing recreational use of PRW could be detrimental to bighorn sheep in PRW.

Although citizens of Tucson value bighorn sheep, the long-term future of bighorn in PRW is not secure (Purdy and Shaw 1981). Purdy and Shaw (1981:4-5) made 6 recommendations as safeguards against human/bighorn sheep conflicts in PRW.

"1. Continue to monitor trail traffic in lower Pima Canyon ... in order to obtain long-term indications of total canyon use.
2. Provide backcountry users of bighorn habitat ... with information that is designed to increase users' level of knowledge of bighorn sheep in PRW. This is perhaps best accomplished ... to make visitors aware of the possible consequences of activities in bighorn habitat in addition to determining the following specific backcountry activities:
    (i) backcountry travel with dogs
    (ii) cross-country travel
    (iii) camping within 1/4 mile (402 m) of wildlife water catchments
3. Enforce existing regulations against camping within 1/4 mile (402 m) of wildlife water ...

4. Provide no improvements of backcountry trails...
5. Obtain accurate PRW bighorn population data...
6. Use information from recommendation 5 as data base for monitoring the physiological and behavioral effects of recreational use on bighorn sheep in PRW."

More recently, Harris and Shaw (1993) and Harris et al. (1994) studied human attitudes related to the conservation of bighorn sheep in PRW. Based on interviews with 403 groups that used PRW for recreation from May 1990 to April 1991 Harris and Shaw (1993) and Harris et al. (1994) described the demographics of users of PRW.

1. More males (57%) than females (43%) used the wilderness trails.
2. Visitors were between 20 and 49 years old (83%).
3. Most (66%) had ≥ a college degree.
4. Most (92%) were caucasian.
5. Most (83%) previously visited the wilderness and the recreational experience PRW provided was important to them.
6. Recreational experiences included hiking (>90%), watching wildlife (except birds) (79%), and bird watching (26%).
7. Only 15% of the respondents observed sheep but 90% were aware that sheep were in the area.

Harris and Shaw (1993) and Harris et al. (1994) also asked wilderness users to respond to management strategies that benefit mountain sheep: dog restrictions, controlled burns, and recreational closures. An estimated 1,650 dogs that are unleashed at least during part of the stay in PRW visit the area annually. Respondents (67%) favored restricting dogs completely from the wilderness. Almost half (46%) favored planned burns to improve bighorn sheep habitat, and 59% of the visitors were willing to give up their wilderness activities to protect bighorn sheep from human pressure. People who use trails in bighorn habitat are concerned about the well-being of the herd. They are willing to accept dog control, controlled burns, and recreational closures as acceptable management strategies (Harris et al. 1994).

As with the biological studies, certain trends emerged from the sociological research.

1. Bighorn sheep are important to citizens of Tucson, Arizona and those that use PRW.
2. Recreational activities by humans will continue to increase in PRW.
3. The same recreational activities are detrimental to the long-term survival of sheep in PRW.
4. Recreational users are willing to give up their activities in the wilderness to minimize human pressure on bighorn sheep.

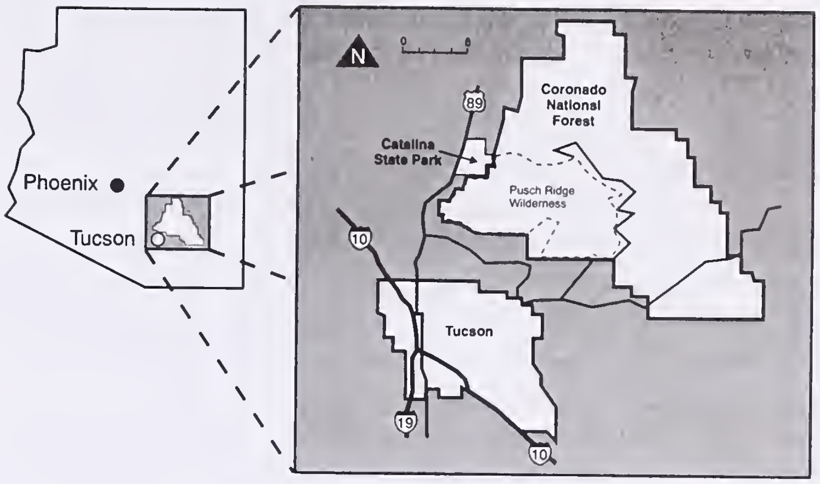

Figure 2.—Pusch Ridge Wilderness in the Santa Catalina Mountains, Arizona.

DISCUSSION

Unfortunately the biological data and sociological data acquired are too little too late. Economic forces have created a human barrier around PRW effectively fencing them in (Krausman 1993) while at the same time reducing their habitat. The decline of desert bighorn sheep in PRW is a surprise to no one and was predicted 15 years ago. Unfortunately, now that the population is nearly eliminated (fig. 2) managers will have to decide if PRW is suitable for the continued habitat for bighorn sheep and if not what modifications need to be made to make it suitable. The other decision would be to do nothing and accept the decline of the herd as human induced.

Berger (1990) examined the extinction of mountain sheep populations in 5 western states and concluded that extinction times were related to initial population size. Native populations of <50 individuals were subject to rapid extinction. Populations with >100 individuals persisted for ≥70 years. Although populations in Arizona do not follow Berger's (1990) predictions (Krausman et al. 1993) the population in PRW declined rapidly after abundance decreased to <100 individuals (fig. 2). Krausman et al. (1993) agree with Berger (1990) that "... it is clear that small (and especially single) mammalian populations are in imminent need of enhanced management to enhance their persistence." Enhanced management has not occurred for bighorn sheep in PRW and the indigenous herd has effectively been eliminated.

The elimination of sheep in the PRW has been gradual. Metapopulations were first eliminated from the surrounding mountains restricting sheep to PRW. Habitat alteration occurred as fire suppression techniques became more effective. In addition, the increasing human population in Tucson has literally pushed bighorn sheep over the brink (Krausman 1993). The bighorn sheep in PRW of the Santa Catalina Mountains may be the next indigenous herd to be replaced with transplants. However, prior to any transplant effort, we recommend a complete census of all potential sheep habitat in PRW done on a systematic basis to obtain the best possible census. If <50 sheep exist a transplant may be warranted but only after the human disturbance, including fire suppression that has been instrumental in eliminating sheep and their habitat has been minimized. An unique population of desert bighorn sheep is in jeopardy and may be lost forever; to transplant additional sheep into the area without solving the problems of disturbance and habitat alteration would be akin to a put and take fisheries operation.

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Introduced Aquatic Vertebrates in the Chiricahua Region: Effects on Declining Native Ranid Frogs

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Abstract.—The Chiricahua Mountain region offers an outstanding opportunity to manage an aquatic vertebrate fauna that is widely in decline or already threatened or endangered. The fauna is diverse, and potential economic conflicts with recovery of native aquatic species are few and limited. Including Aravaipa Creek, the San Pedro River, and Cajon Bonito in Mexico, there is excellent potential for interagency and international collaboration to the benefit of biodiversity and open space.

Herein we provide data showing the extensive and expanding distribution of non-native vertebrates in southeast Arizona waters. These introduced species are being spread directly by humans, intentionally and accidentally. Our detailed evidence shows that, like most native fishes, native leopard frogs are negatively affected primarily by introduced aquatic predatory vertebrates, especially bullfrogs, largemouth bass, sunfishes, and probably catfishes, trouts, fathead minnows, and mosquitofish. These non-indigenous species appear to be thriving in human-created habitats, and spreading into surrounding habitats where they are destroying indigenous forms. Recovery of the Chiricahua leopard frog and other native leopard frogs in the region is a viable objective given (1) priority within government agencies, and (2) cooperation of conservation professionals with ranchers and other private stakeholders that control or manage most waters in the region.

INTRODUCTION

Introduced predators are known for their strong negative effects on native animals around the world. Examples include mass extinctions of native cichlid fishes in African rift-lakes (Witte, et al. 1992; Ogutu-Ohwayo, 1993) and of native bird and lizard species on Guam (Savidge, 1987; Rodda and Fritts, 1992), as well as ground iguana and solenodont mammal declines in the West Indies (Burghardt and Rand, 1982; Thornback and Jenkins, 1982; Nowak, 1991). In the American Southwest, the native fish fauna is similarly facing extinction due primarily to introduced predators and competitors, which thrive in tandem with human-caused (anthropogenic) habitat modification (Minckley and Deacon, 1991).

Over the course of the present century, modern technological humans have created many lakes, reservoirs, and stock-watering ponds in the American Southwest, where perennial waters originally consisted of cienegas, springs, streams, rivers and riverine marshes (see Hendrickson and Minckley, 1984). In these natural aquatic habitats, flash-flooding frequently favors native over introduced—more characteristically lacustrine — species of fish (Minckley and Meffe, 1987), whereas frequent drying may favor native leopard frogs (*Rana pipiens* complex) over bullfrogs (*Rana catesbeiana*) because of the longer aquatic tadpole stage of the bullfrog. Habitat modifications producing to deep, still perennial waters, lack of scouring flash floods, and reduced fre-

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quency of drying contribute directly to the negative effects of introduced predators on native species. Further, most of the native animals discussed here evolved in isolation from the introduced predators that currently plague them, and thus may be behaviorally unprepared to select habitats, microhabitats, or activity modes that permit avoidance of the introduced species.

The Chiricahua and surrounding mountains have natural perennial surface waters in greater abundance than other Madrean "mountain islands" (Gehlbach, 1981) along the U.S. and Mexican border. Moreover, the Chiricahuas lack the major dammed lakes (which harbor great arrays of non-indigenous fishes, bullfrogs, and crayfishes) that exist in other mountain complexes of southeastern Arizona. Inclusive of Aravaipa Creek to the northwest and Cajon Bonito to the southeast, this local region contains the least altered natural waters remaining in the American Southwest (Minckley and Rinne, 1991), and presents the best opportunity (with most of the adjoining San Pedro River a Bureau of Land Management riparian conservation area) to establish a natural area with (1) great open spaces, (2) natural water conditions, (3) healthy natural aquatic fauna, and (4) overall high biological diversity.

The native "true frogs" (family Ranidae) of western North America are all suffering range contractions, massive population declines, or both (Vial and Saylor, 1993; Leonard et al., 1993; Blaustein et al., 1994; Jennings, 1995; Sredl and Howland, *this volume*). Many species have disappeared from large proportions of their ranges, several are nearing endangered status, and two or three (*Rana tarahumarae* and, depending on the taxonomist consulted, *R. fisheri* and *R. onca*) are extinct in the United States. Decline of the Chiricahua leopard frog *Rana chiricahuensis* was first reported, but not explained, by Clarkson and Rorabaugh (1989).

Many factors apparently contribute to ranid frog declines and disappearances, including habitat loss (Jennings and Hayes, 1994), regional pollution (Hale et al., 1994), and global ozone depletion (Blaustein et al., 1994). Introduced predators including fishes (Hayes and Jennings, 1986; Bradford, 1989, Brönmark and Edenhamn, 1994) and bullfrogs *Rana catesbeiana* (Hayes and Jennings, 1988; Schwalbe and Rosen, 1988; Rosen and Schwalbe, *in prep.*) appear to play a major role in many frog declines.

In this paper, we describe the expanding distribution of introduced fishes and bullfrogs in the Chiricahua region, and we correlate this in detail with the pattern of decline of the native Chiricahua leopard frog. We offer a series of management recommendations to reverse this expansion of non-natives, and possibly to make federal listing of the Chiricahua leopard frog unnecessary or of short duration. We focus on measures that may be advantageous to the major stakeholders in the area, both private and public.

METHODS

We visited all known localities for the Chiricahua leopard frog and the plains leopard frog *R. blairi* in the Chiricahua Mountains and surrounding Sulphur Springs, San Bernardino, and San Simon valleys, and in the Dragoon and Peloncillo mountains, Cochise and Graham counties, Arizona (fig. 1). These localities were determined from Clarkson and Rorabaugh (1989, and therein),

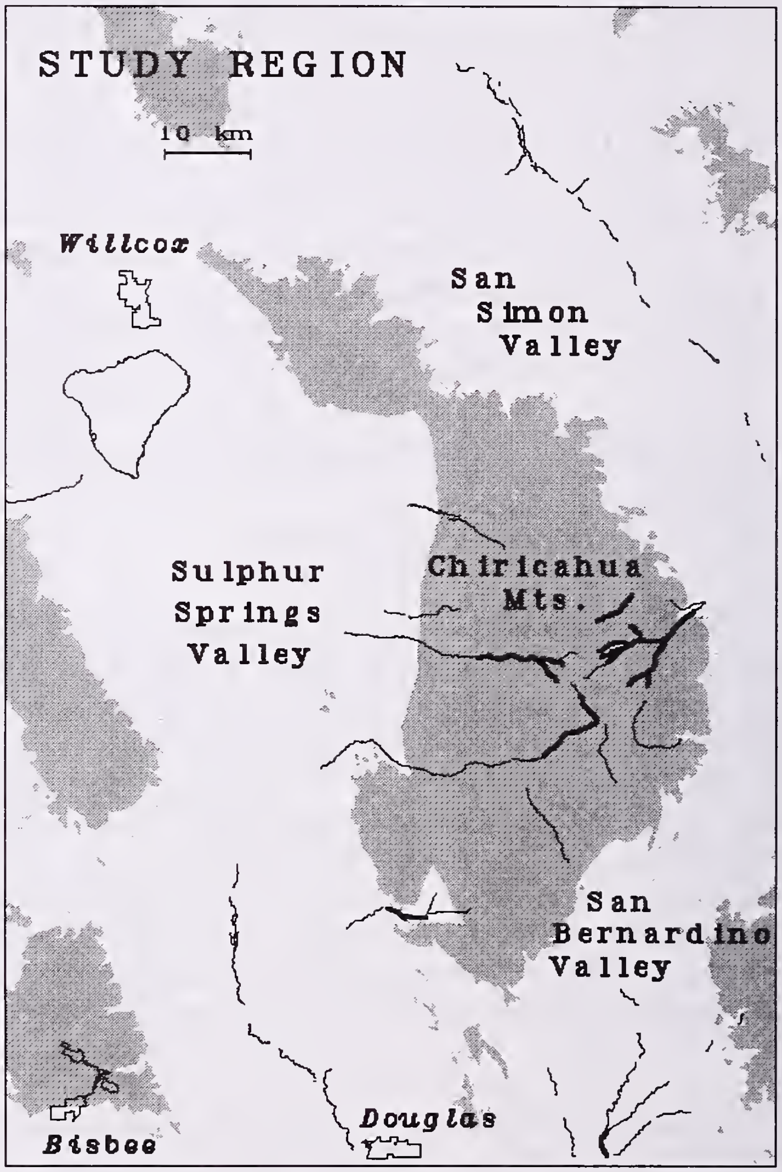

Figure 1.—Footprint of the Chiricahua and surrounding Mule, Dragoon, and Peloncillo mountains, and valley areas, included in this field survey. Major perennial waters are shown as dark lines, major intermittent drainages are light lines.

surveys of museum collection localities, and interviews with herpetologists familiar with the area.

We also sampled other accessible perennial or semi-perennial waters, attempting in sum to visit all potential leopard frog habitat areas; occasionally, site access was denied by private landowners. Whenever possible, we discussed water permanence and faunal observations with landholders, significantly enhancing our ability to locate good sites for frogs. Additional work carried out in the area of the Atascosa Mountains and Altar Valley, in Pima and Santa Cruz counties, Arizona, is reported elsewhere (Rosen and Schwalbe, *in prep.*).

Most of the work reported here was done May-August 1994, a time of drought in southeast Arizona; eleven of the sites were visited only in 1992 or 1993. At each site, we approached slowly, using binoculars for visual observation of frogs or surfacing salamanders and turtles, as well as for fishes. We then walked along the water margin counting frogs or other animals as they moved or were otherwise observed. Finally, we sampled each site with dipnets (6 mm mesh) and seines (3 x 1 m and 8 x 1.8 m; 6 mm mesh) to confirm species identifications and determine relative abundances for tadpoles, salamanders, turtles, and fishes.

Most of the 1994 work was prior to a tardy onset of monsoonal rains, some areas receiving no runoff until at least September—over 2 months late. It was a dry summer following a dry winter in a longer term drought beginning in the mid-1980's. Whereas the aquatic fauna suffered through this drought, we capitalized on the opportunity to determine with some certainty the perenniality for each water source. When we arrived at or near what we estimated to be the drought minimum water level, we recorded the deepest point of each site by wading or diving. These estimates represent 10-20 yr depth minima, based on interviews with resident landholders and land managers. Finally, we revisited a number of sites that were dry in early summer but subsequently filled with runoff, sampling as described above.

Despite our efforts, we may have overlooked some species at some sites, as when fishes may have eluded our small seines or where uncommon species were simply not captured. We think this is a small error, because our results were generally in agreement with interviews with people knowledgeable of the local areas, and with initial visual inspections that revealed the general classes of aquatic animals to be expected. In several areas, we set baited turtle traps and minnow traps to verify species presence.

Reptiles and amphibians were identified in hand using Stebbins (1985) and, for leopard frogs, with Sredl and Howland (1992). Fishes were identified in hand using Minckley (1973) and Page and Burr (1991). Herein we use the term "exotic" to mean exogenous to southwest North American drainage basins, and "introduced species" to be those brought in by man.

RESULTS AND DISCUSSION

Species Observed and Distribution

A total of 103 sites was sampled in the study region. We observed 30 species of aquatic and semi-aquatic ectothermic vertebrates in the Chiricahua region, including 13 exotic species (table 1, figs. 2-6); there were 74 occurrences of non-native

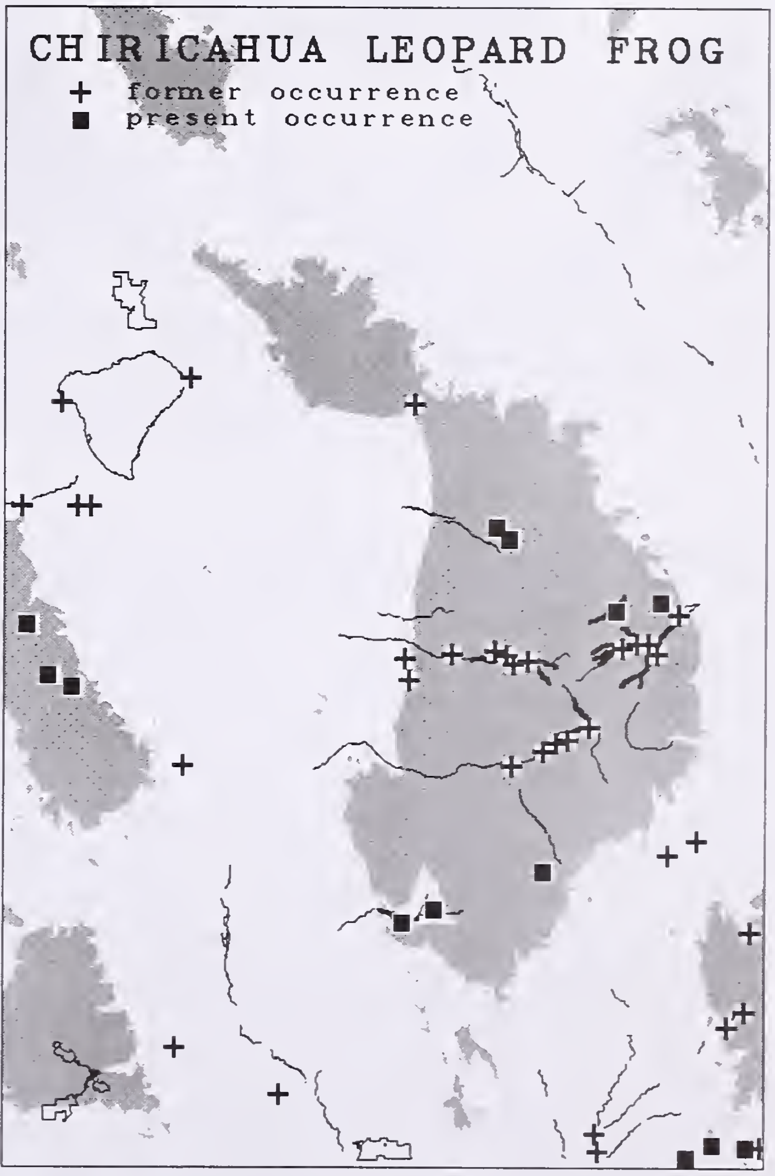

Figure 2.—Present and former known distribution of the Chiricahua leopard frog *Rana chiricahuensis* in the study region as of 1994.

Figure 3.—Known distribution of the introduced bullfrog *Rana catesbeiana* in the study region, 1994.

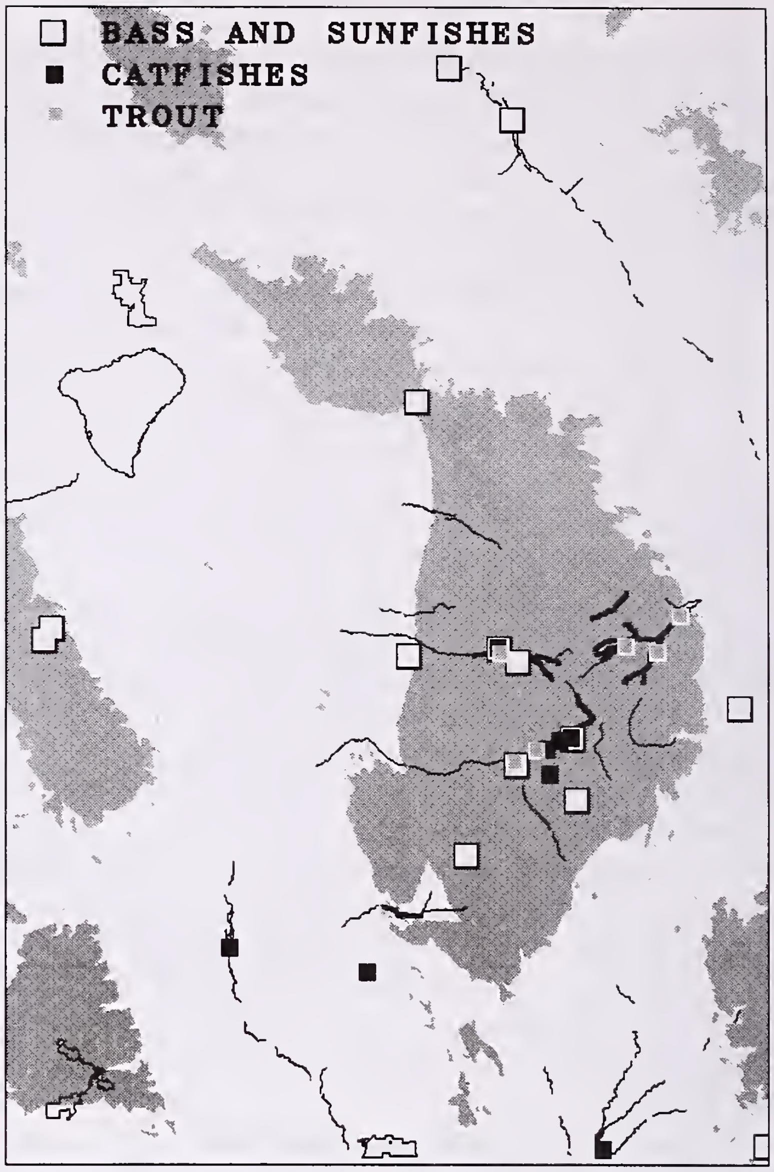

Figure 4.—Distribution of introduced large predatory fishes (largemouth bass *Micropterus salmoides*, green sunfish *Lepomis cyanellus*, bluegill sunfish *L. macrochirus*, black bullhead *Ameiurus melas*, yellow bullhead *A. natalis*, channel catfish *Ictalurus punctatus*, rainbow trout *Onchorhynchus mykiss*, and brook trout *Salvelinus fontinalis*) in the study region in the 1990's.

species at a total of 48 sites and 86 occurrences of native species at 48 sites. Most frequently observed was the introduced bullfrog at 24 localities, double the number of sites for the next most frequently recorded species, the native Sonoran mud turtle (*Kinosternon sonoriense*). Although the Chiricahua leopard frog was observed at 11 sites, this number of occurrences reflects its discovery at some very minor sites, rather than a real abundance of robust populations. This figure is undoubtedly close to the full number of sites at which this species persists in the region.

Introduced fishes were recorded 42 times during our less than two years of sampling with modest collecting gear for this study, compared to a known total of 33 mapped records for the study region as of 1972 (Minckley, 1973). This suggests a recent spread of non-native fishes in the region, despite removal of introduced fishes from two major regional wetland areas—San Bernardino Ranch and Leslie Creek. Available historical records for Rucker Creek also show a marked increase of non-native fishes over the past two decades (fig. 7). In most localities, one or more introduced species had high population densities: for example, effective seine hauls sometimes yielded several dozens or hundreds of adults or subadults of such exotic species as the black bullhead, green sunfish, bluegill sunfish, tiger salamander, and mosquitofish.

Exotic fishes appear to us to have been placed in virtually all reliably perennial waters. Whereas we observed only two partial cases of direct drought-related mortality of these stocked fishes in 1994, heavy, possibly complete, mortality of introduced trout in the Cave Creek drainage followed ash-laden flash floods originating on slopes burned in the 1994 Rattlesnake Fire; similar

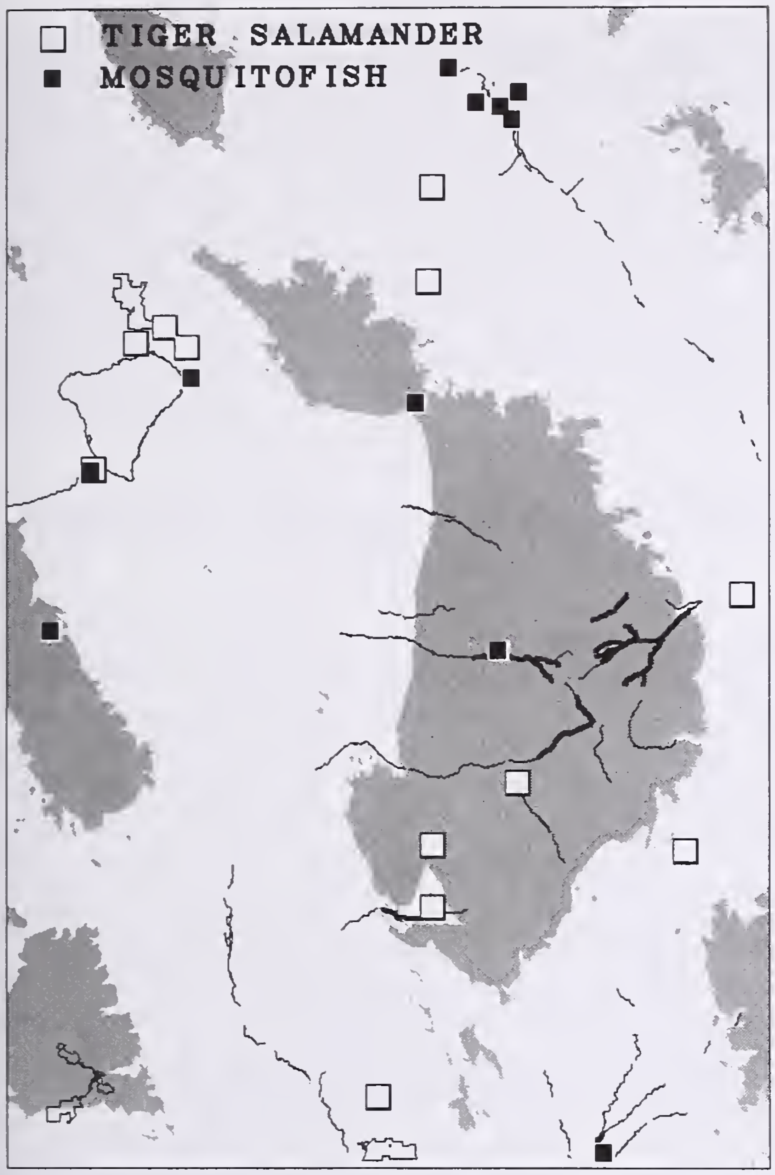

Figure 5.—Distribution of introduced species, mosquitofish *Gambusia affinis* and tiger salamander *Ambystoma tigrinum* in the study region, 1994.

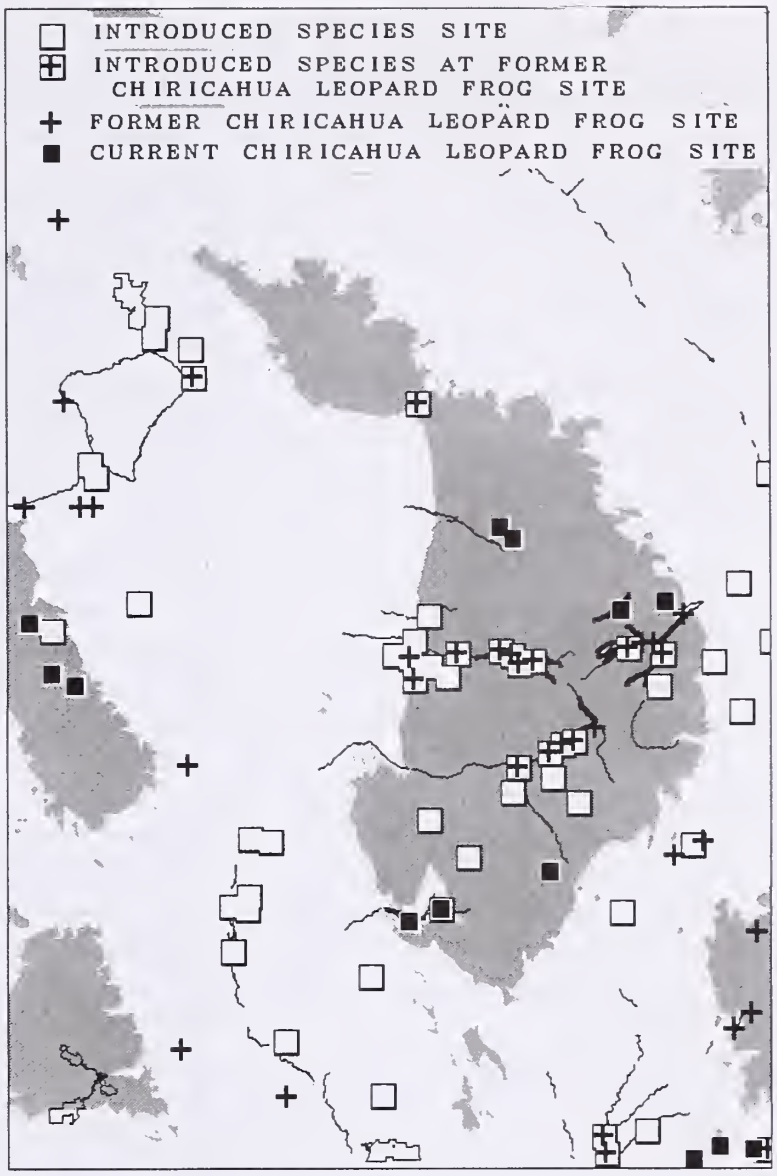

Figure 6.—Occurrence of introduced predatory species at all major perennial waters from which the Chiricahua leopard frog has disappeared. This native frog persists with exotic species in only the single locality shown, as discussed in text.

mortality events occurred in West Turkey Creek; and sediments similarly transported into Rucker Lake largely filled in the lake environment that was a stronghold for introduced fish species.

Regional bullfrog distribution (fig. 3) appears to reflect a limited number of initial introductions, followed by within-drainage dispersal and transplantation. In addition to mapped localities, we observed bullfrogs crossing public roads on five occasions, all within 2 km of known populations. It appears that independent introductions were made at San Bernardino Ranch (1954 or before, personal observations by CHL), lower West Turkey Creek (ca. 1983, J. Austin, personal communication), San Simon Cienega (prior to 1973, R. Zweifel, personal communication), and at Sunsites and near U.S. Rte. 80 and Tex Canyon Road (during the past 10 yr, personal observations by DAP, CRS and PCR). Population groups near Rodeo, New Mexico, Whitewater Draw, and in the Fan region of San Simon Creek are of uncertain origins, possibly involving multiple releases and subsequent dispersal. Possession and intentional spread of bullfrogs continued in 1994, despite its current illegality.

Bullfrogs in southeastern Arizona can be seen at remarkable densities, approaching 1 adult per 2 m of shore at ponds without introduced predatory fishes. In coexistence with largemouth bass (*Micropterus salmoides*) and other centrarchids, yellow bullheads (*Ameiurus natalis*), and other introduced predators (figs. 4, 5), bullfrogs were at far lower abundances, although huge numbers of the unpalatable tadpoles were seen in at least three of these situations (personal observations, PCR).

Minckley (1973) mapped mosquitofish (*Gambusia affinis*) at only three localities within our study region, compared to our 10 sites (fig. 5). Similarly, tiger salamanders (*Ambystoma ti-*

Table 1.—Occurrences of ectothermic aquatic vertebrates in the Chiricahua Mountains region, Arizona, during current survey. The surveyed region included the San Simon, Sulphur Springs, and San Bernardino Valleys and the Chiricahua, Dos Cabezas, Guadalupe, and Dragoon Mountains. An asterisk (*) indicates non-native (introduced) species.

Species	Common Name	Number of Occurrences
*Rana catesbeiana**	Bullfrog	24
Rana chiricahuensis	Chiricahua Leopard Frog	11
Rana blairi	Plains Leopard Frog	4
Hyla arenicolor	Canyon Treefrog	1
Bufo punctatus	Red-spotted Toad	5
Bufo alvarius	Sonoran Desert Toad	4
Scaphiopus spp.	spadefoot toads	8
*Ambystoma tigrinum**	Tiger Salamander	8
Kinosternon sonoriense	Sonoran Mud Turtle	12
Kinosternon flavescens	Yellow Mud Turtle	9
Thamnophis cyrtopsis	Black-necked Garter Snake	10
Thamnophis marcianus	Checkered Garter Snake	7
Thamnophis eques	Mexican Garter Snake	1
*Micropterus salmoides**	Largemouth Bass	7
*Lepomis cyanellus**	Green Sunfish	6
*Lepomis macrochirus**	Bluegill Sunfish	6
*Salvelinus fontinalis**	Brook Trout	1
*Onchorhynchus mykiss**	Rainbow Trout	2
*Ameiurus melas**	Black Bullhead	3
*Ameiurus natalis**	Yellow Bullhead	2
*Ictalurus punctatus**	Channel Catfish	1
*Ctenopharyngodon idellus**	Grass Carp	1
*Pimephales promelas**	Fathead Minnow	3
*Gambusia affinis**	Mosquitofish	10
Poeciliopsis occidentalis	Yaqui Topminnow	2
Gila purpurea	Yaqui Chub	4
Cyprinella formosa	Beautiful Shiner	1
Agosia chrysogaster	Longfin Dace	4
Rhinichthys osculus	Speckled Dace	2
Campostoma ornatum	Mexican Stoneroller	1

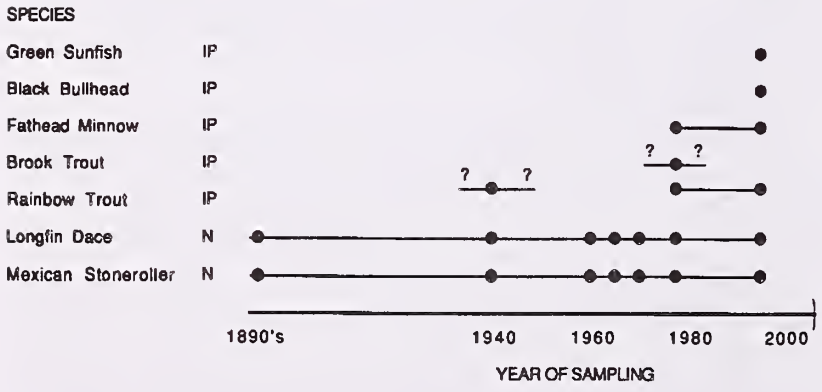

Figure 7.—Time line showing appearance of introduced fishes in Rucker Canyon, Chiricahua Mountains, Arizona. Introduced (non-native) fishes are indicated with an (I), natives with an (N). Species likely to prey on leopard frog tadpoles are indicated with a (P). Occurrence records (dots) 1890-1977 are as summarized by Hendrickson et al. (1980); 1994 records are original here. Question marks on the time lines indicate that stocked game fishes may not have been continuously present.

grinum) were apparently absent prior to the early 1970's (Zweifel, personal communication), but are now widespread in the region (fig. 5). Tiger salamanders are normally eradicated by introduced fishes (Collins et al., 1988), and we found them only once with mosquitofish, in the complex of power plant settling ponds near Cochise. Remarkable abundances were observed for both tiger salamanders (over 40 adults per seine haul) and mosquitofish (several hundred per haul) where they occurred in ponds without additional introduced predators.

During this study, we found tiger salamanders crossing roads four times, all at unknown distances from breeding ponds, and we think they are considerably more widespread than indicated on the map. Branchiate (larval-form) salamanders were found at several sites that nearly dried during 1994, differing from introduced fishes in this regard, and transformed individuals readily live a terrestrial, subterranean existence. Moreover, the animals observed were all probably introduced barred tiger salamanders *A. tigrinum mavortium*, which have been found alive after several months buried over 1 m deep in a dry pond bottom (K. Cobble, personal communication). Thus, we cannot expect to have located a majority of existing population sites in our brief survey focused on perennial waters.

Distribution and Decline of the Chiricahua Leopard Frog

Almost all apparently perennial waters in the Chiricahua region investigated during this study that lacked introduced predatory vertebrates supported moderately sizable populations of Chiricahua leopard frogs (18-ca. 300 observed adult and subadult individuals). All waters having introduced aquatic vertebrates lacked Chiricahua leopard frogs, with a single exception. At Tom Ketchum Tank, Pedregosa Mountains, we found two adult Chiricahua leopard frogs, and 4 large cannibalistic tiger salamanders; the number of both frogs and salamanders was low, and the frogs were within possible dispersal range of a larger population. Thus, we found a nearly perfect pattern of distributional complementarity of Chiricahua leopard frogs and introduced predators in this region.

There were two other probable exceptions to the complementary distribution of Chiricahua leopard frogs with introduced species. Horseshoe Pothole Canyon in the Chiricahua Mountains, a bedrock stream, supported only black-necked garter snakes, red-spotted toads, and canyon treefrogs; a second perennial bedrock stream, Contention Spring in the Peloncillo Mountains, also had black-necked garter snakes, as well as Sonoran mud turtles, but had no ranid frogs. This is also the habitat type from which the Tarahumara frog was extirpated in the 1970's and 1980's (Hale, et al., 1995 *in press)*, suggesting a continuing toxicity problem unique to, or most clearly presenting in, waters that lack mud or other extensive sediment beds.

The consistent pattern of Chiricahua leopard frog absence at sites with introduced species is strong evidence of a negative effect of exotic species on indigenous frogs. The presence of Chiricahua leopard frogs at almost all perennial water sites that lacked introduced predators is strong evidence that these frogs could, in spite of other possible problems including pollution, thrive in most of southeast Arizona if introduced aquatic species are eliminated.

Further evidence for the effect of non-native species on Chiricahua leopard frogs is the presence of introduced predators at all historical, perennial water localities from which Chiricahua leopard frogs have disappeared (fig. 6). All known recent disappearances of these frogs from historically known localities are at (1) perennial waters now supporting introduced predators, or (2) ephemeral waters on valley floors that were dry in 1989 and 1994, and probably in other years of the current drought period.

Decline of the Chiricahua leopard frog was under way by the mid-1980's (Clarkson and Rorabaugh, 1989), whereas numerous healthy, reproducing populations were seen in the Chiricahua region from the late 1950's (Zweifel, personal communication) to the early 1970's (e.g., Frost and Bagnara, 1977). Thus, timing of decline is synchronous with burgeoning of introduced species populations. The simplest hypothesis is that introduced predators eliminated Chiricahua leopard frogs and are currently preventing their re-establishment.

Other hypotheses are possible. Other native ranid frogs, in California, may be strongly affected by tadpole competition from introduced bullfrogs (S. Kupferberg, personal communication), so an assumption that predation is the main or only force remains to be evaluated. Also, during 1974-1984 in the Santa Rita and Atascosa mountains and adjacent regions of Mexico, ranid frogs were found dying, most probably from chemical toxicity derived from smelter-produced air pollution (Hale et al., *in press*). Similar die-offs, involving leopard frogs in at least one previously-affected locality, have recurred occasionally in the present decade (J. Carpenter, personal communication). We might postulate that initial declines or disappearances were pollution-mediated, and that pollution currently affects native frogs more than exotics, thus perpetuating exclusion of the native. Even if this proves correct, removal of introduced fishes and bullfrogs will still help effect recovery of the Chiricahua leopard frog. While delay in acting to save the Chiricahua leopard frog from extinction could risk its extirpation, we would nonetheless be well advised to develop experimental and observational studies on causes and mechanisms of decline, and more appropriately, of survival.

During the mid-1980's there was a temporary resurgence of these native frogs, apparently because wet conditions allowed them to colonize predator-free localities that usually become seasonally dry (personal observations, PCR). This phenomenon offers little hope for the species' survival, as shown by niche occupancy during the drought summer of 1994 (fig. 8). Current niche occupancy shows that Chiricahua leopard frogs are restricted primarily to sites that came close to drying in 1994. Tanks that dried in 1994 were not found to contain leopard frogs if they filled late in the summer. Thus, these frogs have been excluded from optimal habitat by exotics and are thus vulnerable to extinction due to environmental stochasticity, i.e. drought. The habitat occupancy pattern supports a prediction that continuing drought will continue to eliminate populations, and more severe drought might extirpate the species from southern Arizona and southwestern New Mexico.

Almost all current populations of the Chiricahua leopard frog in the Madrean region are in stock ponds that have a significant risk of drying, making the current situation unstable for this species. Only two populations are currently established at better sites. One of these has an anoxic bottom that may wipe out the frogs during a warm, dry winter (R. Jennings, M. Sredl, personal communications). The other is a small perennial stream (Leslie Creek) managed for native fishes by U.S. Fish and Wildlife Service, that may be the only remaining natural population center for the species in southern Arizona: however, at 20-30 adults in 1994, this is inadequate for a boom-bust species that almost certainly requires a metapopulation structure for long term persistence (Gilpin and Hanski, 1991; Sjögren, 1991; Bradford et al., 1993; Sredl and Howland, *this volume*).

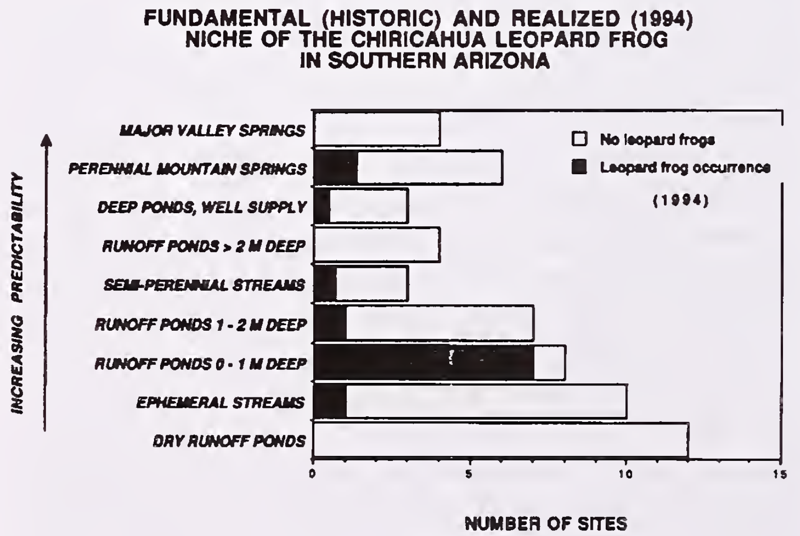

Figure 8.—Habitat occurrence of the Chiricahua leopard frog in southern Arizona, showing 1994 occurrences (shaded) contrasted to existing habitat.

It is clear that introduced predators (in this region bullfrogs, largemouth bass, sunfish, and probably trout and catfish, and possibly mosquitofish and fathead minnows), are the primary causes of decline—and potential listing as a Federally threatened species—of the Chiricahua leopard frog. These frogs may be found to be affected by pollution (Hale et al., *in press*), ultra-violet radiation (Blaustein et al., 1994), or other undetermined factors (Fellers and Drost, 1993) that apparently affect native ranid frogs. In light of our findings in 1994, however, removal of non-native aquatic vertebrates is the most sensible, immediate management action. In concert with control of such exotics, refurbishment of pond habitats to maintain or control water depth is likely to assist recovery of the Chiricahua leopard frog directly.

CONCLUSIONS

1. Introduced predatory vertebrates of at least 13 species now occur widely in the Chiricahua Mountain region. In order of frequency of observed occurrence, these introduced species were the bullfrog, mosquitofish, tiger salamander, largemouth bass, green sunfish, bluegill sunfish, and several species of catfishes and trout.
2. Expansion of these non-native aquatic vertebrates to new localities in this region has been ongoing at an alarming rate for the last 2 decades.
3. Recent decline of the Chiricahua leopard frog, possibly leading to listing as a Federally threatened species, is in this region directly related to interactions (especially predation) with introduced aquatic vertebrates.
4. Remaining populations of the Chiricahua leopard frog exist mainly in habitats subject to drought-related stress, particularly drying or near-drying, where conditions have discouraged the introduction and establishment of non-native aquatic vertebrates.
5. Without corrective action, specifically removal of introduced predatory vertebrates and maintenance of pond and pool environments in predator-free areas, the Chiricahua leopard frog will probably become extinct in this region.

RECOMMENDATIONS

Without doubt, the decline and threatened extinction of native aquatic vertebrates, including fishes, is by far the greatest immediate threat to biodiversity of the Madrean region in the United States. As demonstrated here and elsewhere, this aquatic fauna is being eliminated from historic habitats primarily by non-indigenous sport fishes and bullfrogs. These species, purposefully introduced into lakes created originally for them, are also being spread intentionally and unintentionally into other aquatic environments. If the native aquatic vertebrates are to continue living in southeastern Arizona, wetlands free of these introduced predators must be provided for them.

Below we offer long-term recommendations to aid in recovery of the Chiricahua leopard frog in southeastern Arizona. The survival of this frog in Cochise County is now so tenuous that we also offer shorter term, stop gap measures to maintain the species while longer-term measures are being developed and implemented. Several or all of these long and short-term management recommendations may apply as well to some native fishes of the region, a faunal group even more imperiled than the frogs.

A principal philosophy behind some of the recommendations is that resource managers, conservationists, and private landholders can work together in a spirit of cooperation, with benefits accruing to all parties. Working out this partnership is a challenge that must be met, if the native leopard frogs and fishes are to remain a part of the biodiversity of this unique region.

Many property owners are suspicious of government intentions, especially relating to management of potential threatened or endangered species. Recently, however, several long-time Arizona ranchers have begun working with State and Federal resource management agencies and conservation groups such as The Nature Conservancy to try to insure that the region does retain its biotic as well as cultural components. It is critical that some successes come out of these early efforts—that the landowners, resource managers and, especially, the native wetland ecosystems benefit. Only by demonstrating gains to all sides will we recruit additional participants. Without cooperation of private landowners, efforts to conserve these native aquatic vertebrates in southeastern Arizona are likely to fail.

General Management and Research Recommendations

A management team composed of scientists and resource managers should be created to develop a plan to recover the Chiricahua leopard frog in southeastern Arizona. Such a team should be assembled, regardless of Federal listing status or lack thereof. Actions to be considered in such a recovery plan include:

- Hold off new stocking of sport fishes in the Chiricahua region for at least a decade. The sport fishery in the Chiricahua Mountains is relatively small, yet almost every drainage has a variety of introduced sport fishes.
- Develop standing plans to remove non-native aquatic vertebrates in select areas during severe drought, when such elimination is most likely to succeed.
- Forego the costly and forseeably recurrent dredging of silt from Rucker Lake, permitting Rucker Canyon to exist without the lake habitat that favors introduced species. This "inaction" could save the Coronado National Forest considerable amounts of money in the short and long term. Clear non-natives from the few stock tanks in the Rucker Canyon drainage where they currently occur.
- Maintain the Cave Creek and Portal, Arizona, area free of non-native frogs and fishes for a decade-long experimental period to determine effect on native species. It is timely to begin such a program now, since run-off from the 1994 Rattlesnake Fire seems to have eliminated the non-native fishes. Refurbish key breeding sites for the Chiricahua leopard frog (Herb Martyr and John Hands Dams) by digging out the sediment.
- Cooperate in an attempt to replace non-native with native species of fishes and frogs in West Turkey Creek, Chiricahua Mountains.
- Regularly monitor native and introduced fishes as well as frogs in the Rucker Canyon basin, Cave Creek and South Fork, and West Turkey Creek.
- Initiate research on natural and captive populations of Chiricahua leopard frogs to aid in management decisions affecting recovery.

Recommendations for Landholder Cooperation

- Resource managers and scientists can collaborate with ranchers and other landholders such that all benefit from the frog's need for reliable, clean, perennial waters. Applicable programs available through U.S. Fish and Wildlife Service and Arizona Game and Fish Department should be pursued, wherever clear benefits will accrue to both the resource and the landholder. One such example might be assisting a landholder with the expense or work in installing a new windmill if the landholder agrees (1) to use some of the water produced by the windmill to ensure that leopard frog habitat in the pond is maintained as needed, and (2) to allow and/or assist in keeping his or her ponds free of introduced fishes and frogs.

- Favor management of stock, house, and farm ponds by resident personnel who will help prevent contamination of habitats with introduced species. This could be effected by incorporating inducements to holders of Federal grazing leases into resource management plans in return for commitment to keep ponds predator-free.

We cannot overstate the importance of enlisting cooperative private landholders in this particular effort. Removal of all introduced aquatic predators/competitors from some perennial waters in the area (San Bernardino National Wildlife Refuge, Rucker Canyon, West Turkey Creek, for example) will be a difficult, time-consuming task. Management of stock ponds as leopard frog or native fish habitat may be a relatively simple, cost-effective method of perpetuating the native wetland fauna, while major habitat restoration is in progress elsewhere. Maintaining these man-made wetlands for native species is in keeping with the recent Federal mandate for ecosystem management; even though these wetlands are not the original stream, spring and cienega ecosystems, in most cases they support the only remaining leopard frogs.

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Mike Sredl and Jeff Howland generously shared their knowledge of distribution and ecology of leopard frogs in Arizona, and Richard Zweifel information from meticulously kept field notes on leopard frogs spanning almost 4 decades in the region. Shawn Sartorius participated in most of the field data collection. The following people shared additional important perspectives and data on regional leopard frogs: Josiah Austin, Dixie Bounds, Kevin Cobble, Jim Collins, Phil Fernandez, Steve Gotte, Steve Hale, Jacques Hill, Andy Holycross, Randy Jennings, Tom Jones, Matt Magoffin, Brent Martin, James Platz, Jim Rorabaugh, Norm Scott, Wade Sherbrooke, and Ronnie Sidner. Vicky Meretsky assisted with map production. We thank Mark Jennings, W.L. Minckley, and James Platz for reviewing our manuscript, but we assume full responsibility for the results and management proposals contained herein. The work was supported by funding from Arizona Game and Fish Department Heritage Program and from U. S. Fish and Wildlife Service.

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Aspects of the Life History and Ecology of the Sonoran Mud Turtle in Southeastern Arizona

Richard C. van Loben Sels[1], Justin D. Congdon[2], and Josiah T. Austin[3]

Abstract.—From 1990 through 1994 we conducted a mark-recapture study of *Kinosternon sonoriense* in the West Turkey Creek area of the Chiricahua Mountains in southeastern Arizona. A total of seven were found dead, 573 live individuals were marked, and 913 recaptures were made. Of the total number of marked individuals, approximately 5% were initially captured in stream pools and 90% in stock tanks. Population size is estimated to be approximately 750 individuals. Of the 573 individuals first found alive 18.5% were classified as juveniles; 35.8% and 45.7% were adult males and females, respectively.

The youngest adult female was 5 years old and the smallest had a carapace length (CL) of 106 mm. A minimum of 22% of the females captured twice during the reproductive season produced at least two clutches of eggs. Over all years, clutch size averaged 6.4 eggs; however, clutch size did vary as a function of year and location (e. g., stock tank system). Egg widths determined from X-radiographs averaged 16.5 mm (min. = 13.6 mm, max. = 18.8 mm). Both clutch size and egg witdths were significantly and positively related to body size, but not to the age of females. The dry average mass of egg yolks averaged 0.96 g (min. = 0.73 g, max. = 1.25 g, n = 6), and was comprised of 28.75% (min. = 26.47%, max. = 29.87%, n = 6) non-polar lipids. Egg shells averaged 32.75 % of the total dry mass of the egg and were similar in proportion to eggs of other *Kinosternon*. Four hatchlings captured in early August weighed approximately 3.0 grams and were 22 mm CL.

INTRODUCTION

The mechanisms by which life history trait values of individuals are transduced into population parameters are important in developing life history theories and are of great practical value in formulating conservation and management programs. Major dichotomies in life history traits are predicted to occur in life histories of long- vs. short-lived organisms (Gadgil and Bossert, 1970; Tinkle et al., 1970; Williams, 1966). However, since life history studies are labor intensive, time consuming and expensive, studies that adequately document mean values, and the magnitude and causes of variation in life history trait values are few. Since the problems that impede life history studies are magnified when the species studied are long-lived, the majority of quantitative life history data that exists is on short-lived organisms (Dunham et al., 1988; Tinkle, 1979, Tinkle et al., 1993). As a result, many assumptions and predictions of life history theories remain untested and formulation of conservation and management programs of long-lived organisms will continue to be based on little data.

Turtles of the genus *Kinosternon* are relatively long-lived (Gibbons and Semlitsch, 1982) and are excellent models for life history and demographic studies (Frazer et al., 1991). The Sonoran mud turtle *(Kinosternon sonoriense)* occurs in northwestern Mexico, as well as in the southwestern United States where it ranges from western New Mexico, through central and southern Arizona. It is the only native freshwater turtle that occurs in the Chiricahua Mountains of southeastern Arizona.

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In 1990 we initiated a proposed long-term study of an isolated, single species population of the Sonoran mud turtle (*K. sonoriense*) in southeastern Arizona. The goals of the study were to obtain long-term data on life history trait values and aspects of the natural history of Sonoran mud turtles. Such data will: 1) enhance our understanding of the ecology of sonoran mud turtles in particular and long-lived organisms in general, 2) allow tests of existing life history theories, and 3) expand the life history data base on long-lived organisms to provide a basis for formulating conservation and management programs for long-lived organisms.

MATERIALS AND METHODS

An intensive mark-recapture study of Sonoran mud turtles has been maintained on the El Coronado Ranch in southeastern Arizona for the past five years (1990-1994). The study area is located in the West Turkey Creek and associated stock tanks in Cochise County at approximately 1675 meters elevation in the Chiricahua Mountains.

Some turtles were captured by hand and with dip nets, but most were captured using baited hoop traps fitted with floats to prevent submergence during heavy rains. Each turtle was individually marked by notching the marginal scutes of the carapace, weighed, and measured (straight line anterior and posterior plastron length, carapace length, shell height and shell width at the bridge), and then released at the point of capture.

At first capture, turtles with fewer than 8 obvious growth rings on one of the plastral scutes were assigned an age based on the assumption that these rings were laid down annually in juveniles and young adults. Recaptures of juveniles over all age classes during the past 4 years support this assumption.

All females and larger juveniles were X-rayed to determine if they were carrying oviductal eggs (Gibbons and Greene, 1979). Data from X-radiographs, provided information on clutch size, clutch frequency, the relationships of clutch size to body size and age, and age at maturity. During 1994, 15 females were captured from Rock Creek (approximately 6 km north of West Turkey Creek) and injected with oxytocin (1.5 ml kg^{-1} body mass; Ewert and Legler, 1978) to induce egg laying. All eggs from 6 females (n = 14 eggs) were frozen and transported to the Savannah River Ecology Laboratory where eggs were separated into shells and yolks (includes yolk and albumin). Egg yolks were dried to a constant weight, ground with a mortar and pestle, and non-polar lipids were extracted using a Soxtec apparatus with petroleum ether as a solvent (Fischer et al., 1991).

Parametric statistical tests were used when variables were continuous and assumptions of the tests were met. Otherwise, non-parametric tests, such as Spearman's Rank Correlation (RHO; SAS, 1988) were used. Unless otherwise stated, levels of significance were established at alpha 0.05. Measures of central tendency and dispersion are presented as the mean ± one standard error unless stated otherwise.

RESULTS

From 1990 to 1994, we marked 580 individuals and made 913 recaptures of these individuals. Approximately 5% of the turtles were first captured in stream pools and 90 % in stock tanks. Of the first 573 individuals captured alive, 18.5% were classified as juveniles, 35.8% and 45.7% were adult males and females, respectively.

Minimum age at sexual maturity was 5 years and the smallest turtle that produced a clutch of eggs was 106 mm CL. Mean size of all gravid females was 134.4 mm CL. Data from X-radiographs of gravid females provided direct evidence that between 1991 and 1994, 12 of 55 (22%) of the females captured twice during the reproductive season produced at least two clutches of eggs. However, the actual proportion of adult females that produce more than one clutch annually has yet to be determined. Clutch size averaged 6.4 eggs (min. = 2, max. = 11; SE = 0.125; n = 230; Fig 1a). However, clutch size was significantly lower in 1994 (4.9 eggs) compared to 1991-1992 (7.6 eggs) and 1993 (6.8 eggs). Over all years, clutch size was significantly and positively related to body size of females (Spearmans Rho = 0.622; Fig 1b). Average egg width per clutch determined from X-radiographs (XREW) averaged (16.5 mm; min = 13.6; max = 18.7; n = 241 clutches; Fig 2a). Egg size was significantly and positively related to body size of females (Fig 2b). Neither clutch size nor egg width was related to the age of females (ANOVAS, P >0.05). Egg yolks averaged 60.2 % water by mass. The dry mass of egg yolks averaged 0.96 g (min. = 0.73 g, max. = 1.25 g, n =6 clutches and 14 eggs), and was comprised of 28.75% (min. = 26.47%, max. = 29.87%) non-polar lipids. Egg shells averaged 32.75 % of the total dry mass of the egg.

Four hatchlings were captured August 5, 1993 and one on August 9, 1994; these hatchlings averaged 3.0 grams body mass and 22.2 mm in CL.

DISCUSSION

Twenty four thousand years ago, a large portion of Sulphur Springs Valley was part of Lake Cochise. As Lake Cochise dried, populations of *K. sonoriense* became isolated in the most permanent streams (e. g., West Turkey Creek) originating in the adjacent mountain ranges. The higher densities of turtles presently occupying stock tanks compared to West Turkey Creek stream bed proper, suggests that the turtles prefer the more lentic habitats of stock tanks. Based on simple Lincoln Indices, our first approximation of total population size in the Turkey Creek drainage basin is 700-800 individuals. If our estimation of total population size is accurate, then approximately two thirds of the population had been marked by the end of the 1994 field season.

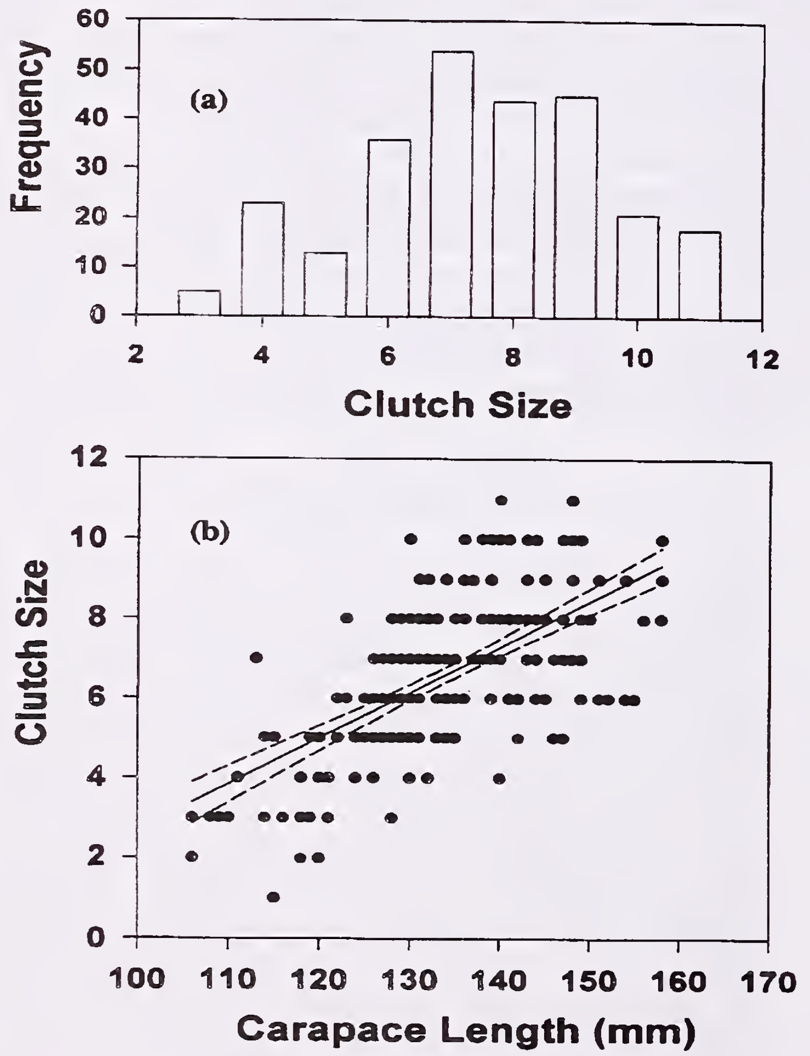

Figure 1.—(a) Frequency histogram of clutch sizes, and (b) the linear relationship (= solid line, and 95% confidence intervals = dashed lines) of clutch size to body size (CS = -0.840 + 0.112 CL; R^2 = 0.42; n = 230 clutches) of *Kinosternon sonoriense* females from West Turkey Creek in the Chiricahua Mountains.

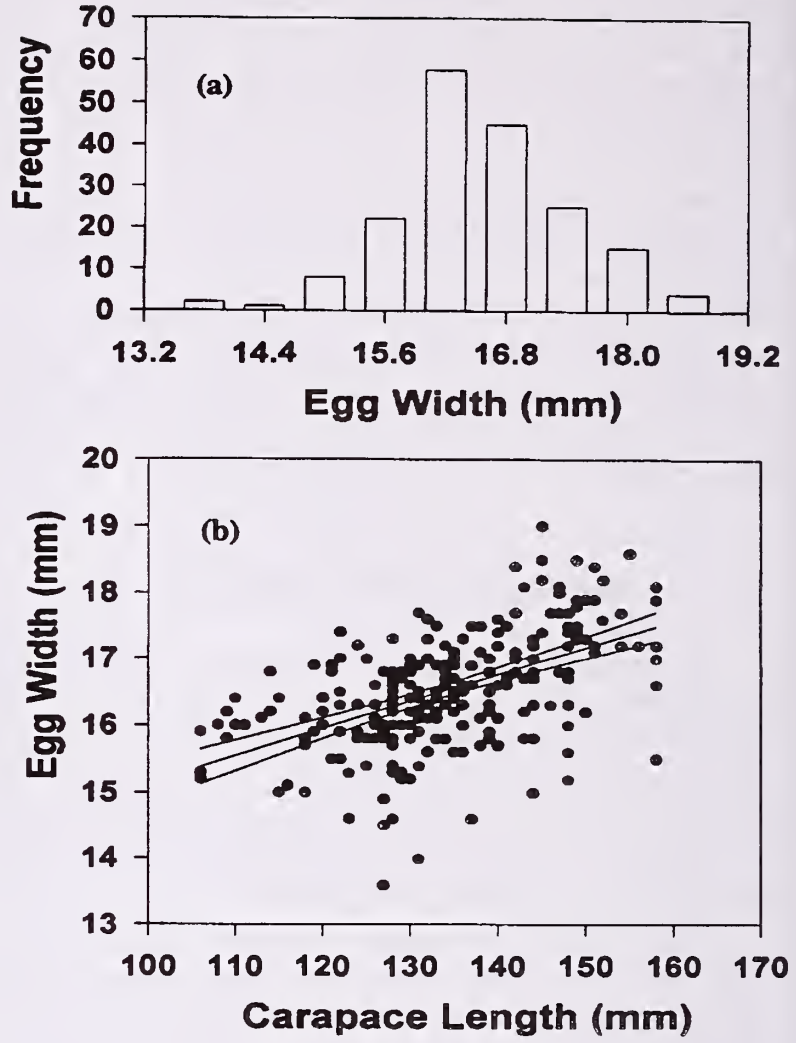

Figure 2.—(a) Frequency histogram of egg widths determined from X-radiographs and, (b) the linear relationship (= solid line, and 95% confidence intervals = dashed lines) of X-ray egg widths to body size (XREW = 10.945 + 0.041 CL; R^2 = 0. 29; n = 241 clutches) of *Kinosternon sonoriense* females from West Turkey Creek in the Chiricahua Mountains.

Since the proportion of known-age individuals in the population will grow each year as we mark more juveniles, we hope to have over 50% of the population as known-age individuals within the next three years. The proportion of juveniles (excluding hatchlings) captured in the El Coronado population (18.5%) greater than that for a population of *K. subrubrum* (10.3% in South Carolina; J. W. Gibbons, unpublished data), and less than that found for painted turtles (*Chrysemys picta*; 40%) in Michigan (JDC, unpublished data). Although the proportion of juveniles captured in the El Coronado is different from other populations of turtles, differential trapping success of juveniles and adults among studies may have caused the differences in the relative numbers of juveniles among studies.

The minimum age at maturity of West Turkey Creek females was 5 years: an age value similar to that reported for other populations of Sonoran mud turtles (Rosen, 1987) in Arizona. Since age at maturity within a population of turtles may be highly variable (Congdon and van Loben Sels, 1993), and such variation can have substantial impact on life table calculations and models of population dynamics (Congdon et al., 1993, 1994), a single minimum value reported for at maturity is not quantitatively adequate description of this important life history trait.

Annual fecundity of females was determined by clutch size and clutch frequency. Based on the assumption of an equal primary sex ratio, an average clutch size of 6.4 eggs, and a reproductive frequency of 1.22, annual fecundity of females from West Turkey Creek is 3.7 female eggs. Average clutch size for the West Turkey Creek population is higher than those reported by Rosen (1987) for five populations of *K. sonoriense* (Beaver Creek, Indian Canal, Montezuma Well, Tule Creek, and Sharp Spring), and slightly smaller than those in three populations (Palm Lake, Granite Reef, and Sycamore Creek). Both body size and clutch size are larger than values reported for species of *Kinosternon* in the eastern United States (Gibbons, 1983). Since body size explains approximately 42% of the variation in clutch size in the West Turkey Creek population, an average increase of 5 eggs is associated with the 75 mm range of body size found between the smallest and largest adult female. The lack of association of reproductive traits with age found in *K. sonoriense* is similar to the lack of such relationships found in most other turtle species examined (Congdon and van Loben Sels, 1993; Frazer et al., 1991).

Size has been implicated as an important component of hatchling survival (Brooks et al., 1991), and is strongly influenced by maternal investment in the egg (Congdon and Gibbons, 1987). Since egg widths determined from X-radiographs were significantly and positively related to body size of adult females, larger females on average would produce larger eggs and thus larger hatchlings. An increase of 3 mm in average egg width is positively associated with the 75 mm range of body sizes found among adult females.

In addition to egg size, the proportional parental allocation of egg components such as water, protein, and lipids are also important aspects of hatchling quality (Congdon and Gibbons, 1990). The proportion of water ,lipids, and shell in eggs of West Turkey Creek females is similar to that found in *K. subrubrum* in South Carolina (Congdon and Gibbons, 1985). In general, females of turtle species with hatchlings that delay emergence from the nest allocate proportionately more non-polar lipids to eggs than do females of turtle species that have hatchlings that do not delay emergence (Congdon and Gibbons, 1985). The proportion of total dry mass of eggs represented by egg shells of *K. sonoriense* (32.75%) was more similar to five other species of turtles having brittle shelled eggs (40.70%) , than to seven species having parchment shelled eggs (19.25%; Congdon and Gibbons, 1985).

The reproductive season for *K. sonoriense* extends at least from June to September (Rosen, 1987). Based on the duration of the reproductive season, and our observations of hatchling emergence in August, we propose the following scenario for egg incubation and embryonic development. Eggs are ovulated beginning in June and are held in the oviducts until the monsoon rains (July through August). Eggs are placed in nests some distance away from bodies of water. Development is postponed through embryonic diapause until the eggs are cooled during winter. Embryonic development remains in diapause through winter and then commences as eggs warm during the following spring. Development takes from 70 to 90 days and hatchlings delay emergence from the nest to coincide with the onset of summer rains . Since both nesting and hatchling emergence coincide with summer rains, the total time from egg laying to hatchling emergence is approximately 11 months.

The results presented here are preliminary as we are only in the fifth year of study. Our results do document that both clutch size and egg size are strongly correlated with body size of females within the population. Based on the size of the population and the proportion of juveniles, the population appears to be in no immediate danger. However, bullfrogs were introduced into the West Turkey Creek drainage about ten years ago, and their population numbers are high enough to be of concern if they are a major predator of turtle hatchlings. Life history studies show that high juvenile survivorship is required for populations of long-lived organisms to maintain population stability (Congdon et al., 1993,1994). We plan to pay particular attention to the numbers, proportions, survivorships, and the age distribution of juveniles in this population over time.

ACKNOWLEDGMENTS

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Unisexual Lizards (Genus *Cnemidophorus*) of the Madrean Archipelago

Charles J. Cole[1] **and Herbert C. Dessauer**[2]

Abstract.—About 20 species of *Cnemidophorus* occur in the vicinity of the Sky Islands of the southwestern United States and northwestern Mexico, in habitats ranging from woodland to desert. Many of these whiptail lizards occur in populations with a 50:50 sex ratio, and reproduction depends on mating and internal fertilization. However, half of the species of the Madrean Archipelago are unisexual species for which only females exist. These remarkable vertebrates are important biological resources for basic research.

Here we review our comparative multidisciplinary research on reproduction, genetics, evolutionary biology, and systematics, integrating field and laboratory investigations. Results include the following: (1) females of the unisexual species reproduce independently by parthenogenetic cloning; (2) a diversity of clones occupies the area, including both diploid and triploid species; (3) the unisexual species originated from F_1 hybrids among bisexual species, and various unique combinations of hybrids were involved; (4) in each instance, the switch from sperm-dependent reproduction to sperm-independent reproduction occurred in a single generation; and (5) these remarkable animals have considerable potential for improving knowledge of reproductive biology and other basic phenomena in addition to revealing the natural history of the Madrean Archipelago and adjacent lands.

BISEXUAL AND UNISEXUAL SPECIES

Whiptail lizards of the genus *Cnemidophorus* (fig. 1) are alert, wary, and fast terrestrial animals that forage actively (usually for insects) in sunny habitats. There are about 50 species in the genus, their composite ranges extending from about the southern two-thirds of the United States southward through Mexico and Central America to and throughout much of South America east of the Andes (for reviews see Maslin and Secoy, 1986; Wright, 1993).

Most species of whiptail are bisexual species (i.e., populations consist of males and females in a 50:50 sex ratio). In these, reproduction requires mating, and fertilization is internal (for the reproductive biology of a bisexual species, see Goldberg and Lowe, 1966).

Figure 1.—*Cnemidophorus sonorae*, a triploid unisexual species (reproduced from Dessauer and Cole, 1989, fig. 2F; reptile specimen number 126976 of the American Museum of Natural History, New York).

Approximately one-quarter of the species of *Cnemidophorus*, however, are unisexual species. In these, only one sex exists; all individuals are females (Minton, 1959; Duellman and Zweifel, 1962; Maslin, 1962).

The whiptail fauna of the Madrean Archipelago includes approximately 20 species (Table 1), of which about half are unisexual. This represents the largest concentration of all-female species and

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their bisexual relatives found anywhere on Earth (Wright and Lowe, 1968). For reviews of unisexual lizards, including those in other genera, see Cole (1975) and Darevsky (1992).

REPRODUCTION IN UNISEXUAL SPECIES

After realizing that certain population samples of *Cnemidophorus* consisted of females only, herpetologists collected additional specimens in expectation of finding males. Nevertheless, males consistently failed to materialize for certain populations. Consequently, several biologists began investigating reproduction of the all-female lizards, particularly after seeing Darevsky's (1958) intriguing pioneering studies of unisexual lizards (genus *Lacerta*) from Armenia, the first report of apparently normal unisexuality in reptiles.

Anatomical and histological studies of field-captured lizards suggested that the reproductive tracts in females of unisexual species were similar to those in females of bisexual species (e.g., Cuellar, 1968, 1970; Christiansen, 1971). However, several questions concerning unisexual species still required attention, such as: (1) are the eggs of these species triggered to develop by sperm from males of other species; (2) do these females actually begin life as males but undergo sex-reversal while growing up; (3) are these females actually hermaphrodites that fertilize their own eggs; and (4) do these females produce offspring from unfertilized eggs (i.e., by true parthenogenesis)? Rare examples for questions (1) through (3) were already under study for other vertebrates, particularly some fishes and salamanders (for reviews, see Reinboth, 1975; Dawley and Bogart, 1989), but true parthenogenesis (development of eggs in the complete absence of sperm) was not documented as the normal means of reproduction in any species of vertebrate prior to 1981.

Table 1.—Species of whiptail lizards (*Cnemidophorus*) in and near the Madrean Archipelago (modified from Table 1 of Dessauer and Cole, 1989, using some names from Wright, 1993).

Species	Reproduction	Ploidy
C. burti	bisexual	2n
C. costatus	bisexual	2n
C. dixoni	unisexual	2n
C. exsanguis	unisexual	3n
C. flagellicaudus	unisexual	3n
C. grahamii	unisexual	2n
C. gularis	bisexual	2n
C. inornatus	bisexual	2n
C. laredoensis	unisexual	2n
C. neomexicanus	unisexual	2n
C. opatae	unisexual	3n
C. scalaris	bisexual	2n
C. septemvittatus	bisexual	2n
C. sexlineatus	bisexual	2n
C. sonorae	unisexual	3n
C. tesselatus	unisexual	3n
C. tigris	bisexual	2n
C. uniparens	unisexual	3n
C. velox	unisexual	3n

The best way to obtain controlled data on these questions was to establish colonies in the laboratory and observe the development of multiple generations within individual family trees (lineages) of known ancestry and relationships. With this approach (for methods of maintaining colonies see Townsend, 1979; Townsend and Cole, 1985), the following has been demonstrated about unisexual species: (1) their eggs develop in the absence of males; (2) all normal hatchlings are immature females that go through the same maturation process as the females of bisexual species; (3) the lizards are not self-fertilizing hermaphrodites and completely lack testicular tissue, spermatozoa, and males; and (4) consequently, we must conclude that their eggs develop parthenogenetically (Hardy and Cole, 1981).

PATTERNS OF INHERITANCE

The fact that unisexual species reproduce parthenogenetically raises the question of whether their offspring exhibit less variation than do those of bisexual species. This requires understanding population genetics both in bisexual and unisexual species.

Population genetics of bisexual species has been studied extensively in lizards of the genera *Sceloporus* (reviewed by Sites et al., 1992) and *Cnemidophorus* (e.g., Dessauer and Cole, 1989, 1991). Patterns of inheritance of chromosomes occurring in heteromorphic pairs (e.g., sex chromosomes and chromosomal aberrations) and of proteins encoded by specific gene loci (including Hardy-Weinberg analyses of frequencies of alternative alleles), show that bisexual lizards are diploid outcrossing species with the same Mendelian inheritance that typifies other vertebrates, such as birds and mammals (including humans). Offspring resulting from different eggs and sperm from the same parents (or different ones) exhibit individual variation due to chromosomal crossing over and random assortment and segregation in meiosis, as well as rare mutations.

In contrast, females of unisexual species of *Cnemidophorus* produce offspring that are genetically identical to each other, to their mother, grandmother, and so-on, excepting rare mutations. In other words, a lineage of these lizards is a clone. This has been demonstrated by analyzing patterns of inheritance at both the level of whole chromosomes and individual gene products in lineages of known ancestry raised through multiple generations in the laboratory (e.g., Cole, 1979; Dessauer and Cole, 1984, 1986). In addition, some of the unisexual species are triploid clones, each individual possessing cells with three sets of functional chromosomes and genes instead of two (e.g., *C. sonorae*; for a review, see Dessauer and Cole, 1989).

ORIGINS OF UNISEXUAL CLONES BY HYBRIDIZATION

The comparative investigations in genetics of *Cnemidophorus* indicated not only their patterns of inheritance, but also hypotheses for the evolutionary relationships of the species. The evidence from chromosomes, individual gene products (with over three dozen independent loci analyzed in the most recent studies), comparative anatomy, geographic distribution, and habitat preferences all demonstrate that the unisexual species in the Madrean Archipelago arose as a consequence of interspecific hybridization among the bisexual species (e.g., Lowe and Wright, 1966; Neaves and Gerald, 1968, 1969; Neaves, 1969; Parker and Selander, 1976, 1984; Dessauer and Cole, 1989).

A preliminary analysis of the relationships of the bisexual *Cnemidophorus* from the Madrean Archipelago was presented by Dessauer and Cole (1989), who used UPGMA clustering of genetic distance data based on about three dozen gene loci. The same clustering of these species was obtained independently from mitochondrial DNA (Moritz et al., 1992b). Currently this hypothesis is being tested again by modern cladistic methods (e.g., Hillis et al., 1994), and it will be modified if appropriate. Meanwhile, we illustrate our hypothesis here in the form of a cladogram (fig. 2), upon which we have also superimposed our preferred hypotheses for the hybrid origins of the derived unisexual species (Dessauer and Cole, 1989).

The diploid unisexual species had one step of hybridization involved in their origin. For example, the unisexual *C. neomexicanus* (NEO in fig. 2) resulted from hybridization between the bisexual *C. tigris* (TIG in fig. 2) and *C. inornatus* (INO in fig. 2). The diploid clone of this hybrid is perpetuated parthenogenetically today, as sterile male hybrids that may also have been produced originally have died out (see below). We have no evidence that new hybrids of this combination have been produced in recent years (Cole et al., 1988).

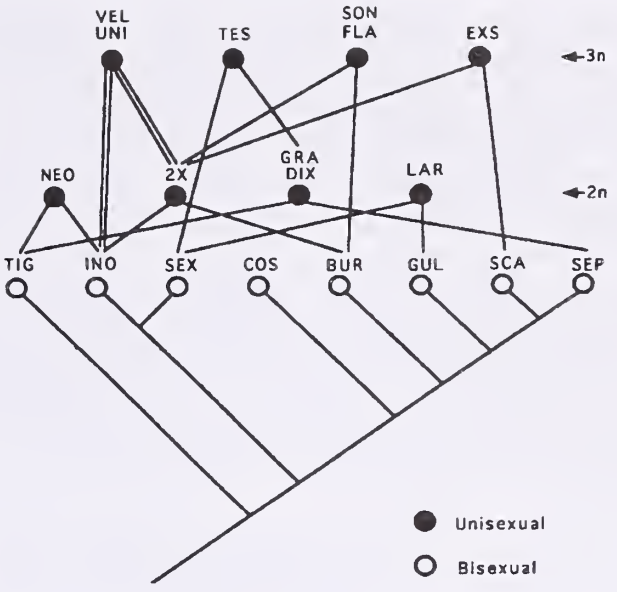

Figure 2.—Hypotheses of phylogenetic relationships of the bisexual and unisexual species of *Cnemidophorus* occurring in and near the Madrean Archipelago, modified from Dessauer and Cole, 1989, fig. 14. Each species is indicated by the first three letters of its name (Table 1), except for 2X, which has not yet been identified in nature. Double lines to VEL and UNI illustrate multiple hybrid origins, based on mitochondrial DNA data showing that 2X was formed by reciprocal crosses between INO and BUR (Densmore et al., 1989b; Moritz et al., 1989b).

Two steps of hybridization were involved in the origin of the triploid unisexual species (fig. 2). For example, the unisexual *C. grahamii* (GRA in fig. 2, using the name applied by Wright, 1993) resulted from hybridization between the bisexual *C. tigris* and *C. septemvittatus* (SEP in fig. 2; Wright and Lowe, 1967; Neaves, 1969; Parker and Selander, 1976; Dessauer and Cole, 1989). While the resulting unisexual clone continues to perpetuate itself parthenogenetically, on at least one occasion in the past a female of *C. grahamii* mated with a male of *C. sexlineatus* (SEX in fig. 2). The sperm added a third set of chromosomes and genes to the diploid egg cloned by the female and produced a triploid hybrid. The triploid clone of this hybrid is perpetuated parthenogenetically today as *C. tesselatus* (TES in fig. 2). Thus, the triploid *C. tesselatus* is comprised of three haploid genomes ultimately inherited from three different bisexual species, through two separate events of hybridization (Neaves, 1969; Parker and Selander, 1976; Dessauer and Cole, 1989). In addition, rare tetraploid hybrids are produced by occasional mating between triploid clonal females and males of bisexual species (e.g., Lowe et al., 1970; Cole, 1979).

Several of the triploid unisexual species originated through an intermediary diploid clone indicated as 2X in figure 2, which resulted from hybridization between *C. inornatus* and *C. burti*. This intermediary diploid clone has not been identified with certainty in nature as yet, although future research may reveal it among the *C. opatae* complex (Dessauer and Cole, 1989; Wright, 1993) or *C. innotatus* (as that name is applied by Wright, 1993). Either hypothesis or both could be correct, as various triploid clones and multiple hybridization events are involved (fig. 2).

INSTANTANEOUS SPECIATION

The process by which ancestral populations of diploid bisexual species diverge over time and produce one or more new species generally requires a minimum of hundreds, thousands, or tens of thousands of generations to complete through mutation and natural selection, particularly to the extent of developing reproductive isolation. In stark contrast, all of the evidence suggests that parthenogenetic clones of hybrid origin arise in a single generation (e.g., Cole, 1985).

In situations today where hybridization occurs among bisexual populations distinguished by low genetic differentiation, a hybrid zone of fertile hybrids is formed (e.g., Dessauer and Cole, 1991). Panmixia is sufficiently extensive that F_1 generation hybrids are rare or absent. All lizards in the center of the hybrid zone are F_2 and subsequent generation hybrids or backcross hybrids with various combinations of alleles from the parental populations. This kind of hybrid swarm is not the situation from which parthenogenetic cloning emerges.

Parthenogens are derived from hybridization among bisexual populations distinguished by high genetic differentiation (but not so high as to prevent development of viable hybrids; Dessauer and Cole, 1989; Moritz et al., 1989a). The most detailed analyses of the combinations of genomes and morphology in clonal lizards (*Cnemidophorus* and other genera as well) indicate that the clone in each instance most likely arose instantaneously from a first-generation hybrid female. This suggests that the F_1 hybrid males that might have been produced were sterile and became extinct after contributing no genes to subsequent generations while one or more F_1 hybrid females perpetuated the F_1 state by parthenogenetic cloning. Given the number of independent cases where hybridization has led to clones (e.g., fig. 2), it seems unlikely that in each case the two rare events of unusual hybridization and an even rarer mutation conferring a new capacity for parthenogenesis on a hybrid female occurred simultaneously. Consequently, it seems likely that there is a cause-and-effect relationship between hybridization among well-differentiated populations and the origin of parthenogenesis, perhaps through dysfunction in meiosis (e.g., Densmore et al., 1989a; Moritz et al., 1989a, 1992b). It is a staggering thought that the switch from sperm-dependent to sperm-independent reproduction occurs in a single generation. Together with Wade C. Sherbrooke at the Southwestern Research Station in the Chiricahua Mountains, we are now conducting experiments to address this question.

CLONAL DIVERSITY

Considering that the bisexual species of *Cnemidophorus* show various differences in their genetic material, it is clear that hybridization among different combinations of bisexual species results in various genetically distinct clones (fig. 2). There are other sources of clonal diversity also.

Comparative studies of individual gene products by protein electrophoresis have revealed two or more minor genetic variants in otherwise similar clones within unisexual species (e.g., *C. tesselatus*, see Parker and Selander, 1976; *C. neomexicanus*, see Parker and Selander, 1984; and *C. cryptus*, see Cole and Dessauer, 1993). For the cases cited, the allelic variants observed in the unisexual species appeared also in one or the other of the parental bisexual species. This suggests that the slightly different unisexual clones arose from separate F_1 hybrids resulting from different combinations of eggs and sperm from the parental species, even though in some cases the same individual mother and father could have been involved.

The laboratory of Wesley M. Brown at the University of Michigan has produced some elegant work on comparative analyses of mitochondrial DNA (mtDNA). The beauty of this is that mtDNA is inherited in the cytoplasm of the egg, contributed by the mother and not the father. Consequently, when the parental species of a clone differ in mtDNA, identification of the mtDNA in the unisexual clone determines which parental species was the maternal ancestor of the clone (e.g., Brown and Wright, 1979). By such analyses, Densmore et al. (1989b) and Moritz et al.

(1989b) determined that the diploid unisexual intermediary clone referred to as 2X in figure 2 probably was created by hybridization at least twice, by reciprocal crosses (INO female x BUR male, and BUR female x INO male).

By conservative estimate, adding up the strong indications for separate hybrid origins of diploid unisexual species (Densmore et al., 1989a, b; Dessauer and Cole, 1989; Moritz et al., 1989b, 1992a; Cole and Dessauer, 1993), parthenogenetic cloning probably had at least 10 independent origins within *Cnemidophorus*, but the actual number may be considerably higher. The majority of these occurred within or near the Madrean Archipelago, where there may have been more separate origins of parthenogenetic lizards than in any other comparable-sized area on Earth (but see Moritz et al., 1989c, for data on unisexual lizards in Australia). We suspect that the reason such diversity has arisen here hinges upon the diverse native bisexual species, diverse habitats that have shifted throughout the Pleistocene and Recent (e.g., Lowe et al., 1970), and the fact that mating in *Cnemidophorus* does not involve the more elaborate courtship-related behaviors seen in other lizards. Thus, the local frequency of hybridization is greater in *Cnemidophorus* than in other lizards, and, as discussed above, there may be a cause-and-effect relationship between hybridization and the origin of parthenogenetic cloning.

Finally, genetic mutations can occur in lizards of a clone, just as they can in bisexual species. If a non-lethal mutation occurs within a clonal lizard, both the original gene (still present in other individuals) and the derived mutant will be perpetuated by parthenogenetic cloning (e.g., Parker and Selander, 1976). Examples of such karyotypic clones were discussed in detail by Cole (1979) and of an allelic clone at the transferrin locus by Dessauer in Cole et al. (1988). In the few studies of geographic variation of clones within unisexual *Cnemidophorus* (Parker and Selander, 1976, 1984; Dessauer and Cole, 1989), different clones distinguished by allelic variation have been found. In many cases, the source of this variation (separate hybrid eggs or gene mutations in parthenogenetic lineages?) remains unknown.

CURRENT AND FUTURE RESEARCH

There are several areas of research and experimentation for which unisexual lizards and their bisexual relatives are most suitable, including the following:

(1) As yet, we know nothing about the sections of DNA that affect meiosis and cause parthenogenesis to occur in some hybrid females. With a better understanding of the mechanics and processes involved, it might become possible to convert animals and plants of agricultural importance to parthenogenetic reproduction. This would greatly improve efficiency of production, as all normal individuals would bear progeny of known qualities. Experimental breeding, genetic engineering in other respects, and related activities would still be important for improving stocks, but as desirable stocks were developed they could be cloned. This might seem far-fetched if we were not actually seeing this happen in vertebrates in nature.

(2) As yet, we do not know what activates cloned eggs to initiate embryonic development in the absence of sperm. All we do know about this process is that the mature ovum, after meiosis, is genetically complete in the appropriate environment (Cuellar, 1971), so there seems to be no need to await fertilization. In fact, for haploid, un-cloned ova of bisexual species, do we know enough about the normal processes involved in their brief period of waiting for fertilization before being shed through the system?

(3) In general, we have a great deal to learn about the effects of exposing wildlife and humans to pathogens, pollutants, radiation, and newly manufactured chemicals. In addition, appropriate animals can be used for research on the general phenomena of nutrition and aging, as well as captive propagation of endangered species (e.g., Porter et al., in press). Unisexual lizards are especially suited to such research because all individuals are identical within a clone and the affects of genetic variation are reasonably controlled (e.g., Cole and Townsend, 1990).

(4) While a good start has been made (e.g., Schall, 1978; Price, 1992; various chapters in Wright and Vitt, 1993; Walker et al., 1994), a great deal remains to be learned about the biology of *Cnemidophorus*, including the populations in and around the Sky Islands.

MANAGEMENT CONSIDERATIONS

Unisexual lizards and their bisexual relatives are important biological resources with considerable potential for future, productive research, and as such they should be conserved. In most cases, active conservation activities are not necessary because most species of these lizards are not currently threatened in nature. However, these lizards depend upon the continued existence of their woodland, grassland, desert-grassland, and desert environments (specific habitats and distribution depending on the species), and some populations are quite locally restricted in geographic distribution.

Consequently, our main recommendation is to keep avenues of communication open, as in the spirit of this informative conference. Directors of research stations and herpetologists should be involved as plans are developed to change land uses in relevant areas that could severely impact the lizards and/or scientists' long-term research programs.

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Bats of the Madrean Archipelago (Sky Islands): Current Knowledge, Future Directions

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Abstract.—Twenty-three bat species occur in Arizona's Sky Islands. Each one has specific, seasonally changing requirements for roosts, forage and water. Current knowledge about these species is insufficient for informed ecosystem management. We pose research questions and suggest techniques and resources for answering some of these questions. Managers, in cooperation with researchers, should establish long-term plans and priorities for studying and monitoring bats.

INTRODUCTION

Bats are vital members of most terrestrial ecosystems, yet frequently are ignored in vertebrate surveys and ecological evaluations. Worldwide, bats occupy every major feeding niche except herbivory (Stebbings 1980). Insectivorous bats are major predators of night-flying insects. Other bat species, especially in the tropics, consume nectar and/or fruit. Many are important pollinators and seed dispersers (Cox *et al.* 1991, Gardner 1977).

This paper addresses concerns and responsibilities of those charged with ecosystem management. A key to management is recognition of species diversity. One cannot manage generally for "bats" any more than for "birds." Just as spotted owls, elegant trogons, and Mexican chickadees are each studied and protected within the context of their particular habitats and individual requirements, so must the biology of each bat species be understood to determine its needs.

Although bats comprise nearly a quarter of all mammalian species, our knowledge of most of them is fragmentary. Perhaps because they fly, are nocturnal, and are mostly unseen, bats are among the least studied mammal groups. For most species we know neither total range nor accurate population numbers. We know even less about their ecology and life history. Indications are that most bat species worldwide are probably declining in numbers due to several causes, including losses of habitat, roosts and food, direct or indirect killing by humans, and harmful effects of chemicals (Stebbings 1980).

As Cockrum (pers. comm.) has noted, many past estimates of bat populations, plus speculation about their life histories, came from incidental natural history observations made as part of general biological surveys, most often on summer field trips, and frequently by observers with little expertise in identifying species and estimating numbers. Information on reproductive status, sex ratios, and roost types often was not recorded. For many species we know only general food requirements, such as "insectivorous," but not specific prey or feeding strategies, or "nectarivorous," but not exact plant requirements through different seasons and habitats.

BACKGROUND

Sustaining ecosystem diversity necessitates meeting the individual needs of each species. Three basic requirements of all bat species are: 1) appropriate roosts for their various seasonal and reproductive activities, 2) suitable foraging areas, and 3) adequate water. For each species, these needs are satisfied differently. Variation also occurs within a species, between populations or across geographic regions. The specifics of these requirements for each bat species are relevant to management considerations. Particulars of the three requirements follow.

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Roosts

With few defenses against predators, most bats survive by escaping detection in roosting sites and by restricting their activity to the night. By roosting in sheltered places, bats are protected from predators, large temperature fluctuations, and adverse weather conditions. Roosts also enhance activities such as rearing young, digestion of food, social interactions, and hibernation (Kunz 1982).

In describing types of shelters (as introduced by Verschuren), Gaisler (1979) lists as major distinctions:

1) "external" or "internal," based on "degree of isolation from the macro-habitat," and
2) composed of vegetation, rock or manmade structures, based on environmental conditions of the roost. We would add
3) colonial or solitary, based on tendency of individuals to cluster;
4) day, night, or transient, based on length of time or portion of 24-hour period spent in the shelter;
5) maternity, bachelor, or hibernaculum, based on gender or physiological condition; and
6) summer or winter, based on season.

Few bats use the same day roost throughout the year; the annual cycle usually includes seasonal movements among different roosts. Many species roost in caves or mines, some use rock or tree crevices, others seek cover in tree foliage, and some take shelter in manmade structures such as buildings and bridges. Some bats roost singly, while others aggregate in colonies. Each species has specific humidity and temperature requirements for its roosting sites, which may change seasonally — not just any dark, quiet place will do. Most caves and mines, for instance, do not qualify as either good hibernacula or nursery roosts. Therefore, when bats are disturbed and driven from a roost, they may be unable to find another suitable retreat. Or, if they are able to move within the same cave, for example, the alternate site may not be satisfactory for long-term survival of that population.

Many bats appear to have high individual fidelity to roost sites, returning to the same site year after year. For some species that have been studied, populations appear to be limited by availability of suitable roost sites, and disturbance or destruction of these sites by human activity is a principal cause of population decline. (Kunz 1982.)

Forage

Bats spend a substantial portion of their lives away from their roosts feeding. For insectivorous bats, this activity typically entails flying over a defined area in a "search pattern" hunting for prey. Prey items usually consist of night-flying insects, but for some species include ground-dwelling arthropods such as crickets and scorpions. Two non-insectivorous Arizona bat species feed primarily on agave nectar and on cactus nectar and fruits.

Geographic areas in which bats forage are defined by abundance of food. For example, individuals of *Macrotus californicus* will fly along desert washes (P. Brown pers. comm.) where there is a higher concentration of a primary prey item, grasshoppers. *Myotis yumanensis* forages over streams where it feeds on adult forms of aquatic insects (Brigham *et al.* 1992). Different species use various capture techniques and may feed at different levels of the canopy or in different subsections of the habitat (Neuweiler 1984). Some food partitioning occurs, as different species divide an area specially and tend to consume different sizes or taxa of insects (Herd and Fenton 1983). Extent and location of foraging territories varies according to bat species, seasonal abundance and variety of food, and changing energetic and dietary requirements. A bat's foraging territory may be close to the day roost, or may be many miles distant.

Foraging requirements as well as major roosting sites must be made secure before a bat species is adequately protected. Too often, roost sites are the only aspect of a bat's natural history considered when attempting to protect them. Roost and food requirements should be considered together. Although foraging ecology of a bat species is usually much more difficult to study than roosting ecology, it is equally important to the survival of the animals.

Water

Most bat species need a supply of free water every night during active periods. Water sources are typically ponds, streams, or cattle tanks. Bats drink by flying just above the water, skimming the surface with their jaw or tongue. Different species require different configurations of water source. Some species need a long unencumbered approach to drink, whereas more maneuverable ones can drink from steep-sided tanks, tinajas and even wells. Most bats probably utilize the nearest suitable source of water. In dry seasons, this may be some distance from the day roost and/or feeding area. A few species, such as those feeding on nectar and fruit, acquire most of their water from their food. As with roosts and forage, lack of water sources could be a limiting factor on some bat populations.

BATS OF THE SKY ISLANDS

Sky Island ecosystems constitute a unique biological crossroads. Of the 44 bat species found in the United States, 28 have been recorded in Arizona, and 23 of these are known to occur in the Sky Islands during at least part of the year. Although none of these species is limited to the Madrean Archipelago, the high diversity of bat species is likely due to the diversity of habitats, including desert grassland, Chihuahuan desertscrub, encinal and Mexican oak-pine woodland, and montane conifer forests (Lowe and Brown 1973), in conjunction with deciduous riparian zones, year-round water, and steep rock-walled canyons.[3] Different habitats support different assemblages of species. The topography of the Madrean Archipelago, in which habitats usually separated by large latitudinal distances are brought into close proximity, may also influence species diversity.

Records of Bats in the Sky Islands

Table 1 lists the 23 bat species recorded from the Sky Islands (nomenclature per Jones *et al.* 1992). While this discussion is limited to that part of the Madrean Archipelago which lies in Arizona, management implications should be the same either side of the border.

Hoffmeister (1986) tabulates relative distribution of mammals of Arizona by vegetative community, based on percentage of total number of localities from which records exist for each species. Thirteen vegetative communities are listed, of which three, desert grassland, oak-pine woodland, and montane conifer forest, predominate on Arizona Sky Islands. For twelve bat species (marked with an asterisk in Table 1), the highest percentage of localities occurs in one or more of the three communities, indicating significant association with Sky Island habitats.

Our understanding of most Sky Island bat species is incomplete. To summarize current knowledge, we look at evidence of bat use through the seasons. (Sources are Barbour and Davis 1969, Cockrum and Ordway 1959, Hoffmeister 1986, Cockrum pers. comm., SLS and DCD pers. obs.) Undoubtedly, as more information becomes available this picture will change.

Maternity roosts (individual or colonial) of *Choeronycteris mexicana, Myotis velifer, M. thysanodes, M. volans, Lasiurus blossevillii, Plecotus townsendii* and *Antrozous pallidus* have been observed in Arizona Sky Islands. Pregnant or lactating females of *Myotis auriculus, M. californicus, Tadarida brasiliensis,* and *Nyctinomops macrotis* have been recorded, suggesting that parturition occurs in the Sky Islands, but maternity roosts have not been found. Female *Leptonycteris curasoae,* collected in August and containing tiny embryos, likely give birth in Mexico (Cockrum and Ordway 1959). Maternity roosts of *Myotis yumanensis, M. auriculus, M. volans, M. californicus, M. ciliolabrum, Pipistrellus hesperus, Lasiurus xanthinus, Lasiurus cinereus,* and *Idionycteris phyllotis* have rarely or never been recorded and are not well understood. (Some of these species have been studied elsewhere, but nursery roosts are not well documented for the southwestern environment.)

Other summer records (adult males, non-reproductive females, or gender unreported) exist for *Leptonycteris curasoae, Myotis velifer, M. auriculus, M. thysanodes, M. volans, M. californicus, M. ciliolabrum, Lasionycteris noctivagans, Pipistrellus hesperus, Eptesicus fuscus, Lasiurus blossevillii, Lasiurus cinereus, Idionycteris phyllotis, Plecotus townsendii, Antrozous pallidus, Tadarida brasiliensis,* and *Nyctinomops macrotis.* Little is known about location and requirements of bachelor roosts for most of these species.

Migrating groups of *Leptonycteris curasoae* and *Tadarida brasiliensis* use transient roosts in the Sky Islands. Capture records of *Lasiurus cinereus* are significantly higher in spring, suggesting this species may stop over during migration. *Choeronycteris mexicana, Leptonycteris curasoae,* and most *Tadarida brasiliensis* are thought to winter in Mexico. It is not known to what localities particular populations of these species go, nor what transient habitats are important to their journey. (However, see Cockrum 1969.)

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[3] *Also occurring on some Sky Islands, but more incidental, are Upper Sonoran desertscrub, chaparral and sub-alpine spruce-fir forest.*

Table 1.—Summary of known occurrences of the 23 bat species of the Sky Islands.

SPECIES[1]	MATERNITY ROOSTS[2]	PREG./ LACT. FEMALES[3]	OTHER SUMMER CAPTURES[4]	TRANSIENT ROOSTS[5]	WINTER RECORDS[6]	SCANT RECORDS[7]	PERIPHERAL[8]
Macrotus californicus					✓		✓
* Choeronycteris mexicana	✓				NA		
* Leptonycteris curasoae	NA	August	✓	✓	NA		
Myotis yumanensis						✓	
Myotis velifer	✓						
* Myotis auriculus		✓	✓				
* Myotis thysanodes	✓		✓				
* Myotis volans	✓		✓				
* Myotis californicus		✓	✓				
* Myotis ciliolabrum			✓				
* Lasionycteris noctivagans	NA		✓		✓		
Pipistrellus hesperus			✓				
* Eptesicus fuscus			✓		✓		
Lasiurus blossevillii	✓		✓				
* Lasiurus cinereus			✓				
Lasiurus xanthinus						✓	
* Idionycteris phyllotis			✓				
* Plecotus townsendii	✓		✓		✓		
Antrozous pallidus	✓		✓				
Tadarida brasiliensis		✓	✓	✓	✓		
Nyctinomops femorosaccus						✓	
Nyctinomops macrotis		✓	✓				
Eumops perotis						✓	

NOTES:

1) Species marked with an asterisk have the highest association with Sky Island vegetative communities (from Hoffmeister, 1986).
2) Actual maternity roosts have been located and identified in the Sky Islands for the checked species.
3) Reproductive females of the checked species have been captured in the Sky Islands, but no roosts located.
4) Males, non-reproductive females or unknowns of these species have been summer captured in Sky Islands.
5) Colonial roosts used for short periods of time seasonally are known in the Sky Islands for these species.
6) Winter records of captures and/or roosts of these species exist for the Sky Islands.
7) There are a few records for these species from the Sky Islands, but they are not found regularly.
8) This species is found near to Sky Island habitats, but it is not known from the Sky Islands proper.
9) NA means that these categories are not applicable to this species in the Sky Islands.

A wintering aggregation of *Plecotus townsendii* has been found in one Chiricahua hibernaculum. Individual *P. townsendii* in winter torpor have also been located in several area mines and caves. Very likely other bat hibernacula occur in the Madrean Archipelago, but none have yet been found. Capture records document individuals of *Lasionycteris noctivagans*, *Eptesicus fuscus*, and *Tadarida brasiliensis* overwintering in the Sky Islands, but their winter roosts and requirements are largely unknown. From the often scant evidence he could accumulate for winter records, Hoffmeister (1970, p.12) observed "a tendency for most species of bats in Arizona either to move to the southeast corner of the state or to move out of the state altogether during the months of November through March." Even for such widespread and "common" species as *Myotis velifer, Myotis volans, Lasionycteris noctivagans* and *Antrozous pallidus,* where they go and what they do in winter remains a mystery.

Historic records of the following species are reported from Sky Island localities, but insufficient data are available to determine their status: *Myotis yumanensis, Lasiurus xanthinus, Nyctinomops femorosaccus* and *Eumops perotis.* A winter roost of *Macrotus californicus* is located at a low elevation on the periphery of a Sky Island, but this species does not appear to use Island habitats significantly.

Questions to Answer for Informed Stewardship

Adequate information about a species is needed before protective measures can be taken. Because we do not have sufficient biological information on any of these species to ensure their survival, what questions should we be trying to answer for each bat species.

1) Roosting Ecology: Questions remain about locations of roosts for many species. Most bat species are found in a variety of habitats. Do their roost requirements differ between various habitats or are they the same? Bats using caves and mines have traditionally been the most studied. However, many species use shelters such as rock or tree crevices or tree hollows where human detection has been difficult. Habitat components vital to bats may currently be unknown to us (Saugey 1991). Roost requirements are often poorly understood; for example, mines that seem to us to be perfectly suitable have no bats. To confound the fact that we probably have not yet found some critical roosts in the Sky Islands, we have no accurate method of predicting if a site would be a suitable roost. Until we do, all potential roosts must be examined (Altenbach pers. comm. See Kunz 1982 and Sheffield *et al.* 1992.)

   Maternity roosts are particularly crucial. If maternity roosts are not secure, the population will not survive. Bats are especially vulnerable because of their low reproductive rate of one or two young per year in most species. Even a slight reduction in birth rate could have a significant impact on the population. Bats are also extremely vulnerable during hibernation, when arousal may cause depletion of energy reserves and lead to starvation (Mohr 1972).
2) Foraging Ecology: It is essential to understand foraging ecology as well as roosting ecology, because a different combination of environmental factors is required for each. Foraging ecology encompasses food habits, territory description and extent, necessary proximity of forage to roosts and water, and shift in dietary needs and/or foraging territory throughout the season. (See Fenton 1982 and Fleming 1982.) Not enough is known about foraging requirements of *any* Sky Island bat species.
3) Seasonal Movements: Migratory bats are similar to migratory birds in that an impact to a population at one of its seasonal homes may affect the community at the other. Understanding better the migratory patterns and seasonal movements of bats utilizing the Sky Islands will require, for some species, an international effort including Mexico and Canada.
4) Reproductive Biology: Although information exists about pregnancy, lactation and weaning for some species, mating systems and locations of mating are virtually unknown. This category of reproductive biology needs more attention. (See Bradbury 1977.) Variation in length of gestation, timing of parturition, and rate of development due to differing environmental or geographic conditions must also be considered (Orr 1970, Pearson *et al.* 1952).
5) Population Status: Are numbers increasing, stable, or declining? What keeps a given population from growing larger? Is it limited by shortage of suitable roosting sites, by lack of accessible food or water sources, or by confounding factors such as disease, predation or human activity (Pearson *et al.* 1952).
6) Importance to Ecosystem: The importance of bats in the ecosystem is poorly known for most species. An understanding of their relationships with other organisms is necessary for effective stewardship. As answers to the above questions clarify interrelationships within the web of living and non-living elements of the ecosystem, we can begin to investigate the role played by each species. (See Cox *et al.* 1991.)

RESEARCH

Maintaining a healthy ecosystem requires gathering baseline data and then establishing regular monitoring protocols. We recommend that managers, in collaboration with researchers, examine long-term goals and concerns, and set priorities for monitoring systems. Many individual research projects are conducted for only one or a few seasons. The result is that our knowledge is fragmentary, especially if there are multiannual fluctuations in local population sizes. Managers of public lands have the opportunity to support both basic and applied research (species, population, community, or ecosystem questions) and to ensure that long-term monitoring occurs.

Clearly, we lack basic biological information on most bat species to manage for them. Acquiring such knowledge takes time and careful research design. In this section, we review a variety of methods used in field studies, offer examples where these techniques have been used to answer biological questions, and suggest research to pursue in the Sky Islands.

Field Methods

The techniques discussed below answer different questions and each has its own limitations and biases. It is important to know these limitations and to use the techniques most appropriate for the objectives of the study. In addition, it must be realized that to handle bats or disturb them in their roosts inevitably introduces stress, and potentially shortens their lives (Stebbings 1966). Therefore, effort should always be made to maximize information gained from any study.

This overview is intended as an introduction to research methods, not as instruction for use of equipment nor training in application of techniques. Most basic methods are described in *Ecological and Behavioral Methods for the Study of Bats* (Kunz 1988), which must be supplemented with more recent literature for current information on each technique. Before undertaking a research project, it is necessary to determine which technique (or combination of techniques) is suitable to the question being asked, and to investigate available equipment.

Thomas and LaVal (1988) noted that bat researchers doing population studies often failed to specify and test assumptions, biases, and limitations inherent in the methods used. They urge that future quantitative population studies be conducted with increased rigor and reported with extreme caution, because inaccurate estimates, once published, tend to be repeated as "truth" (Thomas and LaVal 1988). These cautions are equally applicable to any research project. Poorly planned or executed field studies can result in major mistakes. Past examples of which we are aware include roost surveys conducted in the wrong season, leading to inaccurate population estimates, and a nursery roost gated in the middle of the maternity season, which caused a major disturbance to the bats the gate was intended to protect. Proper execution of each technique and correct interpretation of the results require, in most cases, considerable experience.

Capture Devices

Harp traps and *mist nets* are two devices used to capture bats in a particular location by intercepting them in flight (Kunz and Kurta 1988). Bats show differing abilities to detect and avoid nets and traps. The set of the net or trap, location selected, height of the net or trap above the ground, and environmental conditions of the particular night (moon, wind, temperature) will influence the catch. Failure to capture a particular species at a given time and place does not assure that the species was not present. The catch is not, therefore, a random sample of the population of bats in an area. Nevertheless, sufficiently large sample sizes over a long enough time can give a reasonable indication of relative abundance. The advantage to capture is the ability to identify species, sex, and reproductive status, and to make quantitative morphological measurements. Capturing a bat is also a necessary first step for many other techniques.

Tracking Methods

Three marking techniques, *radiotelemetry*, *light tagging* and *banding* are useful for tracking individual bats. (See Barclay and Bell 1988, Wilkinson and Bradbury 1988.) The principal difference between the three methods is the length of time one obtains information from a given marking. Light tagging only lasts for several hours in a single night. Radiotelemetry can last in excess of 20 days and banding can last for the lifetime of the bat.

Light tagging is used to locate roosts by tracking bats to them, and to conduct detailed studies of foraging strategies. Because the location of the light can be visually pinpointed, the bat's movements can be described in great detail. This technique has a limited range of only about 1 to 2 miles and it also requires a minimum of about 10 observers to be effective.

Although less precise than light tagging, particularly for observing foraging behavior and choice of food items, radiotelemetry provides longer-term information on nightly foraging strategies such as consistency (or inconsistency) of foraging patterns and distance traveled from the roost. Telemetry is also useful for locating roosts, especially those in places not traditionally investigated, such as tree cavities.

Banding enables long term tracking of individuals to determine migration timing and patterns, longevity, behavior and alternate roost usage. Several different band types are available; the right type for the species being studied must be chosen. Banding of bats is problematic because of the difficulty of attaching the band in a manner that does not cause wing damage. It is important that field workers applying tracking devices to bats be skilled in the technique and informed on its risks and benefits.

Roost Surveys and Censuses

Under appropriate conditions, internal cave and mine surveys can be an effective method of locating and censusing bat roosts. (See Thomas and LaVal 1988.) However, abandoned mines may be quite dangerous to humans; caves can require a considerable amount of skill and time to survey; and bats being censused may be unduly disturbed by the human activity. The technique should only be undertaken by experienced bat biologists who are also skilled in caving techniques and mine safety. Mist netting (or trapping) and night-vision equipment can be used in place of internal surveys, or to supplement them.

Fecal Analysis

Guano analysis can aid in identification of food items. (See Whitaker 1988, Thomas 1988.) By periodically collecting samples throughout the season, changes in diet can be detected. Bat guano samples can also be analyzed for residues of agricultural pesticides and other chemicals (Reidinger 1972, Clark *et al. 1982*).

Echolocation Monitoring

Ultrasonic detection is a useful tool for assessing comparative habitat use and relative bat abundance (Thomas and LaVal 1988). (See also Barclay and Bell 1988, Fenton 1988.) The technique is used as an indicator of bat presence, followed by another technique, such as mist netting, for positive species identification. For surveys of free-ranging bats, this technique may have fewer biases than other sampling methods. It is appropriate for surveys, not censuses, because the number of bat passes is not an accurate indicator of the number of individuals. With a broadband microphone that picks up all frequencies, echolocation monitoring can be used in conjunction with mist netting as evidence of bats present but not captured. Caution must be exercised when attempting to identify bats to species level using ultrasonic detectors; several species in a given area may have ultrasonic signatures that overlap, and intraspecific variability also occurs (Thomas *et al.* 1987). †

Night-vision Equipment with Near-infrared Video

Night-vision devices (Barclay and Bell 1988), although quite expensive and easily damaged, have proved to be one of the primary tools of bat biologists for emergence counts and behavioral studies. For permanent record and removing observer bias, the night-vision device can be optically coupled to a video system and recorded on magnetic tape.

Other Techniques

Other research methods are available as well. Some are summarized in Kunz (1988). Newer techniques that show promise include DNA analysis and geographic information systems (GIS). DNA analysis from widely separated populations may reveal inter- or intraspecific kinships that would be difficult to determine by any other known technique. GIS, utilizing databases, can be used as a management tool for mapping out ranges and distributions of various species and correlating multiple factors for ecological relationships.

Examples of Information Gained

These and other techniques are used by bat biologists to answer questions important when managing for species and ecosystems. The following reports of research from many localities illustrate information that can be obtained. Techniques used in these examples could be applied to studies in the Madrean Archipelago.

Roost Location

1) In a study of 200 mine features in New Mexico, 42 percent were found to be used by bats (Altenbach and Milford 1991). These included winter hibernacula for six species, nursery colonies of *Plecotus townsendii* and *Myotis thysanodes*, and a migratory stopover roost for *Myotis yumanensis*. Many of the mines had vertical entrances that required specialized equipment and trained personnel. This equipment and training permitted the field workers to discover these roost sites, which would have been undetected by external surveys.

2) An area of the Coronado National Forest containing numerous mines was surveyed for potential roosts. Using a combination of techniques including multi-season internal surveys, mist-netting at entrances, bat detectors and night-vision equipment, a significant usage of one of these mines by lesser long-nosed bats (*Leptonycteris curasoae*, protected as a federally endangered species) was discovered (unpubl. data). A superficial survey, or one in the wrong season, could easily have missed them. The land manager now has information to make decisions regarding future development of the site.
3) "Waves" of silver-haired bats (*Lasionycteris noctivagans*) travel along the southern shore of Lake Manitoba during spring migration (Barclay *et al.* 1988). Historical records suggested that this is generally a crevice-dwelling species, yet little was known of their roost sites because they had rarely been located. During May and June 1984-1986, two to four people conducted almost daily visual searches of trees along a 2-km stretch of ridge. They discovered 177 *L. noctivagans* (90% of which were females) located in 36 different roosts in 32 trees. Roosts typically were crevices in tree trunks: most commonly a narrow space behind folds in heavily furrowed bark, but also splits in tree trunks and narrow spaces between two touching trunks. (Barclay *et al.* 1988.)

It was not known whether females of this species rear their young in isolation or in aggregations. In Shasta County, CA in 1992, Rainey *et al.* (in press) captured reproductive female *Lasionycteris noctivagans* in mist nets over water. They attached radio transmitters to two of them and were able to track them to two day roosts located in tree cavities. Significantly, each roost contained more than 20 individuals. This supported the 1986 discovery in Ontario and Saskatchewan of two maternity colonies of the species also in tree cavities (Parsons *et al.* 1986), suggesting that during maternity season this bat roosts colonially rather than solitarily as previously thought.

Seasonal Movements, Migration and Roost Fidelity

1) From a five-year banding study of Townsend's big-eared bats (*Plecotus townsendii*), Pearson *et al.* (1952) were able to determine that females in nursery colonies exhibited strong roost fidelity, returning to the same site each year. The longest migration distance recorded for these bats was 20 miles. One large cave housed both hibernating and maternity colonies of bats, but in different tunnels winter and summer. Furthermore, banded bats from other summer colonies appeared at this cave to hibernate. Finally, banding records were used to estimate an average age of five years for the populations they studied. (The authors reported precipitous declines, attributed to their disturbance of the bats, in some of these populations; an important cautionary note for anyone contemplating such a study. See also Pierson and Fellers 1993.)
2) Between 1952 and 1967, more than 168,000 Brazilian free-tailed bats (*Tadarida brasiliensis*) were banded at sites in Arizona and Mexico (Cockrum 1969). From the 2% recovered later plus data from other studies conducted in Oklahoma, Texas, New Mexico and California, Cockrum (1969, p. 324) concluded that "four or more behaviorally (and possibly genetically) separate populations of *Tadarida brasiliensis mexicana* occur in the western United States during the summer months." A recent electrophoretic study by McCracken *et al.* (1994) did not support the suggestion of genetically distinct populations.

Food Habits and Foraging Areas

1) In 1986, Dalton *et al.* completed an analysis of guano collected for three years from a *Plecotus townsendii virginianus* roost (Dalton *et al.* 1986). About 97% of the bats' diet consisted of moths. This information set the stage for concern over gypsy moth management measures, since insecticide (Dimilin) used to control gypsy moths would also drastically reduce other lepidopteran species. Subsequently, Dalton *et al.* (1989) carried out a two year study on the foraging ecology of *P. t. virginianus.* Light tagging and radio tracking enabled researchers to identify foraging areas. Land manager foresight led to appropriate research, and the colony's critical foraging territory was worked into management

plans, which refrained from Dimilin use in those areas.

2) A foraging study was conducted in 1993 on a colony of *Leptonycteris curasoae* located near an active mining operation. Through light tagging, critical foraging areas for the bats were identified and plans for expansion of the mine were altered to accommodate these requirements (Dalton and Dalton 1994b).

Habitat Use

In forested mountains of Washington and Oregon, automated ultrasonic detector systems indicated that nearly all common bat species required forest stands for day roosts, apparently traveling to adjacent riparian habitats to feed. Roosting activity was many times higher in old-growth than in young or mature stands, presumably because large, old trees and snags offer the highest diversity and abundance of hollows for roosts (Thomas and West 1988). In a separate study, guano traps suspended in basal hollows of redwoods in California revealed extensive bat use of these old-growth trees for roosts during all seasons (Rainey *et al.* 1992).

In-roost Behavior and Population Trends

1) In 1991, the Air Force became concerned that their training flights in the vicinity of a *Leptonycteris curasoae* roost might be stressing the colony. Dalton and Dalton studied the bats' behavior while Air Force jets flew over the roost. The bats were recorded on video tape using infrared illumination and a night-vision device. In order to observe natural in-roost behavior with minimal disturbance to the bats, remote-controlled equipment was used. Statistical analysis of the video tapes showed no serious adverse effects on the bats. (Dalton and Dalton 1993)
2) In 1993 a federal agency adopted a census protocol for a large colony of *Leptonycteris curasoae* using night-vision and video recording equipment. This method allows the agency to monitor population trends at the roost and be aware of any problems before they become critical (Dalton and Dalton 1994a).

Pesticide Poisoning

In a recent European study, timber, feces and tissue samples were analyzed for pentachlorophenol (PCP) residues, and a striking correlation was found between all three. The researchers concluded that the PCP burden of bats may be estimated from analysis of their droppings (Cordes 1994. See also Clark *et al.* 1982).

Suggested Research for the Sky Islands

The following are a few suggestions of specific problems that need solving in the Sky Islands. These questions are not necessarily more important than others, but do constitute a starting point.

General Questions

1) Many historical records for bats in the Sky Islands were gathered from only a few well-known localities, such as Sabino Canyon in the Santa Catalinas and Cave Creek Canyon in the Chiricahuas. Attention needs to be directed toward less studied areas, such as forested uplands, and some of the less accessible mountain ranges.
2) Foraging ecology studies are urgently needed. Much information can be obtained on foraging ecology with available techniques. Bats can be tracked from known roosts, or captured while foraging (or drinking) and tracked to learn both roosting sites and foraging behavior.
3) As mentioned, winter habits of most bat species in Arizona are unclear. (See Hoffmeister 1970.) The location of overwintering sites for the majority of bats remains a mystery.

Ecosystem Questions

1) How does the topography of the Madrean Archipelago affect bats? Because several habitats occur in close proximity, all are potentially accessible to flying mammals. How do various bat species use these multiple habitats? Do any species undergo altitudinal migrations between seasons? Some evidence for this occurs among *Plecotus townsendii* in the Chiricahuas (DCD pers. obs.), and it has been suggested as a possibility for other species (Cockrum pers. comm., Hoffmeister 1970) .
2) How does forest fire impact bat habitat? Is there a higher occurrence of potential tree roosts in burned areas or in old growth forest? Does fire suppression affect available roosts positively or negatively?

3) Do bats use the grasslands surrounding the montane islands? (Localities recorded by Hoffmeister 1986 indicate they do). Presumably these areas would be used for forage more than roosting sites. What are the effects of differing land use regimes on bat species? While revisiting historic bat roosts, Reidinger (1972) documented a trend toward decrease of available man-made and natural roosts with the increase in human population. He also observed harmful effects from insecticides. "In comparison with other Arizona mammals with residue values reported in the literature, bats suffer by far the greatest insecticide exposure" (Reidinger 1972, p. 137). Development, grazing and pesticides may all impact bat species which inhabit Sky Island habitats during at least part of the year.

Species Questions

All species require more study. We have selected three, suggesting some questions that could be productively pursued.

1) *Leptonycteris curasoae*

Populations of *Leptonycteris curasoae*, a nectar-feeding bat, migrate annually into Arizona from Mexico. With individuals numbering into the tens of thousands in a single cave or mine roost, *L. curasoae* is a highly colonial species. Several important questions about this species remain unresolved. Since the predominant range of *L. curasoae* is in Mexico, studies on both sides of the border are needed.

a. (Demographics) In late April and early May, gravid females arrive at three known maternity roosts in southern Arizona located west of the Sky Islands (Cockrum 1991). During the months of pregnancy and lactation, these females feed almost exclusively on columnar cacti such as saguaro and organ pipe. By late July, transient roosts at higher elevation sites in the Patagonia, Huachuca and Chiricahua mountains are occupied by a mixture of adult females and juveniles and some adult males. These seasonal movements appear to reflect a shift in available food resources from cacti to agaves (Cockrum 1991). It has not been determined whether populations occupying transient sites in the Sky Islands are the same ones found in Arizona maternity roosts or are different populations flying northward from Mexico. Most individuals of *Leptonycteris curasoae* leave Arizona by late September or early October and migrate to overwintering sites south of southern Sonora (Cockrum 1991). The specific migration routes and winter roosts are unknown. In addition, the population status of the species is uncertain; are numbers increasing, decreasing, or stable?

b. (Nectar corridor) Fleming *et al.* (1993) discovered that northern populations of the species feed almost exclusively on CAM plants, Cactaceae and Agavaceae, during summer and during their spring and fall migrations. This suggests that a nectar corridor of CAM plants exists along both of their postulated migration routes. Flowering periods of at least four species of columnar cacti coincide with the bats' northward progression in spring (Fleming *et al.* 1993). However, field studies are needed to confirm whether *Agave* flowering peaks in Mexico are coincident with passage of migrating bats in the fall, and whether the bats depend on these plants. If a nectar corridor indeed supports the seasonal migrations of *L. curasoae*, then loss of plant populations along either migration route could severely impact the bats (Fleming *et al.* 1993).

c. (Bat/agave mutualism) Howell and Roth (1981) postulated an obligate mutualism between *Leptonycteris curasoae* and *Agave palmeri*, but their evidence has been disputed (Cockrum and Petryszyn 1991). Howell and Roth's (1981) conclusion was predicated on *A. palmeri* fruit set and seed set. However, a number of pollination biologists, examining resource-limitation versus pollinator-limitation hypotheses, have suggested that fruit and seed set are not valid indicators of reproductive success in hermaphroditic out-crossing plants such as *Agave palmeri* (Stephenson 1984, Sutherland 1986, Sutherland 1987, Sutherland and Delph 1984, Udovic 1981). Pollination experiments are needed to test the bat/paniculate agave interdependency hypothesis.

It seems generally agreed that *Leptonycteris curasoae* is an important pollinator for *Agave palmeri*, and that *A. palmeri* is a major food source for populations of *L. curasoae* at higher elevations in southeastern Arizona during mid- to late-summer. However, further research must be done to clarify the extent of their interdependence. This information is important to the conservation of both bats and agaves.

d. (Impact of hummingbird feeders) In many Sky Island localities in recent years, both *Leptonycteris curasoae* and *Choeronycteris mexicana* have been observed drinking sugar water from hummingbird feeders at night. Sightings have been made from April into October (Lee and Clark 1993). This phenomenon raises some concerns about the effect of this comparatively new food source on bats. If bats, particularly juveniles, depend too heavily on nutritionally-deficient sugar water, they may not have sufficient energy for migration. Some individuals may delay their migration and subsequently suffer from extreme weather. Feeders which provide a ready source of "food" could in reality be a population sink, if the animals become part of a positive feedback loop under conditions actually negative to their survival (Richter *et al.* 1993).

e. (Reproductive biology) Very little is known of the reproductive biology of *Leptonycteris curasoae*. There is some evidence that parturition is asynchronous, with births reported at various times scattered through the year. The location, timing and system of mating for *L. curasoae* are also unknown (Fleming pers. comm.).

f. (Chiricahua roosts) While most adult males of the species probably remain in Mexico during summer, by May some males are found in high-elevation roosts in the northern Chiricahua Mountains (Cockrum 1991, Cockrum and Petryszyn 1991, Fleming pers. comm.). The function and importance of these roosts need to be determined. Why, when the majority of males appears to remain in Mexico, does this population come to the Chiricahuas? Are *Leptonycteris curasoae* present in the Chiricahuas throughout the summer, and if so, is it the same population for the entire season. What food sources are used by the bats before the flowering of *Agave palmeri* in late June?
Not only does an influx of post-lactating females and juveniles occur at the Chiricahua sites in late summer, but records of reproductive males and newly gravid females captured at these roosts during August (Cockrum and Ordway 1959) also hint that these "transient" refuges may serve an additional role. It is possible the males found in southeastern Arizona may mate with some of the females from northern populations when they move to higher elevation roosts in August and September, before migrating southward. If so, caves and mines in Arizona Sky Islands could be important mating sites for the species (Fleming pers. comm.).

2) *Plecotus townsendii*

a. ("Alternate" roosts) In Arizona, *Plecotus townsendii* is a year-round inhabitant of caves and mines. In summer, females form colonies of up to a few hundred individuals to rear their young. Maternity colonies have been observed relocated in alternate roost sites in the middle of the maternity season. These "alternate" sites may be within the same cave/mine or nearby in a different one (Tipton 1984, Dalton and Dalton pers. obs.). What triggers these movements? Do the requirements of the colony change as the reproductive condition of the bats changes, or do the roost conditions change sufficiently to necessitate these movements? Without an answer to this question, a colony of *P. townsendii* could be lost from destruction of "alternate" roosts despite adequate protection of the "primary" roost.

b. (Winter behavior) In winter, these bats hibernate in higher-elevation roosts which are colder than their summer roosts (DCD pers. obs.). Because milder climates are within nightly flying distance of potential hibernacula, *P. townsendii* in the Sky Islands may arouse periodically throughout the winter to forage at lower elevations. This sort of winter activity has been observed in California (Pearson *et al.* 1952, Pierson *et al.* 1991). A study could be conducted to determine if there are active *P. townsendii* foraging at lower elevations. If this behavior is confirmed, these animals could be used to locate new hibernacula higher in the mountains.

c. (Winter roost requirements) In the eastern United States, a different subspecies is known to hibernate in clusters in excess of 1000 individuals (C. Stihler pers. comm., DCD pers. obs.). Only one hibernaculum with a significant number of *Plecotus townsendii* is currently known in southern Arizona. Other southern Arizona winter sites have only a few to about twenty non-clustering individuals. In New Mexico, a similar pattern is observed, with bats usually hanging singly or in groups up to about ten, with the largest single cluster numbering about 100 (Altenbach pers. comm.). Is this scattering of individuals in winter typical of *P. townsendii* in Arizona, or conversely, are major hibernacula in the Sky Islands still undiscovered? If they are not colonial in winter, identifying roost requirements, and subsequently, determining management actions, become much more difficult.

3) *Lasionycteris noctivagans*

In contrast to *Plecotus* and *Leptonycteris*, *Lasionycteris noctivagans* is a generally solitary species whose preferred day roosts are probably crevices in trees (Barclay *et al.* 1988). Cockrum and Petryszyn (n.d.) have summarized current knowledge about this species. It is seasonally abundant in the Chiricahua Mountains. There are no known records in adjacent northwest Mexico. Males have been recorded in Arizona in every month, but females only from October through June. No gravid females or juveniles have ever been recorded in Arizona. It is thought that females of the species migrate to coniferous forests in the northern U.S. and Canada to give birth and raise their young (Cockrum and Petryszyn n.d.). As best as can be reconstructed from current data, the northern range limit shifts north in summer and south in winter (Kunz 1982). .

Nearly a quarter of the *Lasionycteris noctivagans* reported for Arizona by Hoffmeister (1986) were netted during winter in the Chiricahua mountains. This fact, plus the absence of any records of the species south of the border, raises the possibility that the Chiricahuas may be a significant overwintering site (Cockrum pers. comm.). In New Mexico, an individual was caught in a mist net (i.e. was active and flying) at 28°F (Barbour and Davis 1969). Research into winter habits of this species is suggested.

CONCLUSION

Primary responsibility for protecting the health of Arizona Sky Islands falls to the agencies which administer these largely public tracts of land. Managers must concern themselves with all flora and fauna under their stewardship, leaving them little time to gain an in-depth knowledge of any one species. What are their best sources of information? Books and journals are of course the primary storehouse of knowledge about bats and bat research. A central database, such as that maintained by AGFD Heritage Program, is useful for some regionally specific facts, but is not always up to date. The most useful resources for current information are experienced bat biologists. Knowledge is always in flux. New discoveries disprove long accepted theories. Updated information mandates refinement of research and management strategies. Active bat specialists are most likely to keep up with such changes. Land managers can use the specialized knowledge of these individuals for effective management. Development of monitoring protocols and management plans should be undertaken in collaboration with researchers working in affected areas. Close, on-going cooperation between managers and researchers can lead to better decisions.

The issues involved in managing for bats are not simple. Understanding their relationships with other flora and fauna is central to understanding the natural diversity of the ecosystems in which they live. As example, bats directly affect the plants and insects that they utilize as food. Indirectly, those bats eating insects will have an effect on the plants upon which their insect prey feed. Therefore, it is necessary for zoologists, botanists and entomologists to work together to gain a more complete understanding of these interactions. To ignore ecological relationships is to oversimplify a naturally complex system. In the words of Janovy (1985), "As a role model for society, the biologist above every other kind of scientist should demonstrate the futility of searching for simplistic and purposeful answers to complex natural problems." This point is key to maintaining natural systems.

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Ecological Relationships of the Thick-billed Parrot with the Pine Forests of Southeastern Arizona

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Abstract.—The thick-billed parrot (*Rhynchopsitta pachyrhyncha*) once ranged throughout the high mountains of southeastern Arizona. Disappearance of the species early in the present century may have been due primarily to widespread shooting. Experimental releases of thick-billed parrots back into the region were conducted between 1986 and 1993, and studies of released birds have revealed a strong dependence on certain conifer species for both food and nesting. The data obtained strongly suggest that the high diversity of conifer species found in southeastern Arizona was a critical factor in allowing the former residence of these parrots.

Conifer cone crops vary among species, among years, among seasons, and geographically. The most important foods of released parrots have been cones of Chihuahua pine (*Pinus leiophylla*), ponderosa pine (*Pinus ponderosa*), and Arizona pine (*Pinus arizonica*), although the parrots have also been observed taking cones of other pine species and Douglas fir (*Pseudotsuga menziesii*). Of all these species, Chihuahua pine appears to be the most important, because it bears cones with high regularity and its seeds are held within cones on a year-round basis. Most other species produce cones only irregularly and many offer seeds only during the summer and fall. It seems probable that the northern extent of the historical distribution of the parrot was tied most importantly to the distribution of Chihuahua pine.

INTRODUCTION

The thick-billed parrot (*Rhynchopsitta pachyrhyncha*) is presently limited in range to the Sierra Madre Occidental of Mexico, but formerly also occurred in the Madrean mountains of southeastern Arizona and southwestern New Mexico (Wetmore 1935, Phillips et al. 1964, Forshaw 1989). Whether the species was ever a fully established breeding resident north of the international border, or was only an irregular visitor to the U.S., has been a matter of debate. The historical record is too fragmentary to answer this question conclusively, but the frequency of historical reports in at least the Chiricahua Mountains, coupled with the readiness of the species to breed in Arizona in recent release experiments, suggests that the thick-billed parrot may once have bred with some regularity in at least a portion of its U.S. range (Snyder et al. 1994).

The thick-billed parrot's disappearance from the U.S. early in the present century may have been due largely to shooting (Snyder and Wallace 1987, Snyder et al. 1994). As a large, noisy, social, and relatively tame species, it was highly vulnerable to such pressures, and shooting was noted in essentially all early U.S. accounts of the species (Lusk 1906, Smith 1907, Vorhies 1934, Wetmore 1935). Shooting is not known to have been a major problem for the species in Mexico, and the major conservation concerns south of the border have been the cutting of thepine forests on which the species is tightly dependent (Lanning and Shiflett

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1981, 1983), and a relatively recent upsurge in trapping of individuals for the illegal bird trade (Snyder and Wallace 1987).

GENERAL HABITS

The thick-billed parrot feeds heavily on the seeds of conifers, although it is known occasionally to take other foods such as acorns, buds of various trees, and flowers of agaves (Wetmore 1935, Blake and Hanson 1942, Stager 1954, Lanning and Shiflett 1983, Snyder and Wallace 1987, pers. obs.). Overall, however, the dependency on pine forests is very strong, as it is in crossbills (Benkman 1993). The bill of the thick-billed parrot is quite large, resembling that of a small macaw, and almost surely serves as an adaptation for husking the tough scales of conifer cones.

In apparent accord with a diet limited largely to pine seeds, the thick-billed parrot breeds very late in the year, most usually laying eggs in late June through July and fledging young in late September through October (Lanning and Shiflett 1981, 1983; pers. obs.). Most pines produce cones that first become sufficiently mature for parrot feeding by the early summer. In some species, such as pinon (*Pinus edulis* and *discolor*) and Douglas fir (*Pseudotsuga menziesii*), seeds are shed from cones by mid fall. In other species, seeds are retained in closed or partially closed cones through the winter and spring months. Thus the maximum availability of food is in summer and early fall, while the minimum availability is in late spring. The parrot breeding season coincides with the period of maximum food availability.

Figure 1.—Pair of released thick-billed parrots at their 1989 nest hole in a Ponderosa pine snag along the Mogollon Rim of central Arizona. Two other pairs nested within a kilometer.

Nest sites of the parrots are typically old woodpecker holes or natural cavities in dead pine snags or aspens. Contrary to early reports and conclusions (Bergtold 1906, Thayer 1906, Phillips et al. 1964), the species is not limited to old nest holes of imperial woodpeckers (*Campephilus imperialis*), but perhaps most commonly enlarges old nest holes of flickers (*Colaptes auratus*) or modifies natural cavities to serve its reproductive needs (Lanning and Shiflett 1983, pers. obs., fig. 1). Thus, the retention of snags is presumably an important forestry management consideration for nesting areas of this species. The thick-billed parrot commonly, but not always, nests in semi-social assemblages, and the exact distribution of nests is presumably controlled largely by the distribution of available cavities (Lanning and Shiflett 1983, pers. obs.).

Nesting records for the species have been limited to relatively high-elevation forests — ranging from about 2,300 to 3,070 m — although the species commonly feeds at lower elevations and readily flies distances on the order of 15-20 km between nests and foraging areas (Lanning and Shiflett 1983, pers. obs.). Roosting areas in the non breeding season also tend to be at relatively high elevations (commonly 2,200 to 2,500 m), and are often positioned in well-developed timber on north-facing slopes. The species centers its activities at high elevations throughout the year, and is well adapted to snow cover and low temperatures in winter.

FOOD RELATIONSHIPS

Like other birds feeding on pine seeds, the thick-billed parrot is a highly mobile species capable of dealing with spatial and temporal irregularities in abundance and distribution of its primary foods. Evidence suggests that at least some populations are migratory (Snyder et al. 1994). Under stress conditions, such as are produced by major droughts, large-scale movements of the birds occur from one part of the range to another (see Wetmore 1935, Marshall 1957), presumably correlated mainly with food availability. It is reasonable to hypothesize that the most favorable parts of the range of the species are regions characterized by the conifer species that fruit most regularly and that retain seeds in cones through all months of the year. Areas lacking such conifers presumably do not constitute viable year-round thick-bill habitat.

Different pine species show strong differences in the regularity of fruiting and in their seasonal availability of seeds for parrots. In table 1, we present summary data on fruiting of conifer species that have been important for thick-billed parrots released in southern Arizona since 1986. These data are based on permanent plots in the Chiricahua Mountains and along the Mogollon Rim of central Arizona, as well as upon more casual observations of cone production in other regions of southern and central Arizona. We have directly observed parrots feeding on all but one of the species listed in the table. The exception, southwestern white pine (*Pinus strobiformis*), is included because thick-billed parrots have been commonly observed feeding on this species (equals *Pinus ayacahuite*) in Mexico (Lanning and Shiflett 1983).

Although table 1 does not represent a complete listing of conifers found in Arizona, it is apparent that the diversity of foods available and presumably acceptable to parrots is considerably higher in southern Arizona than in central Arizona. In fact, several species of importance to the parrots — Chihuahua pine (*Pinus leiophylla*), Apache pine (*Pinus engelmannii*), and Arizona pine (*Pinus arizonica*) — are limited to southeastern Arizona and southwestern New Mexico in their U.S. distributions. The vast pine forests of the Mogollon Rim in central Arizona are comprised largely of ponderosa pine (*Pinus ponderosa*), with lesser amounts of Douglas fir, white fir (*Abies concolor*), and southwestern white pine; and with pinon-juniper on relatively dry slopes. The diversity of pines in southern Arizona closely resembles that in many regions of the Sierra Madre Occidental in Mexico (see Marshall 1957, Kearny and Peebles 1960, Bailey and Hawksworth 1983, Perry 1991, Barton 1992). In this paper, we follow the taxonomy of Bailey and Hawksworth (1983).

With the exception of Apache pine and possible exception of southwestern white pine, all species listed appear to be consistently acceptable as food to the parrots — when cones are available and when seed content of cones is reasonably good. However, we saw apparent rejection of an excellent cone crop of Apache pine with good seed content in the winter and spring of 1992-1993. During this period a flock of released thick-bills on the west side of the Chiricahua Mountains fed exclusively on Chihuahua pine cones in a region of mixed Chihuahua and Apache pine. No feeding on the Apache pine cones was observed even after parrots had effectively exhausted the Chihuahua pine crop, in spite of the fact that the flock had been conditioned to feed on Apache pine cones prior to release in the area. In other years and areas, thick-bills were observed feeding commonly on Apache pine cones, so their failure to do so in 1992-1993 was notable. To some extent, a reluctance to feed on Apache pine cones may trace to the large size of cones and the tough cone scales characteristic of the species, but we cannot presently offer a conclusive expla-

Table 1.—Summary of distributional and cone production data of major thick-billed parrot food species in Arizona from 1986-1993.

Species	Arizona distribution	Regularity of cone production	Seasonal availability of seeds
Chihuahua pine (*Pinus leiophylla*)	SE	Most years	All seasons
Apache pine (*Pinus engelmannii*)	SE	<<Half of years	Summer to Spring
Arizona pine (*Pinus arizonica*)	SE	< Half of years	Summer to Spring
Ponderosa pine (*Pinus ponderosa*)	N, Cen., SE	Half of years	Summer to Winter
Pinon pine (*Pinus edulis* and *discolor*)	N, Cen., SE	Half of years	Summer and Fall
Southwestern white pine (*Pinus strobiformis*)	N, Cen., SE	Most years	Summer and Fall
Douglas fir (*Pseudotsuga menziesii*)	N, Cen., SE	All years	Summer and Fall

nation for the failure of the parrots to feed on Apache pine cones in the winter-spring of 1992-1993.

The absence of observations of thick-bills feeding on southwestern white pine cones may in part be an artifact of incomplete observations and a relative scarcity of this conifer in many of the areas that have been occupied by released thick-bills. It may, however, also relate to the large size and sap-covered nature of *Pinus strobiformis* cones. In Mexico, where thick-bills have been seen feeding on cones of this species, they have refrained from clipping cones from branches and have awkwardly worked on them still attached. In the process, the birds have exhibited difficulties in keeping their plumage free from sap (Lanning and Shiflett 1983; Lanning, pers. comm.). With all other conifers, cones are normally clipped free from branches and held in one foot before being attacked by the parrots. The seeds of *Pinus strobiformis* are very large and offer an apparently substantial nutritional reward (see Benkman et al. 1984), but the difficulties in dealing with cones of this species, especially the feather-fouling problems, may make it a species that is sometimes or generally avoided.

None of the released thick-bills observed from 1986 through 1993 was ever observed with sap-soiled plumage, suggesting that use of P*inus strobiformis* cones was rare at best during this period. However, we have received a verbal report of sap-stained plumage of thick-billed parrots observed in the Chiricahua Mountains by Ralph Morrow (pers. comm.) early in the present century (probably 1917-1919). We suspect that the birds he encountered may have been feeding earlier on *Pinus strobiformis,* although he did not observe this directly. Wetmore (1935) similarly assembled sightings of thick-bills with plumage "smeared with pitch" from the Chiricahuas in 1917-1918.

Many of the conifer seeds fed upon are only available during the summer and fall. This has been especially true for pinon, Douglas fir, and southwestern white pine, but also to a large extent with ponderosa pine, which has usually shed nearly all seeds by mid winter. The most favorable species for the thick-bills, with respect to broad seasonality of seed availability have been Chihuahua pine, Apache pine, and Arizona pine, which exhibit year-round or nearly year-round availability. However, both Apache pine and Arizona pine have exhibited low frequency of cone production, making them completely unavailable in many years. The most regular cone producers have been Chihuahua pine, Douglas fir, and southwestern white pine. Douglas fir, the most regular species of all, has produced at least some cones in all years of study.

At this point, however, we with to emphasize that conclusions as to frequency of cone production are limited to relatively few years (1986-1993), and several of these years were high stress years because of drought, especially 1989-1990. Consequently, conclusions should be considered preliminary.

DISTRIBUTIONAL RELATIONSHIPS

Overall, it appears that Chihuahua pine is an extremely important species for the parrots, both by being a very regular cone producer and by offering seeds in all months of the year. Cones of this species normally remain tightly closed until the spring following full maturity and then open only to a variable extent by summer when a new cone crop becomes available. As discussed above, other species offering seeds nearly year-round have been irregular cone producers, while still other species that are regular cone producers have offered seeds only during summer and fall. Thus within Arizona, it may be possible for the parrots to maintain consistent year-round populations only within the range of Chihuahua pine. With the possible exception of an early Spanish record of the species in central Arizona (see Wetmore 1931), all historical records of the thick-billed parrot in the United States fall within the present range of Chihuahua pine.

Nevertheless, a release of thick-billed parrots in the Chiricahuas in 1986 resulted in a flock that migrated regularly to central Arizona, outside the range of Chihuahua pine, during the summer and early fall (see Snyder et al. 1994). This flock always returned to the Chiricahuas (and the range of Chihuahua pine) in winter and spring. However, the released flock of 1986 did not persist for more than a few years. It did quite well, carrying on a number of breeding attempts up until the drought of 1989-1990, but then suffered high mortality and dispersedfrom the region.

DISCUSSION

The thick-billed parrot is a species historically tied to the pine forests of the Sierra Madre Occidental and Madrean Sky Islands of the southwestern United States. Although not a strong specialist on particular conifers and not a species obviously limited by climatic factors, the thick-bill has apparently been unable to sustain viable populations in more northerly conifer forests, unlike other conifer-dependent species, such as crossbills, pinon jays (*Gymnorhinus cyanocephala*), Clark's nutcrackers (*Nucifraga columbiana*), and various squirrel species (see Balda and Bateman 1972, Ligon 1978, Smith and Balda 1979, Benkman 1987, and Vander Wall 1988). Some of the latter species have evolved food-storage behavior to counter the seasonal availability problems with conifer seeds that are characteristic of many of these forests. Such behavior is unknown in thick-billed parrots, although it is well to note that Dirk Lanning (pers. comm.) has observed thick-bills occasionally raiding the food storage granaries of acorn woodpeckers (*Melanerpes formicivorus*) in Mexico. The historical northern limit of the thick-bill's distribution in Arizona may have been determined largely by a steep south to north gradient of declining reliability of year-round food supplies, resulting mainly from a conspicuous drop in diversity of conifer species, especially those species bearing seeds on a consistent year-to-year basis and on a consistent throughout-the-year basis.

Failures in cone crops are a normal course of events among most conifers, and species dependent on these cone crops must generally be able to respond to failures either by moving long distances or by switching to alternative food species that may not be synchronized in patterns of failure. In our observations of cone production of conifers in southern and central Arizona, it has been apparent that cone failures have not been closely synchronized among various species in most cases. Nevertheless, severe droughts, such as in 1989 and 1990, can result in regional cone failures across many species, providing major problems for cone-feeding animals. Potentially, the historical northern limit of the range of the thick-billed parrot may have been determined as much by the frequency of such catastrophic events as by simple presence or absence of conifer species that tend to fruit regularly and provide seeds on a year-round basis.

At the present time the forests of central Arizona are subject to high rates of timber harvest, with unlumbered areas limited largely to steep slopes. Benkman (1993) has discussed the severe impacts of intensive timbering activities, especially short-rotation timbering, on cone production of conifers and on food supplies for species dependent on conifer seeds. If the forests of central Arizona were not known as thick-billed parrot habitat prior to the onset of timbering activities, they seem even less likely to be able to support this species on a sustained basis now, either as resident or migratory populations.

In any event, it seems likely that the historical presence of the thick-billed parrot in the Madrean mountains of the United States is in itself a reflection of the relatively high diversity of conifers found in these mountains, and is yet one more illustration of the unique biological values of the region. Efforts to reestablish the thick-billed parrot in southern Arizona have not yet yielded a self-sustaining population although preliminary experiments suggest that this may be possible if enough high-quality birds can be assembled for release. With the decline of subsistence hunting in this century, the potentially primary limiting factor causing the extirpation of the species in the region — shooting — is no longer a major threat. Equally importantly, the pine forests of the southern portion of the state are still largely intact and free from timbering pressures, although they have suffered some locally significant timbering activities in the past.

ACKNOWLEDGMENTS

The thick-billed parrot program has been a cooperative venture of a number of public and private parties. Principal agency contributors have been the Arizona Game and Fish Department, the U.S. Fish and Wildlife Service, the U.S. Forest Service, WIldlife Preservation Trust International, World Bird Sanctuary, and Avicultural Breeding and Research Center. We wish also to make special mention of the contributions of Josiah and Valer Austin, James Koschmann, and the Southwestern Research Station of the American Museum of Natural History.

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Use of Species/Area Equations to Estimate Potential Species Richness of Bats on Inadequately Surveyed Mountain Islands

Ronnie Sidner and Russell Davis[1]

Abstract.—Species richness of bats on selected mountains in southeastern Arizona was compared by regression to the area of montane habitat in each of these mountains. The resulting equation was then compared to similar equations generated from species-area curves that have been reported for birds in the Great Basin and small non-flying mammals in the Madrean Archipelago. Data from which these equations were calculated were then graphed and compared to the power model (log/log) regression curve. Outlier data points (apparently anomalous mountains), both above and below the regression line, were then examined. Inadequate sampling effort, size of forested area, and perhaps low habitat diversity are shown to be factors contributing to species richness on certain mountains that is lower than that which would be predicted from mountain (island) area alone. For bats, the contribution to species richness of sampling intensity may provide a caveat that could be important in certain management and conservation decisions: recorded species richness is not always the result of biological processes. This analysis also provides information that could prove useful in decisions regarding the most efficient use of funds for faunal surveys—it would allow these to be directed toward those mountains where recorded species richness is most likely to be increased.

INTRODUCTION

In general, the larger the region sampled, the higher the species richness. This positive correlation of the number of species in a region with the area of that region is one of the most ubiquitous and widely accepted ecological principles. The cause of this pattern, and the factors, other than area, that produce it, however, are topics of ongoing ecological debate. In the southwestern United States, patterns of species richness of both birds and mammals occurring on montane islands have received considerable attention (Brown 1978; Davis et al. 1988; Lomolino et al. 1989). In each case, as expected, when the number of species present on each mountain is plotted on the y-axis of a log-log graph, and the area of each mountain is plotted on the x-axis, the corresponding regression line (plotted from an equation determined by regression analysis) graphically displays a highly significant species/area relationship (see the "bird" and "mammal" curves in Figure 1).

Brown (1978) attempted to use the differences in the slopes of the species/area regression equations that were obtained for mammals and birds on mountain islands in the Great Basin to explain the differences in the patterns of species richness. The slope of the regression line for birds showed a flatter slope, he explained, because birds fly and the extent of isolation of the individual mountain ranges is thus inconsequential. The species/area relationship for birds on mountain islands in the Great Basin, therefore, is very much like that from data obtained from samples taken from a "mainland". On the other hand, Brown pointed out, the species/area regression line for small, non-flying mammals on these same mountain islands has a steeper slope—reflecting their lack of mobility and the extent of the relative isolation (to these

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animals) of the various mountain ranges. A comparably steep slope was also obtained by Davis et al. (1988) for small, non-flying mammals on mountain islands in Arizona and New Mexico.

Bats have been omitted from the papers cited above and from most studies of species richness and area, because of the expectation of potential confusion that would result from bats behaving biogeographically much more like birds than other mammals, and because the distribution of bats generally was not well known (Brown 1978). Only recently have analyses of the influence of area on species richness of bats begun to emerge. Findley (1993) gives two examples of positive influence of area on species richness of bats, one from temperate zones and one from the tropics (r^2=0.50 and P=0.0001, and r^2=0.17 and P=0.03, respectively).

The present study is designed to determine first the pattern of species richness of bats on certain selected mountain islands of the Madrean Archipelago, and then to verify the expected role of area. The slope of the regression line obtained from the analysis necessary for that verification will be compared with regression lines reported for birds and small non-flying mammals. This comparison will provide a tentative test of the hypothesis that the slope of the species/area regression line for bats would be most similar to that of birds. An additional objective of this study, one of considerably more importance, is to determine mountain island characteristics, other than area, that influence the montane species richness of bats. Knowledge of such factors could play an important role in management and conservation decisions and thus have an important impact on the bat fauna of the Madrean Archipelago.

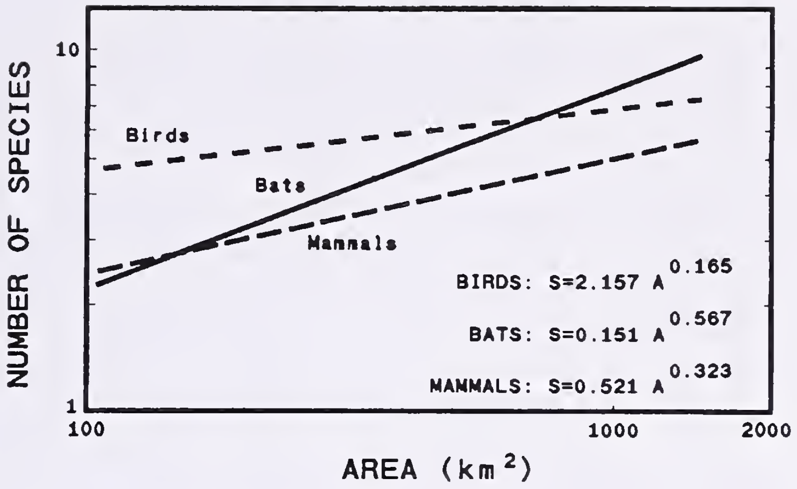

Figure 1.— Species-area curves. Both axes are logged. The equation for birds was derived from Brown's (1978) species-area curve for birds on mountain islands in the Great Basin; his data were first converted from area in mi^2 to km^2. The equation for mammals is from Davis et al. (1988) for small, non-flying mammals (non-bats) on mountain islands in Arizona and New Mexico. The equation for bats is from data provided in this study.

METHODS

We selected ten of the Madrean Islands for which there was either published information regarding bat distributions or for which we had gathered distribution data during recent field work (Table 1).

Table 1.—Characteristics of selected mountain ranges in the Madrean Archipelago. Total area is the area of montane habitat (oak woodland, chaparral, and forest) measured on the Brown and Lowe map (1980). Forest is the area only of forest habitats (pine and mixed conifer, and spruce-fir). Number of montane habitats (including woodland, chaparral, pine or mixed conifer, and spruce-fir forests) in each range are as mapped by Brown and Lowe (1980). Survey effort is a subjective ranking of surveying for bats by biologists. Species richness is the number of montane species of bats recorded from the range (see Table 3).

Mountain Range	Total Area (km^2) [Forest]	Number Montane Habitats	Highest Peak (m)	Survey Effort	Species Richness
Santa Catalina	549 [57]	3	2792	8	7
Rincon	338 [21]	3	2626	5	7
Santa Rita	410 [16]	2	2882	4	5
Whetstone	105 [0]	1	2343	1	2
Galiuro	668 [19]	3	2332	3	4
Pinaleño	537 [162]	3	3267	7	5
Chiricahua/Dos Cabesas/Pedrogosa Complex	1468 [122]	3	2986	10	8
Huachuca/ Patagonia Complex	1056 [36]	2	2886	8	8
Animas	179 [27]	2	2601	6	6
Baboquivari	142 [0]	1	2357	1	1

Using the Brown and Lowe map (1980), we measured the basal area that corresponded to the total area of montane habitats (woodland, and chaparral and forest, if present) on each island and the area of forest habitat alone (excluding woodland and chaparral); see Table 1. The number of montane habitats on each island was counted by considering woodland and chaparral biotic communities each as distinct habitats, while subdividing forest into pine and mixed conifer forest or spruce-fir forest habitats. These habitat criteria resulted in a tally of one to three habitats for each island (Table 1); no montane island had four habitats—none had both chaparral and spruce-fir forest.

From various road and topographical maps we determined the elevation of the highest peak on each island (Table 1). In addition, we compiled, *a priori*, a subjective list of relative survey effort that had been devoted to, or had included, the bat fauna present on each of the mountain islands. The results of this subjective estimate were then ranked from 1 to 10 (Table 1). Criteria used in this estimate of survey effort included: published results of a survey of the mammals (and/or specifically of the bats) of a particular mountain range, accessibility by roads, number of sites known to be sampled, number of biologists known to have studied bats in that range, and the amount of our own field effort there (Appendix 1).

To determine species of Arizona bats that have montane affinity, we used Hoffmeister's table (Table 4.1 in Hoffmeister 1986) of the occurrence in Arizona of each species in each habitat as a percent of the total sites of collection of that species. We chose those species of bats for which a total of 50% or more of their capture localities were in montane habitat: chaparral, oak woodland, and forest habitats (Table 2). Of the 11 species that qualified as "montane" bats, two were not used in our analysis. *Mormoops megalophylla* is known from only one locality in Arizona and was only observed during two nights in 1954. *Myotis evotis* is not known from any of our selected mountain islands nor from any locality in southern Arizona. Species names follow Jones et al. (1992) or Hoffmeister (1986).

We then compiled presence or absence data from the literature for the nine remaining species of bats (Table 3) on each of our selected mountains (Cockrum 1960, Findley et al. 1975, Cook 1986, Hoffmeister 1986, Sidner and Davis 1988, Davis and Sidner 1992, and Hoyt et al. 1994; and from our recent field surveys, Sidner and Davis, unpublished field notes).

Using regression analysis, we log-transformed both species richness of montane bats and total area in order to calculate a power model ($S = c\,A^{z)}$, to allow us to conveniently compare the results of our study with results from Brown (1978) and Davis et al. (1988). Because we converted Brown's area data from mi^2 to km^2 to improve this comparison, the "intercept" portion of the equation for the Great Basin bird distribution data is different from that given in his paper (Brown 1978).

Of four characteristics of the mountain ranges that were tested (total area, forest area, elevation, and number of montane habitats), only forest area and elevation of highest peak were significantly correlated (r=0.836, P=0.003).

Table 2.—Species of Arizona bats for which ≥ 50% of known localities (Hoffmeister 1986) occur in montane habitats: chaparral, woodlands (oak), and forests (pine, mixed, and spruce-fir). Two species indicated by * were not used in the analyses (see text).

Species	% Occurrence in Montane Habitat				No. Sites
	C	W	F	Total	
**Mormoops megalophylla*	0	100	0	100	1
Choeronycteris mexicana	0	64	0	64	25
Myotis occultus	17	0	67	84	18
**Myotis evotis*	7	0	73	80	15
Myotis auriculus	0	30	30	60	10
Myotis thysanodes	9	28	19	56	58
Myotis volans	9	26	31	66	35
Myotis ciliolabrum	9	25	25	59	32
Lasionycteris noctivagans	7	7	58	72	30
Lasiurus cinereus	10	10	32	52	31
Idionycteris phyllotis	6	6	38	50	16

Table 3.—Presence/absence records for montane species of Arizona bats used in this report. Presence is indicated by +, absence by —. Data are taken from Cockrum (1960), Findley et al. (1975), Cook (1986), Hoffmeister (1986), and Sidner and Davis (1988). An asterisk indicates new records of presence verified by unpublished data (Davis and Sidner 1992, and Sidner and Davis—field notes). A specimen of *M. occultus*, designated by ?, was collected by us 7 km south of the Catalina Mtn. and may occur there, but we have not counted it for species richness there. See Table 1 for full names of mountain ranges abbreviated here. See Table 2 for full names of species.

Species	Mountain Ranges CA	RI	WH	SR	BA	HU	CH	GA	PI	AN	Total
C. mexicana	+	+	+*	+	+	+	+	+	+	—	9
M. occultus	?	—	—	—	—	+*	—	—	—	—	1
M. auriculus	+	+	—	+	—	+	+	—	+	+	7
M. thysanodes	+	+*	+*	+	—	+	+	+	+	+	9
M. volans	+	+*	—	+	—	+	+	—	+	+	7
M. ciliolabrum	+	+*	—	—	—	+	+	—	—	+	5
L. noctivagans	+	+*	—	—	—	+*	+	+*	+	+	7
L. cinereus	+	+*	—	+	—	+	+	—	—	+	6
I. phyllotis	—	—	—	—	—	—	+	+	—	—	2
Species Richness of Montane Bats	7	7	2	5	1	8	8	4	5	6	
Species Richness of all bats on Mtn	21	20	8	17	7	18	21	5	15	17	

Stepwise multiple regression was used to test for the influence of the following variables on species richness (untransformed data): total area, forest area, elevation of the highest peak, number of montane habitats, survey effort, and total species richness of bats on the mountain. Survey effort was also tested separately against species richness using simple linear regression.

RESULTS AND DISCUSSION

Species richness of bats for each island is given in Table 3. Values are provided for total species richness on the mountain (including non-montane habitats) and for those species of bats that are here characterized as montane species.

The equation resulting from the regression of species richness of bats and area of mountain islands is $S=0.151\ A^{0.567}$ ($r^2=0.521$, $F=8.70$). However, the semi-log model provided a better fit of the species-area relationship than either the log-log or the unlogged models ($r^2=0.562$ *v.* 0.521 and 0.459, and $F=10.28$ *v.* 8.70 and 6.79, respectively).

As expected, our regression analysis shows a significant influence of area on species richness of bats ($P=0.018$) in the Madrean Archipelago, but the unexpectedly high *z* value is problematic.

The log-log model was used for comparison (fig. 1) with the power models obtained for birds, $S=2.157\ A^{0.165}$ (modified from Brown 1978), and non-flying mammals, $S=0.521\ A^{0.323}$ (Davis et al. 1988). Such comparisons may not be entirely appropriate, but they are at least interesting and they do suggest differences among taxa. We had predicted that the *z* value for bats on mountain islands in southeastern Arizona would be more similar to the *z* value that had been obtained elsewhere for birds than to that obtained for non-flying mammals. This prediction was based on the fact that bats have dispersal abilities more similar to those of birds, while small non-flying mammals have comparably poor dispersal ability. But not only is the *z* value for bats on montane islands not like that for birds, it is also considerably different (much higher) than that for non-flying mammals (fig. 1). The dispersal ability of bats must surely be more similar to that of birds. There must be other variables, in addition to area, that are influencing the species richness of montane bats in southeastern Arizona.

The result of a stepwise regression of six variables on species richness of bats is given in Table 4. We found a highly significant relationship between survey effort and species richness; 82% of the variation was explained by survey effort alone ($F=37.55$, $P=0.001$). The area of forest habitat entered second and significantly improved the r^2 value by 0.091 for a total model $r^2=0.915$. The variable for number of montane habitats entered third but was not significant at the 0.05 level.

Our finding that mountain islands have not been sufficiently surveyed for bats is of no surprise. In fact, in the Great Basin work, Brown (1978) compiled species of mammals on mountain islands in addition to birds but he "ignored bats, because their distributions are incompletely documented."

We graphed the data (fig. 2) from which we calculated the species-area regression equation given above, and drew in the regression line. Each of the data points on the graph represents a mountain range, and each is labelled. Outlier data points (potentially anomalous mountains), both above and below the line, were then examined. Five mountains lie below the line; they have lower species richness than predicted by area. One of these, the Chiricahuas, appears to be spurious and will be discussed below. Of the remaining ones, three of the data points below the line are not surprising because they represent mountains (Whetstones, Baboquivaris, and Galiuros) where little survey effort has been accomplished (Table 1). The fifth point represents the Pinaleños, a range that ranked relatively high for survey effort, but which shows species richness lower than expected. This may also be an anomalous range in terms of distribution of bats. Or it may have been improperly ranked in survey effort; certainly it is surprising that the relatively common *Lasiurus cinereus* has not been recorded there, and this absence may indicate inadequate sampling.

As survey effort is increased, the slope of the species-area regression line will undoubtedly flatten out as more species are recorded from the least-studied mountains. To demonstrate this, we ran the species-area regression again after artificially increasing the species richness on the two least-studied mountains, the Whetstones and Baboquivaris, to that of the lowest diversity on the next least-studied mountain (i.e., four bat species). The resulting curve is shown as a dashed line in fig. 2. Using these artificial data points, the new power model is S=1.606 $A^{0.208}$. The z value (0.208) then is appropriately lower than that for non-flying mammals (Davis et al. 1988) and approaches that for birds (Brown 1978). Note also that the position of mountain data points below the line also changes. The Whetstones and Baboquivaris still have lower diversity values than expected, but they are much closer to the regression line than they were previously. The Galiuros have dropped to the lowest point below the line because they still have much area, but no more effort has been expended at finding new species. And the Chiricahuas, the spurious point mentioned earlier, has moved to where it belonged, above the line, since this range has the highest recorded diversity.

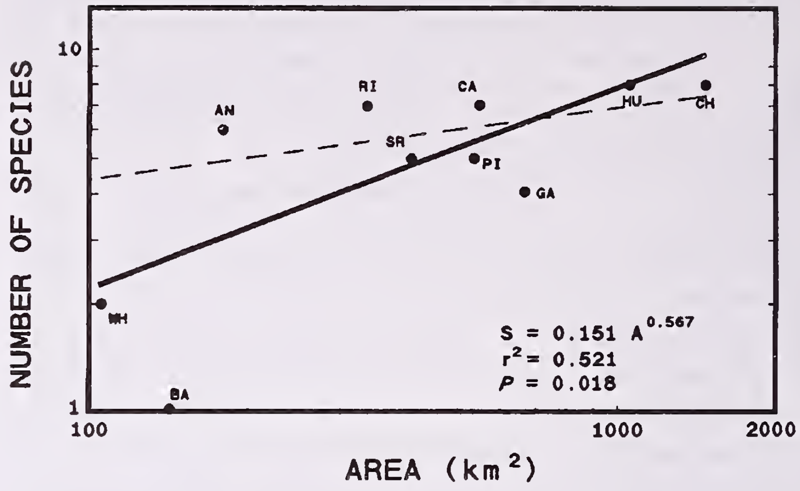

Figure 2.—Species-area curve for montane bats on selected mountains in the Madrean Archipelago. Both axes are logged. Solid curve is the regression line from current data. Dashed curve is a regression line from hypothetical future data with slight increases in the number of species recorded from two mountains ranges. See Table 1 for full names of mountain ranges abbreviated here.

Table 4.—Results of regression analysis of variables that could influence species richness. Mountain characteristics (total montane area, forest area, elevation, and number of montane habitats) were tested for correlation; only forest area and highest elevation were significantly correlated (r=0.836, P=0.003). Stepwise multiple regression was used to test for the influence of the following variables on species richness (untransformed data): total area, forest area, elevation of highest peak, number of montane habitats, survey effort, and total species richness on the mountain. Survey effort entered first, followed by forest area, and number of habitats, but no other variables met the 0.15 significance level for entry into the model (SAS program).

Stepwise Multiple Regression

Variables	Contribution to r^2	F	P
Step			
1: Survey Effort	0.824	37.55	0.001
2: Forest Area	0.091	7.47	0.029
3: No. Habitats	0.033	3.75	0.101

After adequate survey work has been completed so that all ranges have been equally well-studied relative to their size, we predict that all mountains will have nearly the same species richness regardless of island size. Variability in species richness will then be influenced more by other variables. If defined more precisely than we were able to do in our analysis, the number of habitats is then likely to be shown to be an influence of major importance (Rosenzweig 1992).

An examination of the data for non-flying mammals (Davis et al. 1988) shows two points where mammal diversity is zero, both islands that are <100 km^2. There are no islands in the bird or bat analyses that are <100 km^2 in size. It is interesting to speculate, however, whether there would be corresponding zero species richness. We would not predict zero richness for bats or birds.

CONCLUSIONS

For mountain islands in the Madrean Archipelago, inadequate sampling effort, area of forest habitat, (and perhaps low habitat diversity) have been shown to be factors contributing to species richness of bats that is lower on some mountain islands than that which would be predicted from area alone.

With bats, the contribution to species richness of sampling intensity provides a caveat that could be important in management and conservation decisions: the recorded patterns of species richness are not always the result of biological processes.

Distribution data obtained from survey effort may not be the most important information that can be provided by field biologists. Certainly information about roosts, fecundity and mortality data, or the factors affecting species diversity may be more interesting, but they are also more difficult to obtain. Simple faunal surveys, on the other hand, can be accomplished over relatively short periods of time for relatively small amounts of money. And for conservation purposes, as human use continues to affect environments, and where future comparisons will be made between what was and what is, it is critical to know what species exist on defined montane islands.

The analysis provided here provides useful information that could prove important in decisions regarding the most efficient use of funds for faunal surveys. Future effort should be directed toward those mountains where recorded species richness is most likely to be increased. There are some mountain islands in southeastern Arizona that have essentially been oversurveyed—where very little new information will be gained at very high time/effort cost, e.g., in the Chiricahua Mountains. On the other hand, there are other mountain islands where no or very little work has been done, and where even minimal effort will yield much new information about species richness, e.g., the Baboquivari Mountains.

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APPENDIX

Appendix 1.—Survey effort by biologists in selected mountain ranges. A subjective number of points were designated for various criteria. Publications of mammal surveys, or specifically bat surveys, are as follows: Animas-Cook 1986, Druecker 1966; Catalinas-Lange 1960; Chiricahuas-Cahalane 1939, Cockrum & Ordway 1959, Maza 1965; Grahams-Hoffmeister 1956; and Huachucas-Hoffmeister & Goodpaster 1954. The presence of a main road and plentiful auxiliary roads were scored for road access. The presence of some or many known localities where bats were observed was noted for # localities. The number of known bat biologists that worked prominently on a mountain were recorded. The amount of surveying that we have accomplished in each range was added. The totals were then ranked and rank effort was used in regression analysis.

Criteria of Effort	Mountain Ranges									
	CA	RI	SR	WH	GA	PI	CH	HU	BA	AN
Publications	3					3	3+3	3		3+2
Road Access	2		1	1-	1-	2	2	2	1-	1
# Localities	2	1				1	2	2		
Known Bat Biologists	4	2	2		2	2	5	2	1	2
Our Work	1	5	1	1	1	1	1	3		
Totals	12	8	4	1+	3+	9	16	12	1+	8
Rank of Effort	8	5	4	1	3	7	10	8	1	6

Diversity and Importance of Native Bees from the Arizona/Mexico Madrean Archipelago

Stephen L. Buchmann[1]

Abstract.—Pollinating insects, especially solitary and social native bees, play important, often keystone ecological roles in natural ecosystems throughout the world. They not only pollinate flowering plants by vectoring their gametes but contribute to biodiversity and environmental stability by aerating soils, providing food for other invertebrates and vertebrate predators, by utilizing carbon-rich floral resources and widely distributing their nitrogen-rich feces across the landscape. Surprisingly for ecologists, and unlike most other organisms, bees exhibit their greatest species richness not within lowland tropical rain forests, but instead in certain deserts, the Mediterranean region and arid grassland and savannah habitats in general. By far the richest biogeographic region for the Apoidea occurs within the Sonoran desert of Arizona and northern Mexico, along with xeric areas in the Mediterranean. This paper suggests that the Sonoran desert regions south of Tucson, AZ. are perhaps the richest area for bees, with perhaps 1500 spp., for any similar-sized region, worldwide. The "Sky Islands", the Madrean Archipelago, represent climatic regimes and vegetative assemblages of a relictual nature from times when conditions were more mesic. Such isolated mountain tops in a sea of hot, dry lower elevation desert support notable plants and vertebrates (especially birds and reptiles) otherwise not found until much farther south in the Sierra Madre mountains of Mexico. This is not the case for bees. Although there are a few known examples of bee taxa more or less endemic to certain Madrean Woodland communities on AZ. mountains, for the most part the bee communities are depauperate in these regions. It is hypothesized that bees are scarce since the winters are cold, the soils rocky and most importantly, the floral biomass isn't sufficient to support a more diverse bee fauna. Rather, the greatest diversity and abundance of bee species in the Madrean Archipelago occurs as "bathtub rings" in the upper bajadas (Saguaro/Palo Verde association) ringing these isolated mountain ranges. Limited comparative biogeographic data for bees elsewhere in the world is also presented. The first attempt to model community floral resources for both introduced honey bees and native bee species, utilizing Geographic Information System methods, is also discussed for Arizona.

INTRODUCTION

Bees, members of the larger group of "aculeates" (the stinging ants, bees and wasps) in the order Hymenoptera range in size from individuals only 2-3 mm long to giants 40 mm long weighing several grams, more than the smallest hummingbirds. Biogeographical and limited fossil evidence attest to the origin of the bees from their sphecoid wasp ancestors at least by the middle Cretaceous 120 million years ago, if not much earlier possibly even by the latest Jurassic. The oldest fossil bees are about 90 million years old. The proto land masses were united until 180 million years ago, such that the earliest bees could have

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dispersed widely across these hot, tropical continents. By 40 million years ago, we have fossil evidence for all of the extant families of bees. Not only are they diverse in size but also in their lifestyles with free-living solitary to social taxa, many cleptoparasitic forms and even a few known true necrophagous (carrion-feeding) species in the New World tropics. However, most of the approximately 25,000 known species worldwide, feed upon the pollen and nectar of seed plants, including both angiosperms and gymnosperms but predominately upon the rich rewards offered by the flowering plants. Among eusocial bees, such as the familiar honey bee (*Apis mellifera*) or bumblebees (*Bombus* spp.), they feed upon pollen and nectar from the widest variety of flowering plants, and are termed polylectic, due to efficient foraging, long flight ranges, and due to the perennial nature of their populous social colonies headed by a queen. This author suggests that species are being described each year by taxonomists with many more yet to be found, such that the actual number of bee species alive today may be about 40,000. Undoubtedly, many have become extinct in areas of deforestation and desertification where habitat fragmentation has been greatest. To put this diversity into perspective, especially for vertebrate biologists, there are only 9,000 species of birds and 4,000 species of mammals extant today. Within the bees, the genus *Andrena* contains more than 1,000 species, and in the Sonoran desert, the fruit fly-sized panugine genus *Perdita* contains at least 500 species.

The species with the greatest pollen diet breadth may undoubtedly be the honey bee (*A. mellifera*) whose diet breadth can incorporate many dozens or even more than one hundred species at a given location (O'Neal and Waller, 1984) no doubt due to it's advanced "dance language" communication and the ability to non-aggressively pre-empt other species at the most productive floral patches within flight range of their nests. Some stingless bees, especially a few species of *Trigona* (Hymenoptera: Apidae), from Central and South America may have diet breadths as diverse as honey bees. Such species cannot afford to specialize on only one or a few species of flowering plants due largely to their perennial life history strategies.

When asked where to find the highest levels of endemism, diversity and species richness within almost any extant group of animals or plants, any ecologist or lay naturalist will tell you to head toward the equator where amidst the omnipresent green, oppressive heat and humidity the most kinds of everything lives. This simply isn't true or bees, goes against ecological dogma and is little appreciated by most professional biologists or even most entomologists. Why should this "bee"? Although this interesting issue hasn't been addressed by any biogeographer, we can posit some features of bees in general and selected habitats as a thought experiment and to stimulate further discussion. On the whole, bees are largely odalous, simply meaning that their preferred nesting habitat is within soils. Further, many species seem to prefer soils of a certain texture and within a narrow range of edaphic conditions within their natural range. Although there are known examples of tropical bees whose larval cells have hydrophobic linings, and nest under water in flooded forests, most bees select well-drained coarse, usually sand soils in which to construct their nests. Presumably, having waterlogged natal cells is to risk larval exposure to provision spoilage bacteria and fungi, pathogens or simply making longterm respiration difficult under anaerobic conditions. Much larval mortality, even under relatively dry conditions, occurs from attack by specialized entomopathogenic fungi. Thus, we can postulate that having well-drained soils within flight range of one's host plants not only affords protection from soil micro-organisms but facilitates burrow and cell construction by these female solitary bees.

What other environmental features do the biogeographic provinces harboring the greatest bee species diversity have in common? Again, this has not been studied but we note that these areas are equally rich in native angiosperm vegetation. Such floristically rich areas provide a smorgasbord of pollen and nectar sources of varying quality and abundance presented as an ever-changing phenological spectrum within and between years. Very few bees are monolectic, feeding upon the pollen and nectar of only one plant species, instead, most (Schemske, 1983) are specialists upon a few related taxa, or broader "polyleges" feeding upon totally unrelated plants broadly dispersed in time and space. Often, however one plant species can support many dozens of native bees all utilizing the same foodstuffs. This is the case with *Prosopis* and *Larrea* in the deserts of the southwestern United States and in South America which collectively provide food for hundreds of species of native bees. Thus, or these and other reasons, the Sonoran desert of Arizona/Mexico, the Mediterranean, the Cape region of S. Africa along with other semi-arid grasslands support the world's richest bee faunas.

Although the Sonoran desert of southern Arizona and northwestern Mexico may have the richest bee fauna worldwide, the genera and species are not distributed uniformly throughout this region. Most hymenopterists and melittologists, living in other regions, arrive for brief periods and collect bee specimens from flowering plants during the often spectacular spring and summer wildflower blooms. This produces a very uneven record of the Sonoran bee faunas for various sites. Similarly, no intensive longterm collecting efforts, at equal samples intervals and collecting effort, have been made for any location within the Sonoran desert of Arizona or Mexico. Thus, unfortunately, we have no authenticated database examining the bee fauna for any Sonoran desert habitats. Limited data on the bee fauna is available for a site near Silverbell, AZ. an old IBP/IRP biological site (Simpson/Neff, 1985) within the Sonoran desert. Comparative data long-term data for this site or other AZ localities is lacking.

This should be remedied with the establishment of protected, non-disturbed sites where systematic collecting, along with concomitant foodplant utilization studies can begin and continue for multiple years. Surprisingly, bee populations are among the most stable (year-to-year fluctuations) of any organism studied to date (Roubik and Ackerman, 1987) yet this study was for orchid bees and a few other taxa in Panama and we have no comparative data from extratropical regions. This paper reviews the limited biogeographic data on bee faunas worldwide with a call for new taxonomic and ecological studies investigating the rich bee faunas of the Sonoran desert and the Madrean Archipelago.

CLASSIFICATION AND BIOGEOGRAPHY OF BEES

Bees comprise the superfamily Apoidea, an extremely successful and highly specialized offshoot from sphecoid wasps. Their origin and historical record, as fossils, however is poorly known. Surprisingly, the earliest fossilized bee is a worker of the eusocial genus *Trigona* (family Apidae) from early Cretaceous deposits in New Jersey. We hypothesize that the earliest bees were derived from wasps in the family Sphecidae which capture other arthropods as living prey items for their larvae. Bees differentiated from such wasp ancestors by shifting to an herbivorous diet of spores, pollen grains, floral nectar and possibly homopteran exudates. Most bees, like their wasp relatives, construct underground nests with natal cells where their larvae consume "mass provisioned" mixtures of pollen and nectar provided by their mother. Some bees construct free-standing nests utilizing plant debris, mud, resins, saps or gums, or wax, while others excavate soft dead wood or pithy stems (e.g. leafcutter or carpenter bees) or use other natural cavities as their nests. A typical bee is non-social (solitary), constructing her nest burrows and cells and provisioning it with floral foodstuffs alone with no interaction with her developing offspring. Other species form communal nests and still others are truly social (eusocial) wherein some bees forego reproduction (serving as sterile workers). The latter has evolved independently within the bee families Apidae, Anthophoridae and the Halictidae. Examples of eusocial bees are stingless bees (*Melipona*, *Trigona*) of the tropics, bumblebees (*Bombus*) and the honey bee genus *Apis*.

Bee taxonomists generally recognize 9-11 families and about 800 genera of bees, with an informal designation of short-tongued and long-tongued bees. Recently, the number of families has been coalesced with the placement of the immense "digger bee" family Anthophoridae as a subfamily within the family Apidae (now containing anthophorids, stingless bees, bumblebees and orchid bees) and some other taxonomic shifts. Thus, until recently (Michener et. al. 1994) the families of bees included the; Andrenidae, Anthophoridae, Apidae, Colletidae, Ctenoplectridae, Fideliidae, Halictidae, Melittidae, Oxaeidae and Stenotritidae. The above authors recognized 169 genera from North and Central America. Unfortunately, no biogeographic analysis is given as this new book is meant as an identification tool for bee workers and other interested biologists.

The formal biogeographic study of bees has received very little attention from either bee biologists or biogeographers. To date, the only definitive studies are those of Michener (1974, 1979), especially the latter study. In his 70 page monograph entitled; "Biogeography of the Bees", Michener summarizes the available information but only on a very broad level. He presents data on the numbers of genera and species present on a continental basis and outlines major trends at the family level in worldwide bee distributions. Other authors have redescribed and re-emphasized many of these patterns (Duffield et al., 1984; Roubik, 1989) at higher, mostly familial, levels for bees.

Michener (1979) concludes that most bee taxa have distributions which can be explained by ancient dispersion across land masses. Further, these dispersal events likely occurred before the continental land masses had moved, continental drift produced by movement of the tectonic plates, into their relatively modern positions from 200 to 15 million years ago. Deviations from these hypothetical land dispersion patterns are few and are discussed by Roubik (1989). Bee movements especially during relatively cool, dry glacial periods may help to explain some distributional patterns whereas others are indicative of ancient super continental bee distributions prior to their breakup. Except for wood-nesting forms (e.g. some *Xylocopa*) which may accidentally "raft" over great distances, bees are not good dispersers across oceans. Unfortunately, the fossil record for bees is indeed sparse and of little use in reconstructing ancient bee migrations into new areas.

Certain families have global distributional patterns congruent with those of other animals and corresponding with major biogeographic provinces. For example, the Andrenid family are rarely found in the paleotropics and are equally poorly represented in tropical America. Their closet relatives, the oxaeid bees, are distributed in the sub tropical and tropical portions of North and South America. The Anthophoridae, Apidae, Halictidae and Megachilidae are widespread across temperate and tropical areas of most continents. They are quite abundant in tropical regions. Colletids are pantropical, also abundant in temperate areas but reach an unprecedented richness on the continent of Australia (more than 40% of that fauna). The small family Stenotritidae is only found in Australia. Another small family, the Fideliidae, are close relatives of (or are considered members of this family by some taxonomists) the leafcutter bee family Megachilidae, and are only found in Africa and Chile. The small short-tongued bee family Melittidae are primarily found in the Old World with a few temperate New World representatives. The last small, in numbers of species, bee family is the Ctenoplectridae limited to paleotropical regions.

Within the paleotropics there is a recognizable coherent bee fauna that is African. As we travel into the Oriental to the Australasian regions (Michener, 1979) the alpha diversity (number of species present in a region) falls off noticeably. Australia is extremely rich in colletid bees as represented previously. Presumably these bees arrived early and underwent an explosive adaptive radiation on the nectar and pollen-rich dominant myrtaceous flora. According to Roubik (1989); "Between Southeast Asia and Papuasia the bee fauna is largely Oriental, but relatively insular bee faunas of low diversity occur in the Philippines, Madagascar, and Australia." Islands in this area (New Caledonia, New Zealand, the Solomon Islands, Micronesia), and especially oceanic islands, have pronounced depauperate bee faunas (Table 1). Bees experience difficulty in dispersing to islands, especially oceanic islands, and they have not experienced the adaptive radiation they do on mainland areas. The Galapagos islands only have one species of native carpenter bee (*Xylocopa darwini*) which likely rafted there. New Zealand is especially depauperate for its size with only 23 species, while Ireland has 85, Trinidad (relatively close to the mainland forest source areas) has 200 and Britain has 260 species. Australia, a massive island and long-isolated has a colletid-dominanted bee fauna of at least 3,000 species. The only known example of bee adaptive radiation on an island presumably from a single species introduction is the colletid genus *Hylaeus* for the Hawaiian Archipelago. Approximately 100 species of these small bees are found there although honey bees and carpenter bees have been introduced recently. At the higher taxonomic levels of tribes and subfamilies (see Table 3 in Michener, 1979) 36 taxa occur in largely tropical regions while 31 are found in temperate areas. Surprisingly, as pointed out by many authors, bee species formation in wet lowland tropical areas

Table 1.—Compilation of the number of bees species vs. island (oceanic or habitat islands) size from the literature. A calculation of the number of species per square kilometer was made.

Region	Area (km2/sq mi)	No. Bee Species	Spp./km2
Africa	30,323,000	4,000	.0001
South America	17,828,000	7,000	.0004
United States	9,528,318	4,000	.0004
Australia	7,686,850	3,000	.0004
France	547,026	800	.0015
California	411,015	1,985	.0048
New Mexico	315,115	551	.0017
New Zealand	269,057	23	.0001
Michigan	250,687	403	.0016
United Kingdom	244,102	260	.0011
Illinois	150,028	297	.0020
Panama	77,082	352	.0046
Ireland	70,283	85	.0012
Israel	20,325	2,000	.098
Hawaiian Archipelago	16,706	100	.006
Galapagos Archipelago	7,964	1	.0001
Trinidad	4,821	200	.042

lags behind the species richness of semi-arid or desert areas. Many tropical bees do not nest in the soil as do many temperate bees. Possible explanations for this observation will be discussed later.

BEE BIOGEOGRAPHY WITHIN THE UNITED STATES

The continental United States is often suggested to have 3,500 species of native bees, but the actual number is more likely to be 4,000. It has an area of 9,528,318 square kilometers. If we accept the 4,000 bee species estimate, then this represents about 0.0004 species per square kilometer. Of course, all of this area is not suitable as bee habitat. Moldenke (1979) has given estimates of 0.5 -3.0 bee species per 1,000 square miles which I have converted to values for bee species per 1,000 square kilometers (or 0.00019 to 0.00116/km^2). For the entire eastern half of the U.S. he suggests a value of 700 bee species, which would be 0.00019 bee species per square kilometer. From the values in Table 1, the average number of bee species per square kilometer is 0.0098, or 9.8 per 1,000 square kilometers. The highest value, as bees/km^2, for any region is Israel at 0.042 with about 2,000 bee species. Figure 1 presents 16 values for oceanic islands and habitat islands, as number of bee species per unit area (millions of sqaaure km) from the literature. Undoubtedly, the Sonoran desert bee fauna would be as rich, or even more diverse but we are lacking the published data for biogeographic comparisons.

Some of the best bee data comes from pioneering studies of Moldenke (1979a, 1979b, 1979c) in California. Moldenke (see Table 2; 1979) conducted studies in California and this table breaks down bee gamma diversity (number species) into geographic realms (e.g. Mojave desert, montane, cismontane etc.). He finds that California probably has 1,985 species with forested montane California have 12.0 species per 1,000 mi^2 (0.0046/km^2), while mediterranean California, largely chaparral vegetational associations, had the highest at 14.0 species/1,000 mi^2 (or 0.0054/km^2). Further, he suggests that the Chihuahuan and Sonoran deserts of the southwestern United States support about 890 known species, and states that this is undoubtedly a very low estimate for the non-montane desert regions as a whole. According to his estimate about 600 of the state's bee species are found within the forested regions. Moldenke correctly points out that biogeographically, California is a rich mixture of geography and vegetation of ancient and contemporary lineages but the figures for it as a state are misleading due to this artificial political boundary artifact. He attributed the great species richness within the state largely due to the Mediterranean climate and chaparral vegetation in the southern portion of the state. He found a 3-fold difference in bee species richness in the major phytogeographic realms in North America (excluding the depauperate tundra). His Great Basin and Southern Mixed Forest supported the fewest bee species, while the Mediterranean and desert (Mojave and Colorado) regions had the most native bee species. He did not find a clear species/area relationship underlying his conclusion that there was a 6-fold difference in species richness between the tundra and the Mediterranean California biotic province. The paper also explores shifts in pollen diet specialization (oligolecty vs. polylecty) for native California bees.

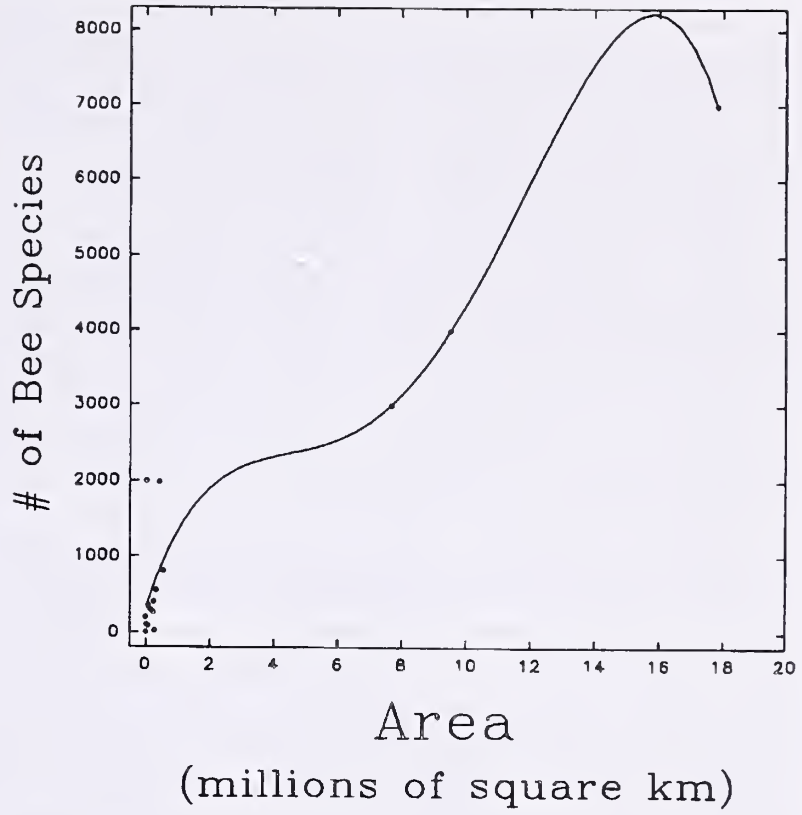

Figure 1.—The number of bee species for 16 regions, oceanic islands and habitat islands, plotted against their area.

MONTANE BEE ASSOCIATIONS

Almost the only comparative data we have for the number of bee species inhabiting montane habitats within the Continental United States are the pioneering papers by Moldenke (1979a,b,c). In one of these studies, he studied, reviewed and classified the "pollination syndromes" (according to their pollinator taxa) for native angiosperms within the Sierra Nevada mountains of California at elevations ranging from 3300 to 4200 meters above seal level. In general, he concluded that most of the bees native to the Sierra Nevada were widespread throughout the mountainous western United States and that endemicity was very low. Of the very few taxa he felt endemic to this mountain range, he felt that their phylogenetic lineages were traceable to California in general or the southwestern deserts and were specialist solitary bees in their pollen-feeding habits. In all, he found 850 bee species at montane flowers in this region. Very extensive observations and collections of all insect floral visitors were made during these studies, with about 1.5 million individuals observed. His team documented a dramatic drop in bee species richness from the lowest to highest elevations. Interestingly, he also linked floral diversity, as an excellent indicator of the floral resource base available to potential pollinators within a community, with concomitant fluctuations in bee species abundance.

In a related study (Moldenke, 1979b) the pollination syndromes, bee and other pollinator diversity was studied at several sites within the Rocky Mountains of Colorado. His group chose five sites from within a 100 mile radius of the Rocky Mountain Biological Laboratory in Gothic, Colorado. Once again, greatly reduced bee species diversity was found at elevations in excess of 3,300 meters. His general conclusion was that only 108 different species for his five sites demonstrates both the tendency for decreased bee species richness at higher elevations and the generally depauperate nature of the Colorado bee fauna in comparison to his California study sites. Regrettably, we have no such extensive quality data sets for the mountainous regions of the mountains of Arizona or Mexico and essentially no quantitative data for the Madrean Archipelago ranges of southeastern Arizona.

Table 2.—Bee genera which are common floral specialists found in the montane western United States.

Genera	Families
Andrena	(Andrenidae)
Anthidium	(Megachilidae)
Anthocopa	(Megachilidae)
Anthophora	(Anthophoridae)
Ashmeadiella	(Megachilidae)
Bombus	(Apidae)
Calliopsis	(Andrenidae)
Ceratina	(Anthophoridae)
Colletes	(Colletidae)
Dianthidium	(Megachilidae)
Dufourea	(Halictidae)
Heriades	(Megachilidae)
Macropis	(Anthophoridae)
Megachile	(Megachilidae)
Melissodes	(Anthophoridae)
Osmia	(Megachilidae)
Perdita	(Andrenidae)
Pseudopanurgus	(Andrenidae)
Svastra	(Anthophoridae)
Tetralonia	(Anthophoridae)

Table 3.—Bee Species Richness for various North American Biotic Realms[1]

Biotic Realms	Tot. Bee Species	Tot. Specialist Species
Desert	890	592
Mediterranean CA.	830	466
Forested CA.	600	252
Rocky Mountains	500	90
Great Plains	500	184
Boreal Forest	450	77
Mixed Mesophytic Forest	450	106
Pacific Northwest	425	104
Oak/Hickory/Pine Forest	25	84
Desert Mountains[2]	395	98
Great Basin	333	165
Southern Mixed Forest	280	63
Tundra & Muskeg	84	13

[1] Modified from Moldenke, 1979

[2] "Desert Mountains" includes montane and subalpine regions of Arizona and New Mexico

BEES ON TROPICAL MOUNTAINS

Recently, a paper appeared (Silveira and Cure, 1993) that present data on the high altitude bee fauna of southeastern Brazil. They compared the bee faunas of two high altitude (1250-1600m) areas in southeastern Brazil. They recognized four different geographic patterns for the bees; 1) widespread in the region regardless of altitude; 2) widespread in the lowlands but not exceeding 1300 m in elevation; 3) restricted to the montane elevations; or 4) common to these mountains and to mountains and/or lowlands south of 24° south latitude. They suggest that the latter set of bee species may represent a remnant (relictual) fauna associated with subtropical and temperate vegetation that advanced northward during Pleistocene glacial periods and that these species may essentially be "trapped" on these high altitude islands.

In all, they found 56 bee species (in 28 genera and 5 families) present at their study sites.

An interesting feature shared by some bee species on mountain tops, especially in cloud forest vegetation, in the neotropics is a tendency for many large species to be dark black and hairy. These large melanic species are especially noticeable in certain bumblebees (*Bombus* spp.) and the colletid genus *Crawfordapis* (Roubik, 1989). Additionally, one highland species of the honey bee genus *Apis* are also markedly darker than their lowland counterparts. Presumably, the melanism is a thermoregulatory adaptation to the cool wet climate on these mountains, although it hasn't been studied from this biophysical standpoint.

BEES OF THE MADREAN ARCHIPELAGO IN ARIZONA

General collecting and observations by hymenopterists and melittologists over the past several decades working in the isolated mountain ranges of southeastern Arizona, along with scattered museum specimen vouchers, reveal a "gestalt" pattern. That is, when in search of native bees, one should stay on the desert floor and not venture too high into the mountain ranges. There are a few notable exceptions to this rule. Bumblebees, the genus *Bombus*, of which Arizona has roughly 5 species (quite depauperate compared with bumblebee faunas from holartic regions) predominate at mid to high elevations within the states mountains. Apart from the largescale patterns of highest bee species diversity and endemism in xeric areas of the world, bumblebees do best in north temperate climes and even manage to exist in the Canadian high arctic tundra where few other bees can survive. The dominant bumblebee of the low AZ desert regions, *B. sonorus*, is omnipresent but not so at higher elevations. Some of the other bee species may be restricted to certain mountain ranges, as relict populations isolated since more mesic climatic regimes but there distributions are too poorly known to form any definitive conclusions.

Like the other mountain ranges previously discussed Sierra Nevada, Rocky Mountains, Brazil), although depauperate there is a characteristic "montane bee guild" at these higher elevations. Species richness is low but a repeatable loose association of high-elevation players usually present on the highly scattered ranges. For example, other than the bumblebees, notable among these taxa are the andrenid genera *Andrena* (an immense largely holarctic genus), *Calliopsis, Perdita* and *Pseudopanurgus*. Similarly, certain megachilid genera (*Anthidium, Anthocopa, Ashmeadiella, Dianthidium, Megachile, Osmia*) are key components of mid and high elevation bee faunas in southeastern Arizona and Mexico. Among the immense family Anthophoridae (now a part of the inclusive Apidae) we find a few general including Anthophora and its subgenus *Clisodon* which nests in rotten wood and not in the soil. These and other "typical" montane genera are listed in Table 2.

Predominating among these montane genera and species are leafcutter bees in the family Megachilidae, especially the anthidiine genera and the Mason bee genus *Osmia* (often a visitor of *Arctostaphylos* spp.). These bees usually nest in pre-existing beetle burrows in wood, although one nest in the ground or on rock/plant surfaces, but the anthidiine genera make extensive use of plant resins for nest-building. In this coniferous realm there are numerous sources of sticky resins. Thus, these "resin-loving" bees do seem to be well represented in our local mountains. Ground-nesting solitary bees at these higher elevations may be at a disadvantage since the native soils tend to be shallow and rocky making them somewhat less suitable for the deeper nests of certain species.

True endemism within the known bee faunas of the Madrean Archipelago of southern Arizona is very rare, as noted for the mountains of California and Colorado by Moldenke in the previously quoted studies. After consulting with numerous bee taxonomists and checking specimens in local museums I consider only three taxa to possibly be endemic to these higher elevations in southern Arizona. Within the former Anthophoridae, the subgenus *Clisodon* within *Anthophora* , these species seem to be found only or mostly at higher elevations in numerous AZ. mountain ranges. Also within this family, the genus *Syntrichalonia* occurs in the Barfoot Park region within the biotically extremely rich Chiricahua Mountains of Arizona. Similarly, *Xenopanurgus* (in the Andrenidae) is only known from Carr Canyon in the Huachuca Mountains. Intensive, directed collecting may expand the known ranges of these taxa and may reveal further bees which may be restricted to the Madrean Archipelago. Whether any of these possible endemics are relict populations of bygone times when a wetter, more equitable climate was widespread across the region, and there was no young (10,000 years B.P. or less) Sonoran desert egetative association at lower elevations can not be determined at this time with our meager data sets.

HONEY BEE COLONIES AS PLANT COMMUNITY (FLORAL RESOURCE) MONITORS WITHIN THE MADREAN ARCHIPELAGO

If, as has been suggested by Moldenke and this author, that the primary limiting factor for native bee species diversity within the Madrean Archipelago of Arizona and northern Mexico (species restricted to or abundant on the mountains not on the valley floors) is insufficient carrying capacity in terms of floral biomass (pollen and nectar), then this hypothesis should be testable. This can be done through tedious phenological and traditional vegetational sampling methods or much simpler using bees. Honey bee colonies may contain from 20,000 to 60,000 individuals as a social colony whose food requirements are staggering. Each year managed or feral honey bee colonies require at least 20 kg of pollen and 40-50 kg of sequestered honey reserves to rear brood and survive the winter cold and floral dearth period. Their colonies are superorganisms whose sterile workers accumulate millions of foraging trips during the year. As central place foragers, these scout and recruited worker bees can fly up to 12 km from their nest. Generally, however, approximately 50% of their foraging occurs within 5 Km of the nest, with 90% within 2-3 Km. This is still a huge foraging area (80-100 km^2) controlled by one social insect colony (Buchmann et al., 1992). Honey bee colonies have been likened to a giant amoeba whose "pseudopodia" find and extract floral resources through space and time and floral patches wink on then fade away to be replaced by others in a patchwork environment. Further, since *Apis mellifera* has perhaps the greatest pollen dietary breadth for any bee species, including up to 30% of the annual diet obtained from wind-pollinated plants in the Sonoran desert, its colonies can be used as perennial sampling stations, biomonitors, of local and regional pollen and nectar resources. This can be accomplished in several ways. Nectar plants used by *Apis mellifera* can be determined by standard melissopalynological techniques. This involves sampling stored honey and identifying pollen grains contained therein to indicated floral resources used for nectar. Similarly, one can extract a rich pollen assemblage from old darkened brood combs and obtain a multiyear representation of pollen diet. Alternatively, a pollen trapping device can be placed on mobile Langstroth bee hives and used as portable ecological sampling device in any community. Pollen influx and the identity of pollen types can be determined, hourly, daily or weekly and are an accurate representation of floral production by the angiosperms within colony flight range. This is an extremely powerful ecological tool which has gone unappreciated by most biologists. By using honey bees, as the ultimate perennial colony floral generalists, to biomonitor Madrean habitats we have a powerful tool to indirectly assess the spatiotemporal changes in abundance and diversity of floral biomass. Floral rewards for bees and ultimately the carrying capacity of any elevation environment for native bees or their introduced alien honey bee floral competitors an be monitored in this way.

If, as I've suggested, that mid and high elevation sites on mountains in the Madrean Archipelago have diminished floral biomass available to all bees with increasing elevation, then we should be able to find this pattern. By using pollen trapping techniques our laboratory has documented just such an altitudinal diminution in pollen/nectar as you ascend mountains in southern Arizona. This pattern is demonstrated for Mt. Lemmon in the Catalina Mountains at three elevations. At the lowest elevation (Pima Cyn. on the upper bajada) we have the richest known area for pollen/nectar production within the United States. Here, colonies routinely harvest 34.5 kg of pollen on average each year. By the time we reach an elevation of 2,438 m at Summerhaven, the bees are only collecting about 7 kg of pollen and 10 kg of honey (see O'Neal and Waller, 1984). In fact, they cannot survive unassisted (without being fed lots of honey) through the winter at this elevation. Feral colonies can survive at 300-1500 m on this mountain but probably not much higher than that (Buchmann, unpubl.).

CONCLUSIONS AND RECOMMENDATIONS FOR FUTURE STUDIES

We have seen that bees are unusual organisms when it comes to obeying biogeographical rules set down by ecologists. They do not increase in species richness as you travel toward equatorial tropical environments. Instead, they are most abundant in semi-arid Mediterranean and true deserts, savannahs and grasslands where they have access to abundant forage and sandy, dry soils in which to construct their nests and rear their brood. I suggest that the low-lying desert valleys within the Sonoran desert of the Madrean Archipelago region support the richest bee fauna anywhere within the United States and likely to be the most diverse bee assemblage in the world, perhaps second only to areas in Israel. I infer that the highest bee species diversity and numerical abundance of individuals can be found at the mountain bases, the upper bajada regions where in southern Arizona the palo verde/Saguaro cactus association predominates. These "bath tub rings" of rich vegetation, soils and nutrients support the most kinds of bees within this area. Within the Madrean Archipelago region, the bee diversity drops off rapidly as you ascend into the mountains. At mid and highest elevation the bee guilds have dwindled into an association of largely twig-nesting megachilids which harvest resin and mud to fashion their nests. In addition to diminished carrying capacity due to much less floral biomass and lessened nectar/pollen production, the combination of poor, rocky soils and cold, harsh winters at the higher elevations all contribute to making the sky islands an environment not entirely suitable for warm-loving bees. Not only is there less pollen and nectar for bees, but much of the pollen comes from oaks and pines which are lower in nitrogen and protein, making them less nutritious for native bees.

Since many mountaintop bees are leafcutter or Mason bees (*Megachile, Osmia*) in the Megachilid family, they will readily accept artificial domiciles and can be "trap-nested" using paper straws or drilled wooden blocks. Using such technology it is possible to assess local montane bee faunas with relative ease (see Krombein, 1967). Increased collecting has already begun to document the bee species within the Madrean Archipelago of Mexico. During the 1980's an ambitious binational consortium known as PCAM (El Programa Cooperativo Sobre La Apifauna Mexicana) and partially funded by the U.S. National Science Foundation began extensive sampling in Mexico to document that country's rich bee fauna. Many trips were made and thousands of specimens were collected within the Sierra Madre of Mexico. Most of these specimens have now been identified and their collection data (including elevation and host plant information) is being entered into a massive computer database for use by PCAM members and other interested parties. The major cooperating institutions in PCAM are the Museum of Natural History at the Smithsonian Institution, the University of Kansas, the Illinois Natural History Survey, the USDA-ARS (Beltsville, Logan and Tucson laboratories) and UNAM (Instituto de Biologia, Universidad Nacional Autonoma De Mexico). There are presently 1,150 species in this extensive database with a total faunal list of possibly 2,000 species. Using these data, within a few years it may be possible to finally accurately determine levels of bee endemism and species richness within the Madrean Archipelago (for Mexico at least). It is hoped that this publication stimulates biologists to conduct similar extensive studies within the sky islands of Arizona.

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Temporal Variation in Pollinator Abundance and Pollinator Foraging Behavior in Response to Robbed Flowers

Sarah C. Richardson[1]

Abstract.—*Xylocopa californica* robs some species of flowers by slitting open the sides of flowers to steal nectar, presumably without pollinating the flowers. Pollinators spend less time on robbed flowers than unrobbed flowers, and do not visit them as often as expected. Of 228 flowers marked over the season in 1993, only 13, or 6% produced fruits. Of those, 10 were robbed before maturing into fruits. Nectar was produced in buds in the late afternoon before they opened, so robbing bees gained access to the resource earlier in the life of the flower than pollinating bees. Since pollinating bees must search for unrobbed flowers and find less nectar in robbed flowers than unrobbed flowers, robbing appears to have a negative effect on pollinators visiting *C. linearis.* However, robbing may have no effect on the plants.

INTRODUCTION

In the plant-pollinator mutualism, pollinators, such as *Apis mellifera,* visit flowers in search of a reward provided by the plant, typically nectar or pollen. At the same time, the pollinators benefit the plant by carrying pollen between flowers.

Other visitors to flowers are cheaters on the plant-pollinator mutualism. Certain cheaters, nectar-robbing bees, make holes or slits on flowers and rob the nectar, usually without touching the anthers or stigma (fig. 1). Thus, nectar-robbing bees take the reward that the plant offers to mutualists, without providing the reciprocal service. When these bees visit flowers, they leave behind a record of their visit in the form of a slit or hole in a flower. Because this damage remains after the nectar-robbing bees have left the flowers, it is possible that the nectar-robbers influence the flower-visiting decisions made by legitimate pollinators of the plant even after the nectar-robbers have removed nectar and left the flower.

Figure 1.— A nectar-robbing bee, *Xylocopa sp.*

Several researchers have investigated the effect of nectar-robbing bees on one or both partners in the mutualism—either plant or pollinators. When flowers are robbed, seed set or pod number of plants can increase (Hawkins 1961, Roubik et al. 1985), decrease (McDade and Kinsman 1980, Roubik 1982), or remain unchanged (Rust 1979, Newton and Hill 1983). A few researchers have shown that floral visitors are attracted to robbed flowers because they gain access to nectar through holes left by robbers (Hawkins 1961, Inouye 1983). Floral visitors that gain access to normally unreachable flowers may increase seed set, either from their own visits (Hawkins 1961) or by causing other pollinators to

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visit more flowers when nectar has been depleted (Heinrich and Raven 1972). in contrast, other studies have shown that pollinators leave plants that have a high proportion of robbed flowers, presumably because the nectar rewards have been depleted (McDade and Kinsman 1980, Roubik 1982, Zimmerman and Cook 1985).

The effect of nectar-robbing bees on plants should vary over time, depending on floral visitors' abundances and the behavior of pollinators in response to robbed flowers. In this study, I measured abundances of pollinators visiting *Chilopsis linearis* (Bignoniaceae) during two flowering seasons. I also investigated the foraging behavior of the two most common pollinators, *Apis mellifera* (Apidae), the honeybee, and *Bombus sonoris* (Apidae), the bumblebee, on plants with robbed and unrobbed flowers. The cheater on the mutualism between *Chilopsis tinearis* and its pollinators is *Xylocopa californica* (Apidae), a nectar-robbing carpenter bee. Future studies will address the effect of robbing and pollinator behavior on plants.

I expected that *Bombus sonoris* would avoid less-rewarding robbed flowers and *Apis mellifera* would not. Individuals of *Apis* may not have evolved the ability to identify and avoid robbed flowers of *Chilopsis,* since *Apis* was recently (by evolutionary time) Introduced into the New World tropics by settlers from Europe (Michener 1979). The historical distribution of *A. mellifera* does not overlap with the distribution of *Chilopsis linearis* (throughout the Southwestern U.S. and northern Mexico, Kearney and Peebles 1960), although the distribution of P. *sonoris* does.

METHODS

Chilopsis linearis blooms profusely for a few weeks in the Ucornucopia" phenology described by Gentry (1974). it produces sympetalous, trumpet-shaped flowers that are visited primarily by bees, but also by hummingbirds and butterflies at the study site. Nectar is produced as flowers open in the late afternoon and again in the early morning (Brown et al. 1981 and Richardson, unpubl. data). The 2-5 m tall trees grow along normally dry washes in the Southwestern U.S. and northern Mexico.

I observed floral visitors to *Chilopsis linearis* during the flowering season from May 20-June 7, 1993 and May 12-May 31, 1994. About 28 trees were located in a dry wash near the Chiricahua Mountains, 5.6 mi. N. of Portal on the San Simon Road, Cochise Co., Arizona. Common plants in the surrounding desert scrub are mesquite *(Prosopis sp.), Acacia Greggii,* and creosote-bush *(Larrea tridentata).*

Patches of flowers on a single tree that varied in size from 16 to 207 flowers were marked before each observation period. All flowers within viewing distance were marked with colored thread to distinguish robbed flowers from unrobbed flowers. Visitors to the plants were observed in 19 half-hour observation periods at nine trees in 1993. The identity of visitors and number of marked robbed or unrobbed flowers visited by each individual within the patch were recorded in 1993. In 1994, numbers of visitors at seven trees were counted during four half-hour observation periods, 3.5 hours of general observations, and four hours of observations during other experiments. Observation periods were conducted at different times of the day over both years, but were concentrated from 6:00 a.m to 11:00 a.m., when rates of visitation to plants were highest.

The frequency of visitation to unrobbed and robbed flowers by individual visitors was determined by counting the number of marked unrobbed and robbed flowers visited during a foraging bout. The numbers of unrobbed and robbed flowers visited were compared with the numbers of unrobbed and robbed flowers available within the marked patch. Using a sign test, the number of unrobbed flowers visited by an individual pollinator was compared with the expected number that would have been visited if the pollinator were choosing flowers within the patch randomly. I assumed that if pollinators were neither avoiding nor choosing robbed flowers, the proportion of visits to unrobbed flowers during a foraging bout would be the same as the proportion available in a patch. Differences between *Apis* and *Bombus* in number of individuals that chose more unrobbed flowers than robbed flowers were analyzed using a Mann-Whitney U test.

RESULTS

Relative abundances of visitors to *Chilopsis IJnearis* are shown in Table 1. In both years, the total number of visitors observed was similar and the number of observation hours was equal, so the overall abundance of visitors was similar in 1993 and 1994. The greatest change in relative abundance was a decrease in *Apis mellifera* from 51.2% of the visitors to flowers in 1993 to 9.1% in 1994. Visits by *Xylocopa californica* increased from

12.5% in 1993 to 41.8% in 1994. The relative abundance of *Bombus sonoris* at flowers increased from 8.3% in 1993 to 30.0% in 1994.

Coefficients of variation shown in Table 1 indicate the variation in abundance of each species over 1993 and 1994. The three most frequent visitors, *Apis, Bombus,* and *Xylocopa,* were more variable between years than the two least frequent groups of visitors, which were hummingbirds and several bee species in the family Anthophoridae. However, bees in the family Megachilidae were the most variable between years, since none was observed at the study site in 1994.

The percentage of unrobbed flowers available during observation periods ranged from 3.9% to 92.2% in 1993. *Apis* visited significantly more unrobbed flowers than expected during each foraging bout (sign test: C = 10, P 0.002, N = 33). in contrast, the number of visits to unrobbed flowers by *Bombus* was not significantly different than the number predicted by the proportion of unrobbed flowers available (sign test: C = 0, P 0.50, N = 7). *Apis* visited more unrobbed flowers than *Bombus* did (Mann-Whitney U test: U = 192.5, P 0.005, Nr s 33, N2 = 7): in observations during 1993, 87.9% of *Apis* individuals visited more unrobbed than robbed flowers within a foraging bout, as compared with 42.7% of *Bombus* (fig. 2).

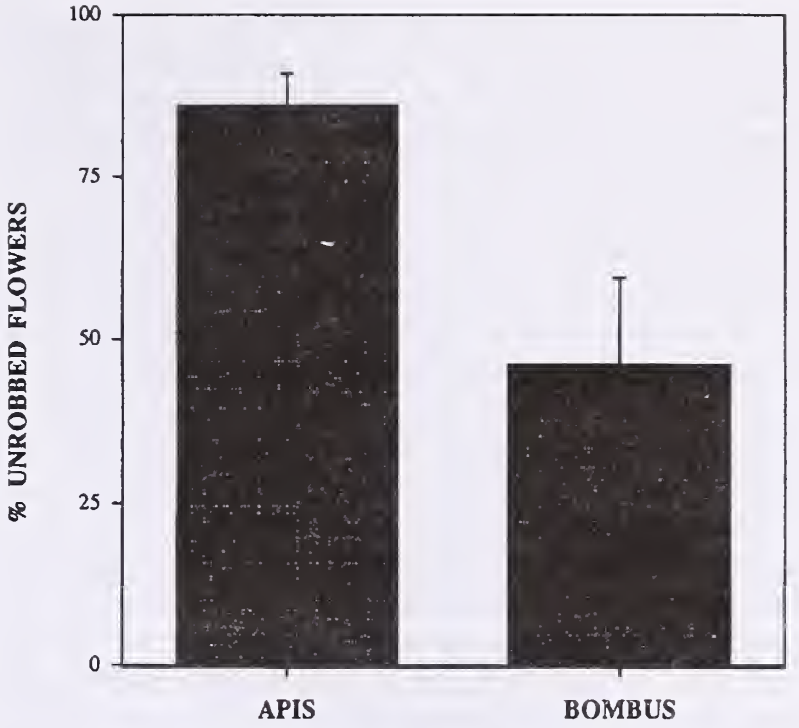

Figure 2.—Visits to unrobbed flowers in a foraging bout (mean t 1 SE, n = 33 for *Apis*, 7 for *Bombvs*)

DISCUSSION

The numbers of individual *Bombus sonoris* visiting C. *linearis* increased from 1993 to 1994 at the same time as visits by *Apis mellifera* decreased. Visits by *Xylocopa californica,* nectar-robbing bees, to plants also declined from 1993 to 1994. In general, more common visitors varied more in abundances between years than did the least common visitors, with the exception of bees in the family Megachilidae. In addition to these changes in relative abundance, I found that individuals of *A. mellifera* avoid robbed flowers, while individuals of B. *sonoris* do not. These observations of behavior are opposite to my original prediction that individuals of *Apis* would not avoid robbed *Chilopsis* flowers because the species have a short evolutionary history together. Though *A. mellifera* has not come into contact with C. *linearis* until recently, its behavior in response to robbed flowers of C. *linearis* may be similar to its behavior in response to robbed flowers of Old World species. First, I will discuss the implications of variation in relative abundance of the floral visitors over time. Second, I will consider the significance of the difference between *Apis* and *Bombus* in foraging behavior in response to robbed flowers.

Table 1.—Relative Abundances of Visitors to *Chilopsis linearis* flowers (in 19 observation hours on 11 trees at one study site).

VISITOR	1993	1994	CV*
Apis mellifera	51.2%	8.3%	112%
Xylocopa California	12.5%	38.3%	53%
Bombus sonoris	8.3%	27.5%	57%
Megachilidae	7.1 %	0.0%	141 %
Anthophoridae	6.0%	10.0%	13 %
Hummingbirds	2.4%	5.0%	28%
Unknown bees	4.8%	2.5%	
Other	7.7%	8.3%	
TOTAL OBSERVATIONS	N = 168	N = 120	

*coefficient of variation

Bombus sonoris increased from 1993 to 1994 at *Chilopsis,* simultaneously with a decrease in *Apis mellifera*. Several workers have hypothesized that the honeybee, *Apis mellifera,* has a negative impact on the abundance of native pollinators by outcompeting them for food (Schaffer et al. 1979, Wolda and Roubik 1986, Roubik 1983). However, in one study, Roubik (1983) found no competition for food measured by brood production between *Apis mellifera* and native *Melipona* after introduction of *Apis* into French Guiana in 1982. Since competition was measured early after the introduction, it may have been too soon to see an effect of the introduction. My data are consistent with the hypothesis that *Apis* competes with native pollinators. However, the reciprocal changes in relative abundance of *Apis* and *Bombus* could be caused by another factor, such as a difference in precipitation between 1993 and 1994 that affected *Apis* and native visitors differently.

Interestingly, high variation in numbers of common visitors to *Chilopsis linearis* conflicts with results reported from other bees in the tropics. Roubik and Ackerman (1987) found that relatively scarce euglossine bees collected from traps at three sites in Panama had more variable populations than more abundant bees did. In the present study, however, the most abundant bees were most variable between years. Differences may be caused by differences in stability of species' population sizes between the tropics and temperate zone or by differences in sampling methods. Perhaps the most abundant species are the fastest to switch to a more productive nectar producer as the season progresses. However, *Chilopsis* appeared to be the only abundant source of nectar in the area during the present study until *Yucca elata* bloomed in mid-June. Correlations between species abundance and speed of resource switching would not be observed by trapping bees (as in the Panamanian study) because resource switching by bees would not affect the likelihood of collection.

Xylocopa californica, the nectar-robbing bee, also changed in relative abundance over the two years of this study. Although more *Xylocopa californica* individuals were observed at plants during observation periods in 1994 than in 1993, many of their foraging bouts were very brief. In 1994, *Xylocopa* often robbed just one or two flowers at the top of a tree while flying across the wash, instead of carrying out the sustained foraging bouts observed in 1993. A possible explanation for this change in behavior is that nest provisioning in 1993 occurred much earlier than in 1994. In 1994, provisioning of nearby nests coincided with the *Chilopsis* flowering season (unpubl. data). To provision nests, a female *Xylocopa* collects nectar and pollen, and shapes it into a ball. she places the ball of provisions in a tunnel inside a hollowed-out yucca or agave stalk. Before sealing the ball of provions in the tunnel, she lays an egg on it. In 1994, female X. *califomica* may have been concentrating foraging efforts on provisioning nestswith pollen from nearby pollen-producing acacia and mesquite, instead of collecting nectar from *Chilopsis*. Even though more X. *califoMica* were observed in 1994 than in 1993, fewer flowers on the trees were robbed (unpubl. data).

In addition to changing reciprocally in abundance, *Apis* avoided robbed flowers during foraging bouts within a plant more than *Bombus sonoris* did. A previous study with conflicting results has been conducted on foraging behavior by *Bombus Pagans* in response to robbed flowers. *B. vagans* departs from patches of *Impatiens capensis* with artificially robbed flowers using a wider angle of flight than from unrobbed patches (Zimmerman and Cook 1985). Measurement of angle of flight after leaving a patch is an indicator of floral visitors' avoidance of similar patches; a wide angle suggests that a bee is leaving the area in search of patches that are different from the one just visited. Three possible explanations for the discrepancy between studies exist. 1) *Bombus sonoris* may simply behave differently than *Bombus vagans. 2)* Avoidance of a patch of robbed flowers involves a different level of decision-making for bees than avoidance of robbed flowers within a patch. 3) *B. sonoris is* restricted to robbed flowers at *Chilopsis* because of competition with *A. mellifera,* whereas pollinators visiting *Impatiens* did not partition resources because *A. meltifera was* not *a* frequent visitor.

Resource partitioning (the third possibility) may occur if *Bombus sonoris* visits robbed flowers because *Apis* cannot obtain the nectar remaining after a visit by nectarrobbing bees, leaving the nectar available to *B. sonoris.* Brown et al. (1981) observed that peak foraging by *B. sonoris* on *Chilopsis linearis* occurred later in the day than the peak of foraging by *Apis mellifera.* Whitham (1977) showed that some of the nectar in *Chilopsis is* contained in deep grooves in the corolla. As a result, Brown et al. (1981) hypothesized that *Apis* cannot reach the nectar in the grooves, whereas *Bombus* can. Brown et al. (1981) suggested that this difference between *Apis* and *B. sonoris* might explain the fact that foraging by *Bombus* peaks later in the day than does that of *Apis.* For the same reason, *Apis* may avoid robbed flowers because they are not able to reach nectar in grooves of flowers.

Several alternative explanations remain for the difference between *Apis* and *Bombus* in the degree to which they avoid robbed flowers. These explanations are not mutually exclusive; one or more may be valid. *First,Apis mellifera* have greater metabolic requirements than *Bombus,* such that for *Bombus,* but not *Apis,* a visit to a robbed flower may supply enough nectar to be worth the visit. At rest at 25□C, a *Bombus vosnesenskii* queen consumes less than 10 ml/g/hr oxygen (Heinrich 1979). In contrast, individuals of

Apis mellifera use more oxygen, about 15 ml/g/hr oxygen at 25□C (Moritz and Southwick 1992). Individuals of *Apis* expend more metabolic energy than those of *B. vosnesenskii up* to about 30□C (Heinrich 1979, Moritz and Southwick 1992). *Apis'* metabolic costs during early morning foraging should be greater than that of *Bombus sonoris* (assuming that *Bombus sonoris* has a metabolism similar to *B. vosnesenskil),* since the peak of foraging by individuals of *Apis mellifera* at *Chilopsis linearis* occurs in the morning, before the temperature reaches 30□C (Brown et al. 1981, and unpubl. data).

Apis may also avoid robbed flowers more readily than *Bombus* because they can sense marking scents that *Xylocopa califomica,* the nectar-robbing bees, leave behind. *X. californica* avoids revisiting some robbed flowers in the greenhouse and in the field (unpubl. data). A related bee, *Xylocopa virginica,* avoids revisiting *Passiflora incarnata* flowers that it pollinates, possibly because females use scent marks to avoid revisiting flowers (Frankie and Vinson 1977). Only marking behavior on legitimate pollinating visits by X. *virginica* has been researched, but *Xylocopa californica* may use scentmarking to avoid revisiting robbed flowers as well. Other research indicates that two species of pollinators in the present study, *Apis mellifera* and *Bombus sonoris,* avoid flowers marked by other individuals within their own species. *A. mellifera* has been shown to avoid flowers scent-marked by other individuals in the same species (Giurfa and Nuflez1992). it has also been suggested that *B. sonoris* avoids scent-marked flowers (Schmitt and Bertsch 1990). in all three cases, the identity of the chemical marking is unknown and the effects of marking on individuals of other species is also unknown. However, as suggested above, it is possible that *Apis mellifera* can sense the mark left behind from a robbing visit by X. *californica* and chooses not to visit, while *B. sonoris* cannot.

Finally, *Apis* may avoid robbed flowers while *Bombus* do not because *Bombus* have lower or slower learning abilities. Several studies have investigated aspects of the learning abilities of *Apis* and *Bombus* separately (e. 9., Dyer 1991, Collett et al. 1993, Greggers and Menzel 1993, Gould 1993, Dukas and Real 1993), but none has yet compared them directly on the same tasks. Duffield et al. (1993) have found that workers of *Apis* discriminate between flowers based on morphology (inflorescence length and number of bracts). One could test whether *Apis* learn to prefer flowers based on morphology or markings more quickly than *Bombus* do.

Whatever the reason for the difference in *Apis* and *Bombus* behavior in response to robbed flowers, that difference may cause the effect of robbing on *Chilopsis linearis* to vary as relative abundances of visitors change. The effect of robbing also depends on the pollination efficiency of the pollinators, the prevalence of robbing, the level of selfcompatibility of *C. Iinearis* and the amount of damage done to a flower during a robbing visit, all of which are being currently investigated. For example, if *Apis* is the least efficient pollinator, taking the reward provided by the plant without providing a reciprocal pollination benefit, the effect of robbing may be positive in years in which *Apis* is common. Willmer et al. (1994) have found that several species of *Bombus* transfer more pollen between *Rubus idaeus* flowers than *Apis* does, but the results may not apply directly to this study because *Chilopsis* flowers are shaped differently than *Rubus* flowers. If *Bombus* is more effective than *Apis* in pollinating *Chilopsis*, the effect of robbing may not be significant when *Bombus* predominates, because *Bombus* do not avoid robbed flowers. When pollinators vary in behavior and abundance, the overall effect of cheaters on the evolution of mutualisms may vary over time.

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Phylogeny and Biogeography of the Land Snail, *Sonorella*, in the Madrean Archipelago

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Abstract.—The Talus Snail, *Sonorella*, includes 79 species and inhabits the Madrean Archipelago and adjacent regions. A phylogenetic analysis of these species, and 5 related genera allow not only an understanding of their relationships, but of the biogeography of the genus as well. Traditional subgenera and species complexes prove to have little relationship to phylogeny. *S. eremita* is probably a junior synonym of *S. papagorum*. *Sonorella*'s ancestors probably derive from the west, perhaps the Mohave Desert. The record of dispersal and vicariance of *Sonorella* is complex, perhaps related to the numerous glacial advances and retreats.

The mountains of the southwest have long been likened to "islands of the Oceans" (Smith, 1827, in Brooks, 1977), or cleverly "sky islands" (Heald, 1951) but no term has captured the biological significance or interest of the region as well as _Madrean Archipelago" (Lowe, 1992). The Talus Snail, *Sonorella,* perhaps best symbolizes this archipelago, as it occurs from the Madrean mainland through both the Madrean and Petran subdivisions. In addition, *Sonorella* ranges from the Lower Colorado Desert to Fir Forest but is limited in this era to the mountain islands and does not occur in the desert and grassland seas.

As presently understood, *Sonorella* consists of 79 species and numerous subspecies. The high diversity is undoubtably due to repeated episodes of vicariance or dispersal (or both) and isolation on their sky islands. This diversity makes *Sonorella* more than just a fit symbol for the Madrean Archipelago. It provides an excellent subject for studies in evolution, speciation, and biogeography.

One prior attempt to reconstruct the phylogeny of *Sonorella* has been made (Miller, 1967a). This phylogeny was in some respects superior in methodology to the one presented here, in allowing a persistent or known ancestor. This assumption permits a more parsimonious arrangement of taxa and, potentially, better character polarity assessment than cladistic methods. The phylogeny presented here is superior to the previous attempt in: 1) expressly stating characters and assumptions employed in its construction; 2) distinguishing primitive from derived characters and phyletically uniting taxa employing only derived characters; and 3) including species not previously known for the genus.

Basic biogeography may be accomplished by comparing taxa in common between two or more areas. A more complete understanding of the biogeography of a taxon or a region is possible only with an understanding of phylogeny. Phylogeny permits us, in effect, to compare taxa in common through time and, thereby, to understand relationships between areas through time. The phylogeny presented here should be regarded as preliminary, made with too many species and too few characters, but it is only through this and future efforts that we can understand how *Sonorella* dispersed though the Madrean Archipeligo and, ultimately, to understand our sky islands.

CHARACTER ANALYSIS

Taxa thought to be related to *Sonorella* have included: *Eremarionta* (Miller, 1973; Hoffman, 1993); *Greggelix* (Miller, 1972; Richardson, 1982); *Mohavelix* (Berry, 1943; Richardson, 1982); *Sonorelix* (Berry, 1943; Miller, 1967a; Richardson, 1982); and, *Tryonigens* (Miller, 1967a; Richardson, 1982). Taxa specifically thought to be ancestral to or sister-groups to *Sonorella* include: *Eremarionta* (Miller, 1973; Hoffman, 1993); *Sonorelix* (Miller,

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1967); and, *Tryonigens* (Miller, 1967). Due to some ambiguity as to whether the various taxa are in-groups or out-groups in respect to *Sonorella*, all were included in this analysis. Because of this same ambiguity, a hypothetical ancestor was constructed employing only characters generally recognized as being primitive for the Family. This ancestor assured correct character polarity assessment and correct positioning of *Sonorella*'s various relatives.

Character states for *Sonorella* relatives were determined by the literature. Taxa include: *Eremarionta* (Pilsbry, 1939); *Greggelix* (Miller, 1972); *Mohavelix* (Berry, 1943; Miller, 1970); *Sonorelix* (Berry, 1943; Gregg, 1948; Miller, 1972); and, *Tryonigens* (Tryon, 1863; Pilsbry, 1927; Solem, 1959; Miller, 1971). Character states for *Sonorella* were determined by personal observation or from species descriptions (Berry, 1948; Christensen and Reeder, 1981; Fairbanks and Reeder, 1980; Gregg, 1951; Gregg and Miller, 1969, 1974; Miller, 1966, 1967a, 1967b, 1967c, 1967d, 1968, 1976; Naranjo-Garcia 1988b, 1988c, 1989; Naranjo-Garcia and Miller, 1986; Pilbry, 1939, 1948). Character states were coded as "?" or unknown for two reasons. The first was simply ignorance of the author. The second is when the character was non-applicable, for example: "grooves on verge" when no verge is present on that form.

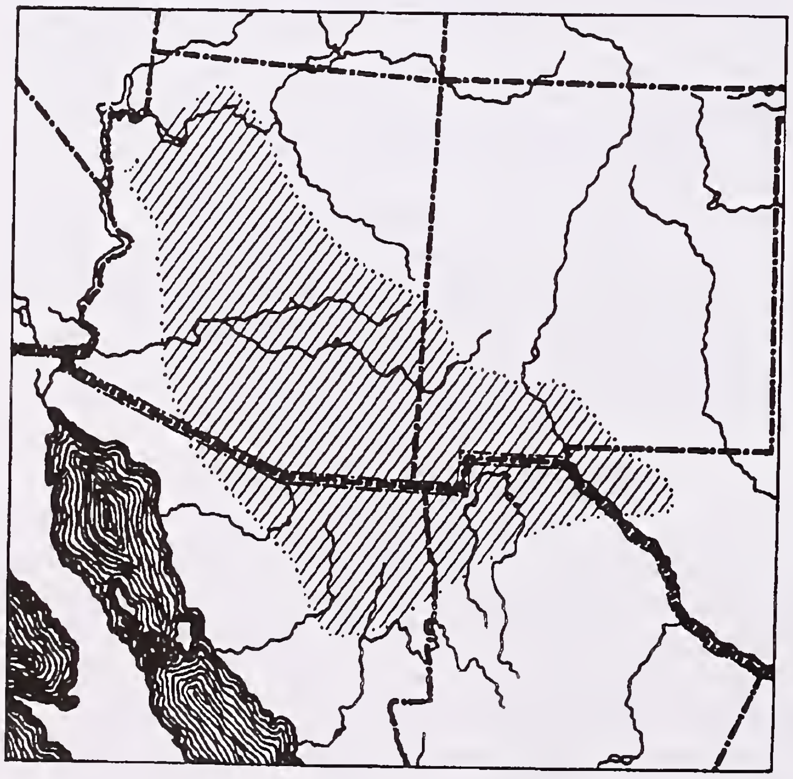

Figure 1.—Distribution of *Sonorella*. Adapted from Maranjo-Garcia, 1988a.

Reproductive Characters:

1. Dart sac - Present (0); absent (1). There is concensus that presence of a dart sac is primitive in Xanthonychidae (Miller, 1971; Bequaert and Miller, 1973; Nordsieck, 1987). For this reason, presence of dart sac is employed in the hypothetical ancestor.
2. Mucus glands - Present (0); absent(1). The presence of the mucus glands are considered to be primitive in the Family (Miller, 1971; Bequaert and Miller, 1973; Schileyko, 1979; Nordsieck, 1987) and is so employed in the hypothetical ancestor.
3. Spermathecal diverticulum - Present (0); absent (1). A spermathecal diverticulum is considered to be primitive in the Family (Miller, 1971) and is employed in the hypothetical ancestor.
4. Penis length/vagina length - Penis length less than vagina length (0); penis length at least as great as vagina length, but less than twice vagina length (1); penis length twice or more the length of the vagina (2). Coding is based on population means. As the species in this analysis are hermathrodidic, both measurements may be made from one individual.
5. Verge length/penis length - Verge minimal or absent (0); verge less than one half of the penis length (1); verge greater than one half the penis length (2). This character was coded as ordered. Values based on population means.
6. Penial retractor insertion - Penial retractor inserts on epiphallus (0); penial retractor inserts on the extreme distal portion of the epiphallus or the apex of the penis (1); penial retractor inserts on penis (2). This character was coded as ordered.
7. Epiphallus length/penis length - Epiphallus less than penis length (0); epiphallus at least as long as penis, but not as much as twice as long (1); epiphallus twice or more the length of the penis. Value based on population means.
8. Penial sheath/penis length - Penial sheath one half or less the length of the penis (0); more than one half, but less than equal to the length of the penis (1); equal to or greater the length of the penis (2). The character was coded as ordered and was based on population means.
9. Penis length/shell maximum diameter - Penis less than the maximum shell diameter (0); penis equal to or greater than maximum shell diameter (1). Value based on population means.
10. Verge shape - Verge slender and narrow (0); verge club-shaped and wrinkled (1); verge thick and bluntly rounded (2); verge thick, wrinkled, and truncated (3); verge spherical (4); verge

spindle-shaped (5). Character states were unordered.

11. Verge with glandiform tip - Glandiform tip absent (0); present (1).
12. Verge with spiral grooves - Spiral grooves on verge absent (0); present (1).

Shell Characters:

13. Mean maximum shell diameter - Shell maximum diameter less than 15mm (0); shell maximum diameter at least 15mm, but not 25mm (1); shell maximum diameter equal to or greater than 25mm. Values based on population mean. Character states were ordered.
14. Periostracum - Periostracum is smooth and silky lustrous (0); periostracum is granulose (1).

Ecological Characters:

15. Precipitation - Precipitation was ranked from lowest to highest as follows: Lower Colorado, Central Gulf Coast, Mohave and Great Basin (1); Chihuahuan Desertscrub, Arizona Uplands, Plains of Sonora and Viscaino (2); Thornscrub, Semidesert Grassland, Pinyon-Juniper and Chaparral (3); Madrean Woodland, Pine Forest, Spruce Forest, Fir Forest and Short Tree Forest (4). Character states were ordered.
16. Temperature - Temperature was ranked from hottest to coldest as follows: Thornscrub and Short Tree Forest (1); all subdivisions of the Sonoran Desert, Chihuahuan Desertscrub, Mohave Desertscrub, and Semidesert Grassland (2); Madrean Woodland, Great Basin, Pinyon-Juniper and Chaparral (3); Pine, Spruce, and Fir Forest (4). Character states were ordered. Note that rank classes are similar, but not identical to Merriam Life Zones (Lowe, 1964).

Other Characters:

17. Haploid chromosome number - Haploid chromosome number 29 (0); 30 (1). A haploid number of 29 is thought to be primitive in Xanthonychidae (Babrakzai, 1975) and is so employed in the hypothetical ancestor.
18. Mantle collar mucus - Mantle collar mucus is white (0); orange (1).

PHYLOGENETIC ANALYSIS

The data were analysed using PAUP, version 3.0q (Swofford, 1990). Due to the large number of taxa in this analysis, exhaustive or branch-and-bound algorithms were not feasible. Instead, heuristic branch swapping with the tree bisection-reconnection (TBR) option and MAXTREE=600 was used. Trees obtained in this fashion are not guaranteed to be the shortest possible. MacClade, version 3.0 (Maddison and Maddison, 1992) was used to edit the character matrix and manipulate trees.

RESULTS

Over 600 equally parsimonous trees with a tree length of 146 were generated. A strict concensus tree of the retained trees showed almost no resolution. A 50% concensus tree (Figure 2) shows almost complete resolution. The concensus of most nodes on this tree exceeds 85%. Consistancy index (CI) for this tree is 0.43 and retention index (RI) for this tree is 0.75.

DISCUSSION

All indications are that it is extremely unlikely that the tree presented here represents the true phylogeny of *Sonorella* - especially in every detail. Nevertheless, broad patterns revealed by the tree may be discussed with reasonable confidence.

The positions of the related genera offer a few suprises and at least one artifact of the data matrix. *Eremarionta, Sonorelix,* and *Greggelix* all prove to be out-groups, as expected, and all suggest a systematic reduction of reproductive structures in the group. This is contra the concept that the reduction had multiple, independent origins (Miller, 1973; Hoffman, 1993). The clade, ((((*Tryonigens, S. burgessi*), ((*S. pratti, S. seri*), *Mohavelix*)), *S. rothi*), *S. waltoni*), is almost certainly largely an artifact of missing data. All of the species of *Sonorella* in this clade have a large number of unknown (to the author) characters. The algorithm attempts to obtain a most parsimonious solution for these taxa, which is, of course, one that minimizes homoplasy. Paradoxily, *Sonorella* as a rule, exhibits a great deal of homoplasy. The result is that taxa with missing data are artifically united at or near the base of the *Sonorella* tree. Conversely, we can not discount that *Tryonigens* and *Mohavelix* may represent de-

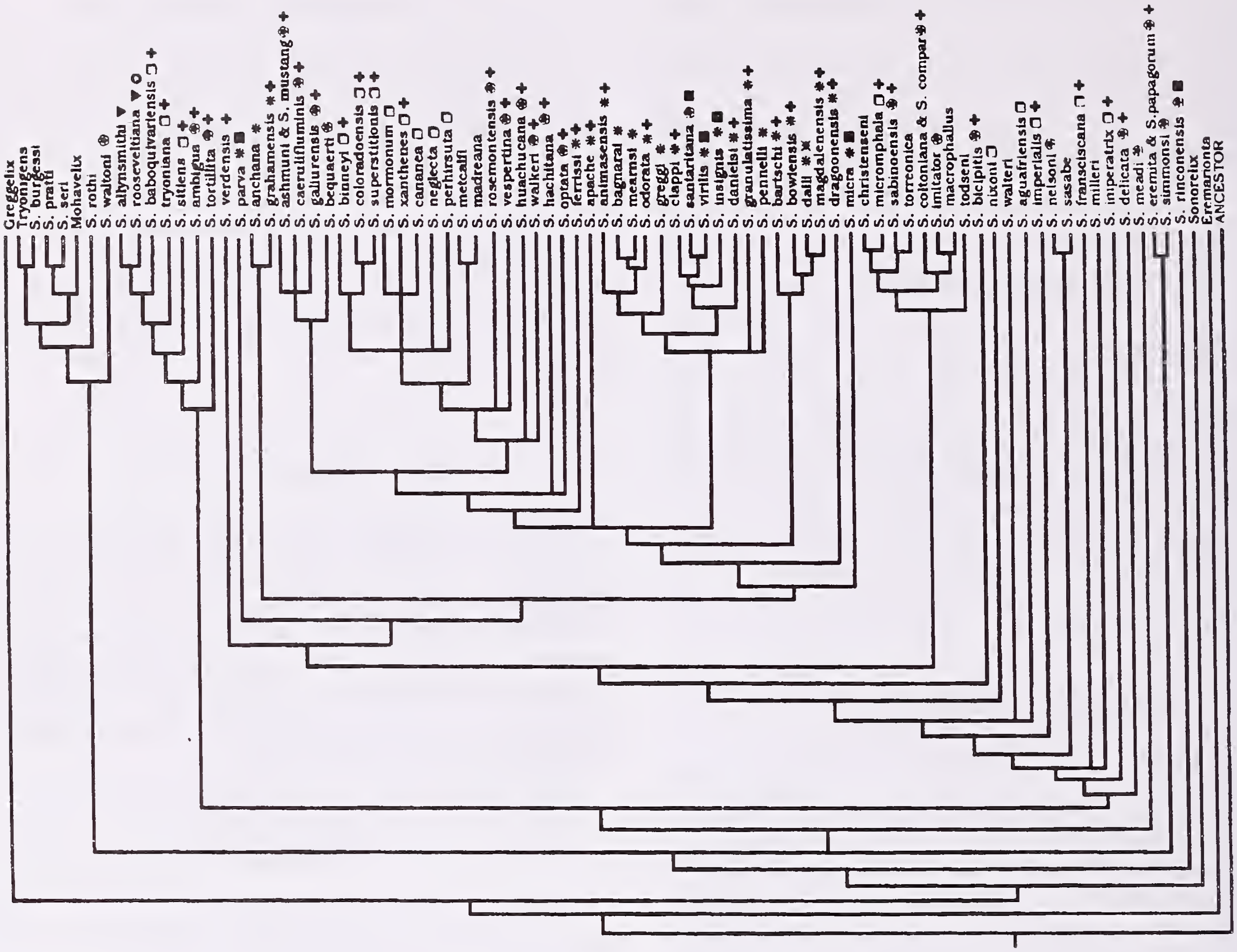

Fig. 2. 50% concensus tree for *Sonorella*. +=*Sonorella*, ■=*Masculus*, ✳=*Sonoranax*, ○=*Myotophallus*(Pilsbry,1939). ⊛=*S.hachitana* Complex, □=*S.binneyi* Complex, ✻=*S.granulatissima* Complex, ▼=*S.rooseveltiana* Complex(Bequaert and Miller,1973).

scendents of *Sonorella*. *Mohavelix* was originally described as a subgenus of *Sonorella* (Berry, 1943; contra Miller, 1973). On the other hand, *Tryonigens* has been viewed as an out-group (Miller, 1967a; contra Miller, 1973). Although phenetically different and geographically remote, no derived traits remove this genus from *Sonorella*.

The previously proposed subgenera (Pilbry, 1939) and species complexes (Bequaert and Miller, 1973) appear to be largely aphyletic. The *S. rooseveltiana* complex (Bequaert and Miller, 1973) appears to be holophyletic, but the utility of uniting two species among 79 is little. The *S. granulatissima* complex (Bequaert and Miller, 1973) appears to be largely paraphyletic, and it is possible that with more or better characters it also may prove to be holophyletic. This species complex might be retained for convenience, pending better analysis. The remaining species complexes and subgenera appear to be remarkably polyphyletic, or uninformably monotypic. The artifical nature of the subgenera and species complexes has been noted before (Richardson, 1982).

An unexpected (for the author) result of this analysis is the close relationship between *S. eremita* (federally listed, catagory 1) and *S. papagorum*. As coded in the character analysis, these species are identical. Detailed examination of the situation indicates that *S. eremita* differs from *S. papagorum* largely in smaller overall size. This, coupled with their close geographic proximity, suggests that *S. eremita* is , *at best*, a subspecies of *S. papagorum* (by page priority).

The intent of this paper was originally to reconstruct the phylogeny of *Sonorella* in order to reconstruct the biogeographic history of the genus. As is so often the case, our picture of the Talus Snails' history is complex, but certain broad patterns emerge. It is probable that *Sonorella's* ancestors came from the west. *Eremarionta* and *Sonorelix* are primarily Mohave Desert forms and *Greggelix* lives in Baja. It is possible that a more tropical form, *Tryonigens,* may have derived early in *Sonorella's* history and proceeded south, a possiblity that has been noted before (Miller, 1973). This overall picture of west to south derivation is contra our general picture of a Mexican origin for the Madrean Archipeligo fauna, but is suggestive of the rich and complex history of the region.

In detail, no clear picture of the dispersal or vicariance of *Sonorella* emerges. Sister groups are often not on adjacent ranges and no north-south or east-west trend is evident. This could be due, in part, to a flawed phylogeny, but it also is likely to be representative of the true complexity of their history. In the Pleistocene alone, there may have been as many as 21 glacial advances and retreats (van Donk, 1976) which may have resulted in conditions alternately suitable for dispersal and vicariance. The probability of this involved pattern has been postulated before (Fairbanks and Reeder, 1980) albet with the here discredited species group.

The mountains of the Madrean Archipeligo in southeastern Arizona are inhabited by a snail-eating beetle in the genus *Scaphinotus* (Ball, 1966; McCleve, 1979). Throughout about half of this beetle's range, *Sonorella* is the only large snail and, presumably, an important prey item. It would be pleasant to show congruence between the phylogeny of these *Scaphinotus* (Ball, 1966) and *Sonorella,* but no close agreement exsists. Improvement in the phylogenies of both genera may yet reveal congruence between predator and prey.

CONCLUSION

Sonorella originated from ancestors to the west, perhaps from the Mohave Desert. Sister groups include *Sonorelix, Greggelix,* and *Eremarionta.* The subgenera and species complexes of previous authors have little systematic reality, however, the *S. rooseveltiana* complex is a holophyletic grouping and the *S. granulatissima* complex in part appears to be paraphyletic. Both of these complexes might be retained pending a throuough phylogenetic and systematic review of the genus. *S. eremita* and *S. papagorum* are almost certainly conspecific.

The biogeographic history of the genus appears to be extremely complex. This complexity probably reflects repeated dispersal and vicariance events throughout the Pleistocene. Further work to resolve and perfect *Sonorella's* phylogeny is merited.

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APPENDIX I. This matrix shows the distribution of the 18 characters among 85 taxa that were analyzed using the heuristic algorithm of PAUP. Characters appear in the order they are discussed in the text. Numbers represent character states; "?" denotes that the character state is unknown to the author or when the character is nonapplicable.

	Characters																	
Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
ANCESTOR	0	0	0	?	0	0	?	?	?	?	?	?	?	?	?	?	0	?
Eremarionta	0	0	0	0&1	0	0	0	?	0&1	4	?	?	0&1	?	1	2	1	?
Greggelix	1	1	0	0	1	0	2	?	0	4	0	0	1	?	2	2	0	?
Mohavelix	1	1	1	1	2	1	0	0	?	?	?	?	?	?	1	2	?	?
Sonorelix	1	1	0	0	2	0&2	0	?	0	?	?	?	1	?	1&3	2&3	0	1
Tryonigens	1	1	1	1	2	1	1	0	?	?	0	0	1	?	1&3	1&2	?	?
S. allynsmithi	1	1	1	2	0	0	0	1	0	?	?	?	0	0	2	2	?	?
S. ambigua	1	1	1	1	1	0	0	?	0	1	0	0	1	0	2&4	2&3	?	?
S. anchana	1	1	1	1	2	0	0	1	0	3	0	0	1	1	4	4	?	?
S. animasensis	1	1	1	0	2	0	1	1	0	3	1	0	1	1	4	3	?	?
S. apache	1	1	1	0	2	0	?	0	0	3	?	?	1	1	4	3	?	?
S. aguafriensis	1	1	1	1	1	0	0	0	?	2	0	0	1	?	3	1	?	?
S. ashmuni & S. mustang	1	1	1	1	2	0	0	0	?	0	0	0	2	0	4	3	?	?
S. baboquivariensis	1	1	1	1	0	0	1	1	0	2	1	0	1	0	2	2	?	0
S. bagnarai	1	1	1	0	2	0	2	2	0	?	0	0	1	1	4	4	?	1
S. bartschi	1	1	1	2	1	0	0	?	0	3	0	0	1	1	4	3	?	1
S. bequaerti	1	1	1	0	2	0	1	0	0	0	0	0	2	0	4	3	?	?
S. bicipitis	1	1	1	0	2	0	0	0	0	1	0	0	1	0	4	3	?	?
S. binneyi	1	1	1	1	1	0	1	1	?	2	1	0	1	0	4	3	?	?
S. bowiensis	1	1	1	1	1	0	1	0	0	3	0	0	1	1	4	3	?	1
S. burgessi	1	1	1	1	2	0	1	0	0	?	?	0	1	0	1	2	?	?
S. caerulifluminis	1	1	1	0	2	0	0	0	?	0	0	0	2	0	4	3	?	?
S. cananea	1	1	1	1	2	0	1	1	0	2	0	0	0	?	4	3	?	?
S. christenseni	1	1	1	1	2	0	0	1	0	0	0	0	1	?	4	4	?	?
S. clappi	1	1	1	1	2	0	1	0	?	0	0	0	1	1	4	3&4	?	?
S. coloradoensis	1	1	1	1	1	0	1	1	?	2	0	0	1	0	1	3	?	?
S. coltoniana & S.compar	1	1	1	1	2	0	0	0	0	0	0	0	1	0	4	4	?	?
S. dalli	1	1	1	1	1	0	1	0	1	3	0	0	1	1	4	3&4	?	0
S. danielsi	1	1	1	1	2	0	1	0	0	3	0	0	1	1	4	4	?	?
S. delicata	1	1	1	0	1	0	1	1	0	0	0	0	1	0	2	2	?	?
S. dragoonensis	1	1	1	1	2	0	0	0	0	3	0	0	1	1	4	3	?	?
S. eremita&S.papagorum	1	1	1	0	2	0	1	0	0	0	0	0	1	0	2	2	?	?
S. fersissi	1	1	1	0	2	0	0	0	0	0	0	0	1	1	4	3	?	?
S. frenciscana	1	1	1	0	1	0	1	0	?	2	0	0	1	0	2	2	?	?
S. galiurensis	1	1	1	0	2	0	0	0	0	0	0	0	2	0	4	3	?	?
S. grahamensis	1	1	1	1	2	0	0	0	0	5	0	0	1	1	4	4	?	0
S. granulatissima	1	1	1	0	2	0	0	0	0	3	0	0	1	1	4	4	?	?
S. greggi	1	1	1	0	2	0	1	0	0	3	0	1	1	1	4	3&4	?	?
S. hachitana	1	1	1	0	2	0	0	0	?	0	0	0	1	0	4	3	?	?
S. huachucana	1	1	1	0	2	0	1	0	0	0	0	0	1	0	4	2&3	?	1
S. imitator	1	1	1	1	2	0	0	0	1	2	0	0	1	0	4	4	?	?

Appendix 1, continued...

Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
S. imperatrix	1	1	1	0	1	0	1	1	0	2	0	0	1	0	2	2	?	?
S. imperialis	1	1	1	0	1	0	0	0	0	2	0	0	1	0	2	2	?	?
S. insignis	1	1	1	1	2	0	1	?	?	?	?	0	1	1	?	?	?	?
S. macrophallus	1	1	1	1	2	0	0	0	0	2	1	0	1	?	4	4	?	?
S. madreana	1	1	1	1	2	0	1	1	0	?	?	0	1	?	3	2	?	?
S. magdalenensis	1	1	1	1	1	0	1	0	0	3	0	1	1	1	2&3&4	1&2&3	?	0
S. meadi	1	1	1	0	2	0	0	1	0	0	0	0	1	0	2	2	?	1
S. mearnsi	1	1	1	0	0	0	2	1	?	?	?	?	?	1	4	3&4	?	1
S. metcalfi	1	1	1	1	2	0	1	1	0	0	0	0	1	0	3	2	?	?
S. micra	1	1	1	1	2	0	0	0	1	3	0	0	1	1	4	3	?	?
S. micromphala	1	1	1	1	2	0	1	1	?	0	0	0	1	0	4	4	?	0
S. milleri	1	1	1	1	1	0	1	0	0	?	?	?	1	1	2	2	?	?
S. mormonum	1	1	1	0	2	0	1	1	0	2	0	0	0	0	4	3	?	?
S. neglecta	1	1	1	1	2	0	1	1	?	2	0	0	1	0	4	3	?	?
S. nelsoni	1	1	1	?	?	0	?	?	?	?	?	?	?	0	3	2	?	?
S. nixoni	1	1	1	0	1	0	0	0	1	2	0	0	1	0	4	3	?	?
S. odorata	1	1	1	0	2	0	1	1	0	1	0	0	1	1	4	4	0	?
S. optata	1	1	1	0	2	0	0	0	0	0	0	0	1	0	4	3	?	?
S. parva	1	1	1	1	2	0	0	0	?	?	0	0	1	1	4	3	?	0
S. pennelli	1	1	1	0	1	0	0	0	0	3	0	0	1	1	4	4	?	?
S. perhirsuta	1	1	1	1	2	0	1	1	0	2	0	0	1	?	4	3	?	?
S. pratti	1	1	1	1	2	0	0	0	1	2	0	0	1	?	1	2	?	?
S. rinconensis	1	1	1	0	2	0	0	0	1	0	0	0	1	0	2	2	?	?
S. rooseveltiana	1	1	1	?	0	0	?	?	?	?	?	?	1	0	2	2	?	?
S. rosemontensis	1	1	1	0	1	0	1	1	0	0	0	0	1	0	4	3	?	1
S. rothi	1	1	1	1	2	0	0	0	0	0	0	0	1	?	1	2	?	?
S. sabinoensis	1	1	1	1	2	0	0	1	0	0	0	0	1	0	2&4	3	1	?
S. sasabe	1	1	1	0	1	0	1	0	0	?	?	0	1	?	3	2	?	?
S. santaritana	1	1	1	1	1	0	1	0	1	0	0	0	1	0	4	4	?	?
S. seri	1	1	1	1	2	0	0	0	1	?	?	0	1	0	1	2	?	?
S. simmonsi	1	1	1	0	2	0	1	0	0	1	0	0	1	0	2	2	1	?
S. sitiens	1	1	1	1	1	0	0	1	0	2	0	0	1	0	2&4	2&4	?	?
S. superstitionis	1	1	1	1	1	0	1	1	?	2	0	0	1	0	3	5	?	?
S. todseni	1	1	1	1	2	0	0	0	0	0	0	0	1	0	4	3	?	?
S. torreonica	1	1	1	1	2	0	0	1	0	?	?	0	1	?	4	3	?	?
S. tortillita	1	1	1	1	1	0	0	1	0	0	0	0	2	0	2	2	?	?
S. tryoniana	1	1	1	1	1	0	0	1	?	2	1	0	1	0	2	2	?	?
S. verdensis	1	1	1	1	2	0	0	0	0	1	0	0	2	1	?	?	?	?
S. vespertina	1	1	1	0	2	0	1	2	0	0	0	0	1	0	4	3	?	?
S. virilis	1	1	1	1	2	0	0	0	1	?	0	0	1	1	4	4	1	1
S. walteri	1	1	1	0	1	0	0	0	0	?	?	0	1	?	3	2	?	?
S. waltoni	1	1	1	1	2	0	0	0	0	?	?	?	1	0	2	2	?	?
S. walkeri	1	1	1	0	2	0	1	0	0	0	0	0	1	0	4	3&4	?	1
S. xanthenes	1	1	1	2	2	0	1	1	0	2	1	0	0	0	4	3	?	?

Helminths of Yarrow's Spiny Lizard in the Madrean Archipelago

Stephen R. Goldberg[1], Charles R. Bursey[2], and Robert L. Bezy[3]

Abstract.—Eight isolated montane populations of Yarrow's spiny lizard, *Sceloporus jarrovii*, in Arizona and New Mexico harbored a total of seven species of helminths. For each lizard population, the species composition of the helminth communities differed, except for the Santa Ritas and the Grahams. Examination of species composition of the helminth communities did not yield a geographically coherent pattern. There is a strong west to east increase in the abundance of heteroxenous (multiple host life cycle) nematodes relative to monoxenous (direct life cycle) nematodes.

The Sierra Madre Occidental of Mexico supports a distinctive and diverse assemblage of amphibians and reptiles (McCranie and Wilson, 1987; Webb, 1984). Of the ca 25 species of the Madrean herpetofauna that reach the northern outliers of the range in the southwestern United States, Yarrow's spiny lizard, *Sceloporus jarrovii* is one of the most abundant and widespread. It is found in a dozen isolated mountain ranges in southern Arizona and New Mexico (Lowe, 1964; Stebbins, 1985) from the Quinlans and Baboquivaris on the west to the Hatchets on the east, extending north to the Grahams, but (like most Madrean reptiles) not to the Rincons and Santa Catalinas. Elsewhere we have reported in greater detail on the helminth communities found in the isolated populations of this lizard (Bursey and Goldberg, 1991a, 1991b, 1992, 1994; Goldberg and Bursey, 1990, 1992); here, we focus on aspects of these communities relevant to biogeography of the Madrean Archipelago. We thank Michael E. Douglas (Arizona State University, Tempe Arizona) and Howard L. Snell (Museum of Southwestern Biology, University of New Mexico, Albuquerque, New Mexico) for allowing us to examine Yarrow's spiny lizards from their institutions and Peggy Firth for figure 1. Collecting in Arizona was by permission of the Arizona Game and Fish Department.

METHODS

A total of 302 specimens of Yarrow's spiny lizards were examined from eight montane populations (Quinlan, Santa Rita, Huachuca, Dragoon, Chiricahua, Graham, Peloncillo, and Animas; fig. 1). The samples collected for the study were augmented by material from museum collections (Appendix 1). The gastrointestinal

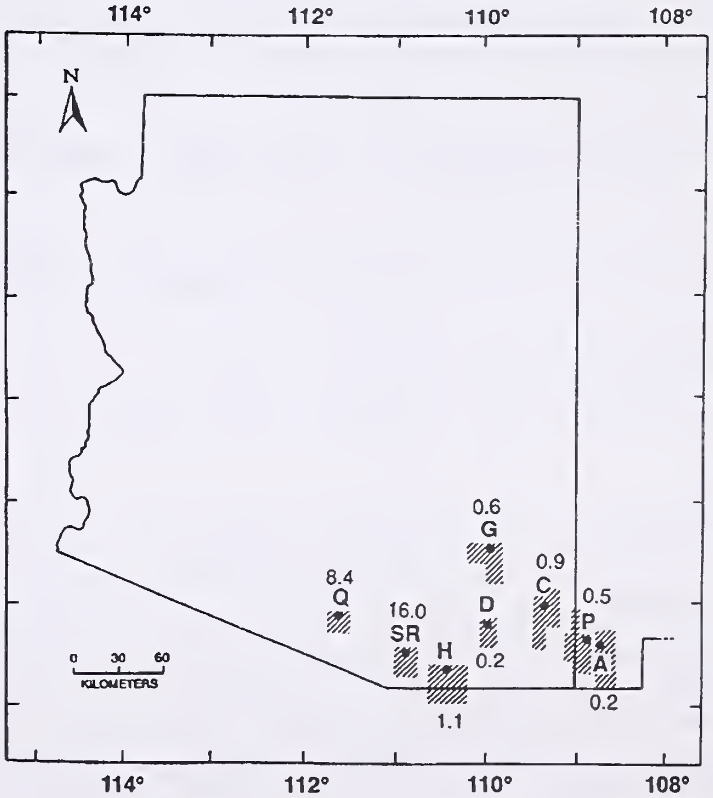

Figure 1.—Map showing the location of the Yarrow's spiny lizard populations examined and the ratio of monoxenous (direct life cycle) to heteroxenous (multiple host life cycle) helminths in each population. A = Animas; C = Chiricahua; D = Dragoon; G = Graham; H = Huachuca; P = Peloncillo; Q = Quinlan; SR = Santa Rita.

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tract, liver, and body cavity were examined and each helminth was removed and identified using the standard glycerol wet mount procedure. All helminths were deposited in the United States National Museum Helminthological Collection (Appendix 2).

RESULTS AND DISCUSSION

Helminths were present in 84% (255/302) of the lizards and represented five species of nematodes and two species of cestodes (Table 1). Two of the helminths (*Physaloptera retusa, Spauligodon giganticus)* were found in all eight of the populations. These two species were also the most abundant, together comprising 75% of the helminths recovered from Yarrow's spiny lizard. At the other extreme, *Strongyluris similis* occurred only in the Dragoons.

There is no clear correlation between mountain (island) size and the number of helminths found in the Yarrow's spiny lizard populations. The Chiricahuas harbored six species; the Animas, Dragoons, Grahams, Huachucas, and Santa Ritas had four each; and the Peloncillos contained three (Table 1). Only the Dragoons contained a helminth species, *Strongyluris similis,* not shared with any other ranges, or with any sympatric species of reptile. It does however occur in another member of the *torquatus* species group (*Sceloporus torquatus*) in Mexico, suggesting the possibility that this helminth species may have a phylogenetic distribution pattern within the genus *Sceloporus.* How long these northern populations of Yarrow's spiny lizards have been isolated can be inferred from the record of Holocene vegetation changes in the Southwest (Van Devender, 1977, 1990; Van Devender and Everitt, 1977; Van Devender and Spaulding, 1979; Van Devender et al., 1984). This record indicates that areas dominated today by Chihuahuan, Sonoran and Mohave Desert vegetation supported woodland communities (containing pinyon, juniper and oak) in the late Pleistocene to about 8,000 years ago.

The populations of Yarrow's spiny lizards in Arizona and New Mexico were likely interconnected during this period and became isolated in the last 8,000 to 10,000 years as a result of the shift from woodland to desert-grassland that now separates these ranges. Although these montane populations of Yarrow's spiny lizard are geographically isolated, this may not necessarily be the case for the helminth species. The arthropod intermediate hosts of some of the helminth species may be distributed more or less continuously across the intervening valleys or be wind-carried between the ranges. Moreover, at least four species of lizards (bunch grass lizard, *Sceloporus scalaris*; striped plateau lizard, *Sceloporus virgatus*; Sonoran spiny lizard, *Sceloporus clarkii* and tree lizard, *Urosaurus ornatus*) that occur in sympatry with Yarrow's spiny lizard share with it one or more helminth species.

Table 1. —Prevalence (%) and abundance (A) for helminths from each of the eight montane populations of Yarrow's spiny lizard examined in this study.* denotes monoxenous (direct life cycle) species.

	Chiricahua		Dragoon		Graham		Huachuca		Quinlan		Santa Rita		Animas		Peloncillo	
Sample Size (N)	53		27		57		43		50		36		22		14	
Helminth	%	A	%	A	%	A	%	A	%	A	%	A	%	A	%	A
Cestodes																
***Mesocestoides* sp.**	6	382	—	---	7	672	—	---	4	53	3	1	9	302	—	—
Oochoristica scelopori	4	2	4	1	2	4	12	12	6	67	8	7	—	—	—	—
Nematodes																
Abbreviata terrapenis	4	76	—	---	—	---	2	72	—	—	—	—	14	225	36	27
Physaloptera retusa	41	229	100	1121	45	247	30	201	20	20	8	15	54	175	100	304
Spauligodon giganticus*	64	501	85	264	77	534	72	305	92	1427	69	368	64	116	85	176
Stongyluris similis*	—	---	11	9	—	---	—	---	—	—	—	—	—	—	—	—
Thubunea intestinalis	2	1	—	—	—	---	—	--	6	30	—	—	—	—	—	—

The Sonoran spiny lizard and tree lizard are widespread in the region and are found between the ranges where suitable habitat exists. At this point we cannot evaluate the degree, if any, that helminth transmission may occur between these lizard species. However, there is no obvious correlation between the presence or absence in Yarrow's spiny lizard populations of particular species of helminths and the presence or absence of particular sympatric lizard species. When the presence and absence of species is used to compare the helminth communities of the eight montane populations of Yarrow's spiny lizards, each community is found to have a different species composition, except that the Grahams and Santa Ritas are identical (Table 1). The helminth fauna distribution among the mountain ranges does not present a coherent geographic pattern (Table 1). For example, the Santa Ritas are identical to the Grahams, although they are closer geographically to the Quinlans, Huachucas and Dragoons.

The lack of a coherent distribution pattern among the mountain ranges may be the result of random colonization or of random losses of species from the ancestral helminth community that may have been shared by the lizard populations prior to isolation of the ranges. Of the seven helminth species infecting Yarrow's spiny lizard, five are heteroxenous (involving arthropod intermediate hosts), whereas two are monoxenous with direct life cycles and no intermediate hosts (Table 1). For the latter two species, infection requires direct contact among hosts and is directly related to gregarism. In the eight montane populations of Yarrow's spiny lizard, heteroxenous helminths were most abundant in the eastern populations, whereas monoxenous helminths were strongly dominant in the western populations (fig. 1).

In the Huachuca population heteroxenous and monoxenous helminths were found in about equal numbers. This striking west to east shift in the abundance of heteroxenous helminths relative to monoxenous species presumably relects differences in mountain spiny lizard diet, behavior or ecology (e.g., population density or aggregation patterns). That broader ecogeographic factors may play a role in this shift from predominantly monoxenous to predominantly heteroxenous species is suggested by the fact that the transition occurs in the Huachucas which are near the boundary between the Sonoran and Chihuahuan Deserts.

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Appendix 1.

Museum catalog numbers for Yarrow's spiny lizards examined. Museums: Arizona State University (ASU), Museum of Southwestern Biology, University of New Mexico (MSB), Natural History Museum of Los Angeles County (LACM).

Animas Mountains, Hidalgo County: MSB 4014-4017, 4019-4023, 4025, 8886-8887, 8889, 8892, 8894, 11412, 11530, 41244, 48856; LACM 133290-133291.

Chiricahua Mountains, Cochise County: ASU 1057, 1059, 1060, 1069, 3575-3577, 14325-14326, 14328, 14347, 15349, 15352; LACM 17484, 61856, 62170-62171, 95909-95910, 95916, 95919-95920, 95923, 95925, 140298-140327.

Dragoon Mountains, Cochise County: LACM 140806-140832.

Graham Mountains, Graham County: ASU 6869, 6893, 9376, 9380, 9383, 9385, 9402, 9407, 22440, 22442-22446, 22448-22449; LACM 140242-140282.

Huachuca Mountains, Cochise County: ASU 3344, 3368-3370, 3376, 3663, 9131, 9157, 13442; LACM 17480-17481, 74212-74213, 75243, 95897-95900, 140283-140297, 140843-140867.

Peloncillo Mountains, Hidalgo County: MSB 6314, 10556; LACM 4462-4468, 113573-113574, 123360-123361, 126640.

Appendix 2.

Accession numbers for helminths from the eight populations of Yarrow's spiny lizard deposited in the USNM Helminthological Collection.

Animas Mountains: *Mesocestoides* sp., 83526; *Abbreviata terrapenis*, 83527; *Physaloptera retusa*, 83529; *Spauligodon giganticus*, 83530.

Chiricahua Mountains: *Mesocestoides* sp., 83535; *Oochoristica scelopori*, 83536; *Abbreviata terrapenis*, 83537; *Physaloptera retusa*, 83539; *Spauligodon giganticus*, 83540; *Thubunaea intestinalis*, 83541.

Dragoon Mountains: *Oochoristica scelopori*, 83542; *Physaloptera retusa*, 83544; *Spauligodon giganticus*, 83545; *Strongyluris similis*, 83546.

Graham Mountains: *Mesocestoides* sp., 83547; *Oochoristica scelopori*, 83548; *Physaloptera retusa*, 83550; *Spauligodon giganticus*, 83551.

Huachuca Mountains: *Oochoristica scelopori*, 83552; *Abbreviata terrapenis*, 83553; *Physaloptera retusa*, 83555; *Spauligodon giganticus*, 83556.

Quinlan Mountains: *Mesocestoides* sp., 83686; *Oochoristica scelopori*, 83687; *Physaloptera retusa*, 83688; *Spauligodon giganticus*, 83689; *Thubunaea intestinalis*, 83691.

Santa Rita Mountains: *Mesocestoides* sp., 83557; *Oochoristica scelopori*, 83556; *Physaloptera retusa*, 83560; *Spauligodon giganticus*, 83561.

Peloncillo Mountains: *Abbreviata terrapenis*, 83531; *Physaloptera retusa*, 83533; *Spauligodon giganticus*, 83534.

Hydrology and Watershed Management in the Madrean Archipelago

Malchus B. Baker, Jr., Leonard F. DeBano, and Peter F. Ffolliott[1]

Abstract.—Interactions among hydrologic processes, soils, and vegetation that has been subjected to a wide array of watershed management activities have not been well studied in the Madrean Archipelago biogeographic region. As a result, better measurements of storm runoff, soil erosion, and sediment yields are needed to adequately characterize many of the representative ecosystems hydrologically. Many sensitive ecosystems are sustained in a delicate balance under a limited water regime and a highly variable climate. This balance has frequently been overwhelmed by land uses and abuses, resulting in severe and widespread watershed degradation. This paper discusses existing hydrologic and watershed information for the Madrean Archipelago, and supplements this information with data from similar ecosystems located outside of this region. It also provides suggestions for the restoration of severely degraded watersheds.

INTRODUCTION

The climate of the Madrean Archipelago is mainly arid, with the higher-elevation mountain ranges subjected to a more semiarid climate. This biogeographic region is thus especially sensitive to climatic fluctuations and human impacts. Therefore, knowledge of the hydrologic processes regulating these water-limited ecosystems is essential to understand the soil-vegetation relationships responsible for sustaining landscape stability. The overall hydrologic response of this region to potential global climate changes is also important because of the delicate equilibria and interrelationships existing between precipitation and soil-vegetation assemblages.

Only a few comprehensive hydrologic studies have been reported for the Madrean Archipelago region (Lopes and Ffolliott 1992). One notiable exception is the long-term research effort at the Walnut Gulch Experimental Watersheds in southeastern Arizona. This paper characterizes the hydrology of the Madrean Archipelago by summarizing existing information obtained from within, and supplements this information with data extrapolated from similar ecosystems located outside the region.

VEGETATION

The Madrean Archipelago is the area in the southwestern United States and northern Mexico where scattered, isolated mountains occur in a sea of largely evergreen woodlands and semidesert grasslands. According to Brown (1982), the cold-temperate forests occupying the mountain tops are Rocky Mountain montane forests, which extend from southern Colorado, Utah, and Nevada through Arizona, New Mexico, Chihuahua, and Sonora. These forests, which are recognized as recreational centers, unique wildlife habitat, critical watershed areas, and sources for lumber and livestock grazing, reach their characteristic development between elevations from 2,300 to 2,650 m (fig. 1).

The lower limits of the pine forests, which make up a significant portion of the montane forest type, interface with evergreen oak woodlands and, to a lesser extent, coniferous woodlands. The evergreen woodlands are centered in the Sierra Madre of Mexico, reaching northward to the mountains of southeast Arizona and southwest New Mexico (Brown 1982). Elevations range from 1,200 to about 2,200 m. These woodlands are open

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stands of evergreen oaks, or intermixtures of oaks, alligator and one-seed juniper, and Mexican pinyon. The lower contact of the evergreen woodlands is semidesert grasslands, or desertscrub. This boundary is influenced largely by the soil depth and type, since these types occupy similar elevational ranges.

Brown (1982) indicates that the semiarid grasslands in the Madrean Archipelago region were historically encountered at elevations of 1,000 m on level plains and along the larger river valleys. These areas are typically grass-dominated systems with scattered woody plants—a savanna landscape. Since grasses have intensive and woody plants extensive root systems, respectively, the removal of grasses by livestock overgrazing can reduce water loss near the soil surface. As a result, more water becomes available for use by woody plants, and scrub or bush encroachment begins. If grasses are not allowed to recover and increase the likelihood of lightning or human-caused fires, woody plants continue to invade at the expense of the grass species (Brown 1982).

Desert grassland vegetation generally grows on alluvial soils (Hendricks et al. 1985). These are well-drained soils on valley plains and wide floodplains in the Santa Cruz, Sulphur Springs, and San Simon Valleys. These soils support some of the best rangeland in the Madrean Archipelago.

The two desert biomes found in the Madrean Archipelago are those associated with the warm-temperate Chihuahuan Desert, centered in the arid highland plains and basins of north-central Mexico, and the subtropical Sonoran Desert, centered at the head of the Gulf of California (Brown 1982). The Chihuahuan desertscrub is dominated by cresosotebush, and over 80 percent of the type resides on limestone parent material. This biome maintains a recognizable homogeneity in its dominants and receives most of its scanty precipitation during summer months.

The unifying theme of the Sonoran Desert is that of an unreliable and uneven biseasonal rainfall pattern, separated by periods of spring and fall drought. This desertscrub type merges in southeastern Arizona with the semidesert grassland type, and occasionally with the Chihuahuan desertscrub. Its flora is clearly derived from subtropical elements and its affinities are to the south.

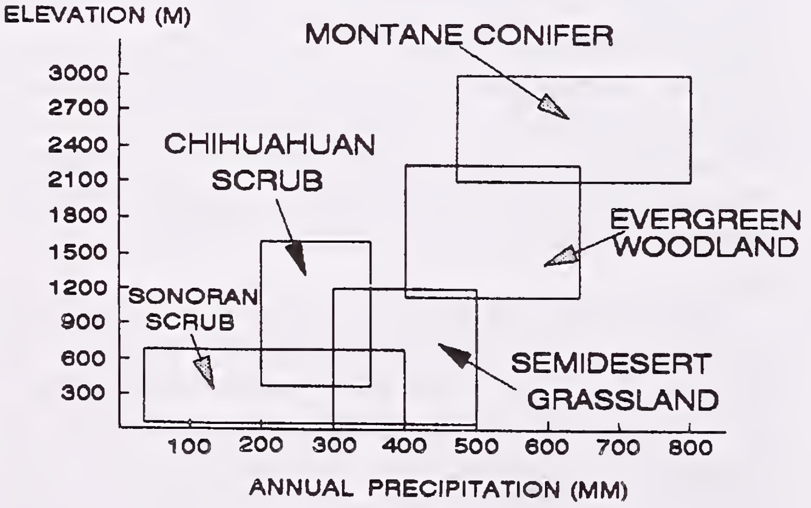

Figure 1.—Elevation and precipitation relationships of biotic communities in the Madrean Archipelago Region.

HYDROLOGY

Precipitation

The Madrean Archipelago receives from less than 100 mm of annual precipitation (on the average) in the lower desertscrub to over 800 mm on the higher mountain peaks (Sellers et al. 1985; Brown 1982) (fig. 1). One-half or more of the annual precipitation falls during the growing season from July to September (Osborn et al. 1987). These precipitation events are mainly high-intensity, short-duration convectional storms originating in the Gulf of Mexico. Winter precipitation is generally rain that comes during November through April, with occasional snow in the higher elevations. Moisture for winter precipitation normally comes as frontal storms from the Pacific Ocean.

The high-intensity precipitation events that frequently occur in this region often create overland flow from both vegetated and nonvegetated areas, and as a result, significantly increase erosion.

Plants growing in the Madrean Archipelago are engaged in a race against time. Green and Martin (1967) show that the effectiveness of precipitation in relation to plant growth in the semi-desert grassland-shrub community varies with season. The length of time that the soil remains wet after a rain is much longer in winter than in summer. Evaporation from a free water surface in Tucson is 8 times greater in June than December, and soil moisture after each rain is available only until it evaporates or is used in plant growth. Plants grow little in December and January, regardless of the availability of water, because ambient temperatures are low. Athough plants can grow rapidly in the summer, they only have a few days to use water made available by rain because of high evaporation losses.

Green and Martin (1967) pointed out that heavier rains will often produce visible growth on shrubs or perennial grasses, and germinate annual grass and forb seeds. A deep wetting of the soil in summer can produce significant amounts of perennial grass herbage, but it rarely produces substantial usable annual plant growth. Most southern Arizona soils require from 6 to 8 mm of precipitation to wet the surface 8 cm of soil. However, rains of 6 mm or even less a day or two apart, interspersed with heavier rains, can maintain usable soil moisture levels. The surface layers of many soils in the region hold about 38 mm of water per 30 cm of soil at field capacity, and 13 mm of water per 30 cm of soil at the point where herbaceous plants wilt. Therefore, about 25 mm of water per 30 cm of soil is required to support rapid plant growth.

Summer rains produced 90 percent of the perennial grass herbage on the Santa Rita Experimental Range (Culley 1943) and are responsible for major plant growth in New Mexico (Nelson 1934). Green and Martin (1967) showed that the amount and distribution of rainfall affects not only the amount of forage produced, but composition as well. Perennials account for only 20 percent of the grass herbage at the lower elevations, compared to 70 percent at the higher elevations where rainfall is greater. An additional 25 mm of summer rainfall can increase average perennial grass yields by about 140 kg/ha.

Temperature

Brown (1982) reported that nighttime freezing temperatures in the montane forest type usually begin by mid-September and do not end until the end of May. Freezing temperatures in the evergreen woodlands range from occasional in the south to an average of almost 150 days per year at the northern limits of its range. Freezes in the grassland savanna can be expected during any winter, but these freezes are not of long duration and temperatures rarely drop far below -4°C. Killing frosts are infrequent. Therefore, evaportranspiration loses can occur all year long at the lower elevations in the Archipelago.

Evaporation

Information on water losses from the soil, by both evaporation from the soil surface and transpiration from vegetation, has been used to calculate water balances. Buol (1964) calculated annual potential evapotranspiration (PET) values (by the Thornthwaite method) for Arizona from available climatic records. Calculated PET in the Madrean Archipelago ranges from 760 to 1,020 mm of water per year, and actual evapotranspiration ranges from 250 to 760 mm per year. In general, these values agree with measured annual ET values of 989 mm from an area supporting riparian grasses along the Gila River (Leppanen 1981), and 493, 389, and 335 mm for actual ET measured in a 150-day growing period from a forested area, clear cut area, and cienega, respectively, in the White Mountains (Thompson 1974). Estimates of evaporation from a free water surface in the Madrean Archipelago range from 1,525 to 1,780 mm (NOAA 1982).

Interception and Throughfall

Precipitation falling on a watershed is partitioned into water intercepted by leaves, twigs, or stems and returned to the atmosphere by evaporation; water channeled to the soil surface as stemflow, or drip from the foliage; water passing through the foliage to the soil surface as throughfall; and water falling directly on the soil surface in areas having sparse vegetation.

Throughfall in taller vegetation can be intercepted by low-growing vegetation, litter, or the soil surface. Crouse et al. (1966) indicated that the water storage capacity of grasses is proportional to the product of the average plant height and percent of ground cover. Interception losses in storms with total rainfall greater than the storage capacity of the plants varies from 0.2 to 9 mm. Corbett and Crouse (1968) found that the amount of water evaporated from surface litter is governed primarily by the moisture-holding capacity of the litter, and the evaporation potential during and following storms. Interception losses from small storms are high, while those from larger storms range between 2 and 5 percent. Approximately 20 percent of the gross precipitation intercepted in the coniferous woodland canopies is lost to evaporation (Skau 1964) and from 10 to 25 percent from the ponderosa pine canopies (Aldon 1959).

A study of rainfall distribution in the evergreen woodlands of southeastern Arizona showed that up to 70 percent of the late summer-early fall rains are intercepted directly under the canopies of Emory oak trees (Haworth 1992). Throughfall varied from 100 percent (all trees, large storms) to about 30 percent (large trees, small storms). Rainfall was distributed evenly under and around trees in storms generally larger then 25 mm.

Infiltration

Once precipitation reaches the land surface it can infiltrate into the soil, evaporate, or contribute to overland flow and eventually runoff. The rate that water enters the soil depends upon the nature of the precipitation, vegetation, topography, and soil properties. Important soil properties are texture and restricting subsurface layers.

Montane forests in the Madrean Archipelago grow on soils that are shallow to deep, gravelly and cobbly, moderately coarse-textured, and hilly to very steep (Hendricks et al. 1985). The soils are well-drained and formed in residuum weathered from granite, gneiss, schist, and other igneous rocks.

Soils in the evergreen woodlands are similar to those found in the San Rafael Valley and Canelo Hills areas (Lopes and Ffolliott 1992). Dominant soils in the San Rafael Valley are formed from old alluvia developed largely from mixed sedimentary and igneous parent materials (Hendricks et al. 1985). They are deep, moderately fine to very finely textured, gravely, and have moderate rates of infiltration. Soils in the Canelo Hills area are typically shallow, moderately fine to moderately course in texture, gravely and cobbly, and also have moderate infiltration rates. Soils typically supporting evergreen woodlands often have a layer that impedes the downward movement of water, further influencing the pathways of water flow through this ecosystem.

Beutner et al. (1940) studied infiltration in a wide range of Arizona desert soils. All of their infiltration curves for dry soils began with high infiltration rates, which declined rapidly for the first 10 minutes until a nearly constant infiltration rate was reached. Final infiltration rates varied from 7 to 56 mm/hr when rainfall was applied to dry soils, compared to from 5 to 32 mm/hr when applied to soils at field capacity.

Infiltration rates are influenced by grazing animals that remove plant material and compact the soil (Branson et al. 1981). As a result, runoff often increases as range condition deteriorates. Hendricks (1942) found that infiltration is improved if grazing management allowed for the accumulation of grass litter on semiarid rangelands.

In more arid climates, water-repellent soils found under various oak, chaparral, and coniferous woodland communities may affect infiltration (DeBano 1981).

Runoff

If water reaching the soil surface does not infiltrate or evaporate, it becomes runoff. Of the three major components of runoff—surface or overland flow, storm seepage or interflow, and groundwater flow—surface runoff is the most common component in arid environments. Surface runoff normally occurs only briefly during summer rainfall events when intensities exceed the infiltration capacity of the soil, or during periods of rapid snowmelt in the spring.

Studies of runoff relationships in arid and semiarid areas are complicated by infrequent runoff events and variable precipitation. Studies using comparable amounts of artificially applied rainfall on adjacent small areas show that differences in runoff can be attributed to variations in soils, plant type, and range condition (Branson and Owen 1970; Kincaid and Williams 1966; Schreiber and Kincaid 1967).

Much of the surface runoff originating on the mountain tops of the Madrean Archipelago flow into ephemeral stream channels in the lower evergreen woodlands, and finally into the semidesert grassland and desertscrub types. Therefore, it is important that these areas be protected from accelerated erosion and sedimentation which impact water quality and can eventually lead to a decrease in long-term site productivity (Lopes and Ffolliott 1992; Marsh 1968).

Osborn et al. (1980) reported that normally dry ephemeral stream channels in arid and semiarid regions can accommodate large volumes of runoff. Storm movement has little effect on major flood peaks from small watersheds. However, storm movement can affect flood peaks and volumes for smaller runoff events. If storms move too rapidly across a watershed, the reduced surface runoff can be entirely (or mostly) absorbed by the channels above the watershed outlet.

Surface runoff in the Madrean Archipelago is often linked directly to groundwater regimes (Davis, 1993b), as is illustrated by the upper San Pedro River Basin (Jackson et al. 1987). Both inhabitants of this river basin and government officials are concerned about groundwater depletion resulting from accelerated pumping. Water use throughout the upper portion of the basin, which reduces streamflow in the San Pedro River, is also a major concern. A University of Arizona study (1991) indicated that pumping from the regional aquifer in the Sierra Vista area is depleting stored groundwater reserves, and future pumping will only accentuate this trend. Although the depletion rate is small compared to the total volume of water in aquifer storage, these withdrawals directly affect surface flows, which are particularly important in stream reaches supporting riparian habitat vegetation (e.g., the BLM's San Pedro Riparian National Conservation Area).

Erosion and Sedimentation

Streamflow in the Madrean Archipelago is generated mainly from higher elevation forests, while the majority of the sediment originates in ecosystems at lower elevations (Branson et al. 1981). For example, Dortignac (1956) found that the Rio Puerco, which represents less than 20 percent of the Upper Rio Grande Basin, contributes nearly half of the sediment but produces less than 8 percent of the water yield from the area. Langbein and Schumm (1958) concluded that maximum sediment yields occur at about 300 mm of annual precipitation, and decrease on the dry side because there is a lack of runoff to transport sediment, and on the wet side because denser vegetation protects the soil and reduces sediment production. Sediment is frequently the major source of non-point pollution in streams (Branson et al. 1981).

Information on sediment yields in the Madrean Archipelago is generally lacking. However, some insight can be gained by data from similar vegetation types outside this biogeographic region. For example, in coniferous woodlands, a type that intermingles with the evergreen woodlands, Clary et al. (1974) reported annual sediment yields from volcanic soils of 2,000 to 4,500 kg/ha. Conversion treatments on these volcanic soils did not increase sedimentation. Sediment losses, however, from coniferous woodlands occupying other soil types (such as sedimentary soils) were greater.

Chaparral brushlands intermingle with evergreen woodlands on the flanks of isolated mountain ranges in southeastern Arizona. Sediment yields from chaparral watersheds with soils derived from granitic parent materials are often of the same magnitude as those observed in the coniferous woodlands. Sediment production, however, can be accelerated immediately after conversion treatments, especially when burning is involved (Hibbert et al. 1974; Morenno 1968).

Sediment yields at Walnut Gulch went from an average annual production of 3,740 to 290 kg/ha following vegetation conversion of brush to grass (Simanton, Osborn, and Renard 1977). Although runoff increased during the transition period, it decreased once grass became established—contributing to the reduction in erosion.

Sediment yields depend upon the magnitude of overland flow and stability of stream channels. Important climatic, geomorphic, and hydrologic parameters controlling sediment production and transport are: high intensity thunderstorms, which can produce large peak discharges per unit area; limited areal extent of rainfall, which can result in partial area runoff; transmission losses in normally dry stream channels, which can decrease downstream sediment transport capacities; steep channels, which can produce high flow velocities with increased potential for transporting sediment; and unconsolidated stream channel material and unprotected stream banks, which supply sediment (Lopes and Ffolliott 1992).

WATERSHED MANAGEMENT

Watershed management in the Madrean Archipelago region must consider the soil and water resource as related to forestry, livestock production, wildlife habitats, and recreational use within the context of sustaining the uniqueness of this biogeographic region. Conservation of the soil and water resource is important because of the fragile nature of the soils and limited amounts of available water in the region (Lopes and Ffolliott 1992). Therefore, watershed management practices should be carefully planned and implemented to ensure protection and (wherever possible) enhancement of the soil and water resource.

Soil and Water Conservation

Numerous attempts have been made to control erosion, particularly on rangelands, but failures have been frequent (Branson et al. 1981). Peterson and Hadley (1960) reviewed the effectiveness of a number of erosion abatement practices (including nearly 200 erosion control structures) on semiarid rangelands in the Upper Gila River Basin. They found vegetation was not benefitted appreciably by structures. In addition, excessive maintenance costs would likely limit widespread use of this practice.

Peterson and Branson (1962) evaluated the effectiveness of various land treatments undertaken by the Civilian Conservation Corps in the mid-1930s. Treatments included earth fill dams, earth dike spreaders, loose rock spreaders, hand placed rock spreaders, brush spreaders, "cement worm" spreaders, cable and wire spreaders, and rock rubble gully control structures. More than half of these structures breached within a few years after construction. However, vegetative cover was improved where earth dikes were not breached and water was distributed by the spreader system.

Lusby and Hadley (1967) studied the influence of low dams and barriers on sedimentation. They concluded that slope of deposition was largely dependent upon the particle-size distribution of transported sediment, and the rate steep-sided gullies filled was dependent upon availability of material approaching the size of the original channel bed material. Deposits behind low permeable barriers had steeper surface gradients than the original stream channels, and deposits behind low dams had lower gradients than the original channels.

The extreme variability in climate in the Madrean Archipelago region makes it difficult to isolate natural erosion and sedimentation rates from those induced by human activities. However, much of the severe erosion and sedimentation observed in the woodlands and semidesert grasslands in southeastern Arizona has been attributed to overgrazing by livestock, mainly during the last half of the 19th century.

Cox et al. (1984) estimated that cattle numbers in the desert southwest exceeded 500,000 between 1830 and 1840, and increased to a peak of about 1.5 million in the late 1880s. Large areas of sacaton and grama grass existed here prior to 1870, and beaver dams often restricted water flow. But, human disturbances between 1870 and 1901 (including the plowing of sacaton bottoms, channeling of rivers to provide irrigation water, overgrazing by livestock, and extermination of beaver by trappers) dramatically changed this landscape. Most of the water sources were dried up by 1893, and about 65 percent of the cattle had died because of these changes, which were amplified by a severe drought. Although the drought ended by 1895, the added effects of overgrazing, farming, drought, and subsequent flooding resulted in accelerated sheet and gully erosion throughout the region.

Restoration efforts in the San Simon Valley illustrate the benefits arising from the implementation of proper engineering and land management practices. Historically the area was a broad grassy valley that was bisected by an intermittent stream with little apparent erosion prior to the 1880s. The broad, flatter areas were covered by sacaton and tobosa grass with few trees. Willows grew in the wetter areas, and cottonwoods were found in San Simon Cienega, near the current Arizona-New Mexico state line. Little channel erosion was present, and the bottom was well vegetated.

From 1883 to 1916, head cutting of San Simon advanced 60 miles up the channel, and ranged from 3 to 10 m in depth and 12 to 245 m in width. Factors contributing to this rapid erosion included overgrazing by livestock, widespread drought, subsequent flooding, and construction of a drainage ditch, a wagon road, and a railroad. By 1919, the San Simon had been recognized (by the U.S. Government) as needing extensive restoration.

Numerous erosion control measures have been implemented on San Simon since 1934, including diversion dikes, water spreaders, detention dams, gully plugs, and rangeland seedings. After 50 years of observing the results of the various control measures, main channel structures were judged to be most effective. Side channel structures have been largely ineffective in regrading steep channel slopes, although these structures stopped further headcutting of the side channels, and reduced water velocities.

Watershed Improvement Practices

Watershed improvement practices can be grouped into three general categories: those which minimize adverse impacts to the soil and water resource; those designed to increase water yields; and rehabilitation practices used to improve watershed condition.

Minimizing Adverse Impacts

Fragile soils and limited water make it important to protect the Madrean Archipelago from further deterioration of the soil and water resource. Past degradation has been contributed to overgrazing by livestock, reduction in wildfires by man, and precipitation events at both extremes—high intensity rains, and droughts. Therefore, a positive plan of action is needed to protect this unique resource from further degradation. Management practices that minimize adverse impacts on the soil and water resource are similar to those used to prevent excessive rates of erosion (Lopes and Ffolliott 1992). Roads should not be constructed in or near stream channels. When roads are closed to public travel, roadways should be seeded with herbaceous plant species to protect against erosion. Logging operations should be restricted during periods of excessive rainfall, and grazing and recreational use should be monitored to minimize impacts on stream channels, riparian areas, and water quality. These practices are all essential components of an integrated watershed management program that accommodates multiple uses.

Increasing Water Yields

Vegetative management was advanced during the 1950s and 1960s to increase water yields. Experiments conducted throughout the world (and more specifically in Arizona) demonstrated that water yields could be increased (to varying magnitudes and duration) by changing the structure and composition of the vegetative cover on a watershed (Baker 1986; Bosch and Hewlett 1982; Clary et al. 1974; Davis, E. A. 1993a; Hibbert 1979; Hibbert et al. 1974; Rich and Thompson 1974). Additional water yields, when obtained, were attributed largely to decreases in transpiration.

An analyses by Hibbert (1979) showed that vegetative manipulations could increase water yields only on areas receiving more than 480 mm of annual precipitation. His reasoning was that precipitation below 480 mm is efficiently utilized by any remaining overstory vegetation and subsequent increases in herbaceous plant cover. This finding suggests it is unlikely that water yields can be increased in the Madrean Archipelago by vegetation manipulation. Vegetation manipulation thus does not appear to a viable watershed management option.

Watershed Rehabilitation

Management practices used to rehabilitate watersheds include: controlling gullies and mass wasting with properly constructed check dams (Heede 1970); establishment of protective tree, shrub, or herbaceous plant covers on degraded sites (Cox et al. 1984); and (when necessary) curtailment of wood harvesting, livestock grazing, and other exploitative practices (Lopes and Ffolliott 1992).

Artificial seeding of rangeland plants has been studied for nearly a century in the Madrean Archipelago. The results of these studies provide information necessary for rehabilitating severely degraded watershed. For example, Cox, et al. (1984) found several grass species that can be successfully established in the Chihuahuan and Sonoran deserts. Unfortunately, frequent drought and continual abuse by man has caused the deterioration of semidesert grasslands through accelerated erosion, brush invasion, and reduced forage production. However, even though revegetation is difficult and costly, it is possible.

CONCLUDING REMARKS

The ecosystems in the Madrean Archipelago represent a wide assemblage of hydrologic conditions within the context of an arid to semiarid environment. Many sensitive ecosystems are delicately balanced within an environment having limited water and a highly variable climate. This balance has frequently been overwhelmed by past land abuses, resulting in severe and widespread watershed degradation. Careful implementation of existing watershed and hydrologic information has successfully restored some highly degraded sites. However, widespread application of existing technology will depend on a more thorough understanding of the fundamental hydrologic processes operating in this unique environment.

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Riparian Zones: Neither Mountain Nor Desert

Jack Whetstone[1]

Abstract.—The analogy has been made the Madrean Mountains are like islands floating in desert seas, high points of diversity surrounded by the relative monotony of grassland and scrub. But, unlike islands, the Madrean Mountains are linked by lower elevation streams and rivers that are wildlife corridors and ribbons of diversity. These corridors, from mountain to desert, contain most of the plant species and virtually all of the wildlife found in the surrounding habitats.

INTRODUCTION

Riparian areas are often the most impacted by human uses; the water is pumped out, roads cross, dams and flood control projects are built, vegetation is cleared for agriculture. How much of our riparian habitat has been lost has been a controversial subject for the past few years. The figure of 90% lost, degraded or altered has been quoted and challenged. We probably don't know how much has been lost but is probably safe to say that virtually all of Arizona's riparian areas have been altered, and a strong case could be made that virtually none of that alteration has been to the benefit of those areas.

From the beginning of man's history in the Southwest, the San Pedro River has been a focal point. The highest concentration of Clovis sites is found within the San Pedro Riparian National Conservation Area especially at Lehner Ranch and Murray Springs where Paleoindians trapped and Killed Mammoths and other large mammals by driving them into bogs. Paul Martin has theorized that by trapping the young of these large mammals with low reproductive rated it was possible, even likely, that a relatively small population of Paleohunters could have driven the megafauna to extinction in a relatively short period of time, perhaps 500 years. During this period the valley floors between the Madrean Islands were oak woodland and savanna.

At about 8000 BP the climate warmed and dried to the point where grassland replaced oak woodland on the valley floors and the mountains became "islands". Archaeohunters now pursued smaller game like deer and antelope and by about 2000 BP were living in pit houses and experimenting with agriculture in the floodplain. Then followed the Hohokam, Mogollon and Salado cultures, villagers in semi-permanent houses with pottery, the bow and arrow, floodplain irrigation and agriculture as their main means of support. The entire length of the San Pedro shows signs of settlement and it is likely there were lots of these folk.

When the first European explorers reached the upper San Pedro (Fray Marcos de Niza in 1539 and Coronado in 1540) they found the Sobaipuri peoples living along the river in pueblos like Quiburi and Gaybanipitea in the area of Fairbank. The Sobaipuri were probably a Piman people related to modern Tohono' odam who farmed the river bottom. Like other pueblo dwelling Indians the Sobaipuri were converted to Christianity. Father Eusebio Kino made his first visit to them in 1692.

Perhaps the Sobaipuri were eager to embrace Christianity to gain the Spanish as allies against the newly arrived Apache or Dine' as they call themselves. The Dine' were Athapaskan raiders who arrived almost simultaneously with the Spanish. Quickly adapting to horses stolen from the Spanish they became the terror of the entire Southwest. Initially the Sobaipuri and Spanish were successful in repelling the Apache attacks, the Presidio of Santa Cruz de Terrenate was established near Quiburi to protect the new Christians. But within 4 years the first two commanders and over half of the garrison had been killed and the fort was abandoned. By 1780 the Spanish and the Sobaipuri had abandoned the entire San Pedro

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Valley to the Apache. With brief exceptions they were to have the valley to themselves for nearly a century.

In 1833 the two Mexican Land Grants were awarded that eventually would become the nucleus of the National Conservation Area, San Rafael del Valle in the south and San Juan de las Boquillas in the north. The new land owners brought in large herds of cattle and for a brief period were able to bribe the Apache to leave them alone, but by 1840 they were gone, abandoning an estimated 85,000 head of cattle to the Apache and the Grizzly.

The earliest Anglo accounts of the area come from James Ohio Pattie who wrote of his beaver trapping adventures along the Gila and Lower San Pedro Rivers. He describes the Mesquite forests of the lower river but did not explore the upper stretches. During the Mexican War the Mormon Battalion, looking for a route to California, followed the San Pedro from what is now the Mexican Border to present-day Benson. Their description of the river is the earliest account we have of what is now the NCA. The vegetation was described as a few ash trees and "...when twenty pace off, a fine bold stream!", this in the vicinity of Palominas. Near Charleston the account continues "... a dense thicket of bramble bush, mostly muskeet, with which millions of acres are covered". Early accounts mention not seeing the river until the horses were standing in it and having to detour well south into Mexico to cross during the rainy season. Other repeated elements from descriptions of the San Pedro show that it was perennial throughout most of it's length, in fact there are accounts of riverboats on the river, and that marshy areas and beaver were common. The last beaver were apparently trapped out by 1900.

By the end of the 1870s the Chiricahua Apache were largely pacified, the railroad connected Arizona with the rest of the country, silver had been discovered in Tombstone and Bisbee, and the stage was set for major change. Heavy livestock grazing removed the groundcover, fuelwood and timber cutting removed the trees and road and railroad building caused gullying from the disruption of washes. Because of the railroad it was now possible to ship cattle anywhere to market and cattle were stocked at way beyond the carrying capacity, there were probably close to 100,000 head in the upper valley and at least one writer referred to it as one vast cattle ranch. Everything from cooking to pumps ran on firewood, it is estimated that Tombstone alone used 4 million cords of fuelwood. By the end of the 1880s wood haulers were cutting well into Mexico. Because of the availability of water, towns like Charleston, Contention, Emory City and Fairbank sprang up along the river, most as mill sites for the various mines in Tombstone.

The Tombstone boom was short-lived. By 1886 Tombstone and the surrounding area had a population of 20,000 but that same year silver production cam to a virtual standstill and by 1889 there were only 1900 people left in Tombstone. Miners, and mining town settlers drifted off the other areas, mills and businesses closed and the towns along the river almost became ghost towns overnight. The following May a major earthquake hit a short distance south of the border at Batepite leveling much of Charleston. In 1891-92 drought struck the valley. Apparently the overstocking had been done during good years and now there was to be reckoning. From 1890 to 1893 little rain fell and cattle died by the thousands. It was said you could walk for miles on the carcasses. The range was devastated, the grass was gone and with it the lands ability to hold what rain fell. Then in 1893 the rains returned with a vengeance. By the end of the century the river had changed from a stable, slow-moving, marshy perennial river to an unstable, flood-prone, incised, intermittent stream and the lower elevations of the watershed from rich grassland to Chihuahuan Desert Scrub. After Indians had lived for 11,000 years along the river with little impact, Anglo settlement had wrought major change in 20 years.

At the turn of the century litigation involving the Mexican Land Grants was finally settled forcing many of the residents to move. Juan Pedro Camou received the San Rafael del valle Grant which was sold to Wm. "Cananea" Green and Wm. Randolph Hearst received the San Juan de las Boquillas Grant. Eventually Hearst bought the Green holdings as well. Kern Land and Cattle acquired the property in 1958 and Tenneco in 1972. Tenneco used the land for ranching and other agriculture, pumping over 18,000 acre feet on to farm fields along the west side of the river from Hereford to Lewis Springs.

A front page article on the Tucson Citizen on Jan. 13, 1978 first explored the idea of fringing the San Pedro into Federal control. Bill Quimby, the outdoor editor stated "an 80 to 100 mile stretch of the San Pedro river from a point south of Tombstone almost to Winkelman has been targeted as a 'unique wildlife area' by the U.S. Fish and Wildlife Service and is being considered for purchase under President Carter's National Land and Heritage Program. It was the Bureau of Land

Management and then State Director Dean Bibles who arranged the land deal that transferred the San Pedro to the Public Domain. On Nov. 18th, 1988 Congress passed the Arizona-Idaho Conservation Act that created the San pedro Riparian National Conservation Area.

The acquisition of the Upper San Pedro by BLM and its designation as a National Conservation Area marked a new beginning for the river. Several bold decisions were made eliminating some traditional Public Land uses. It was decided that ORBs would not be allowed off road in the NCA and that no new mining leases would be permitted. Existing gravel quarries were phased out and their sites reclaimed. By far the most radical departure from tradition was in the elimination of grazing for at least 15 years.

I don't think any one was prepared for the speed of the recovery of the vegetation. As an initial part of the monitoring process readily repeatable photo points were established. Photos are taken in late June or early July when vegetation has attained most of its foliar growth but hasn't been knocked down by monsoon flood pulses. From the before pictures it is obvious what an effect grazing was having. From the after pictures it is obvious how quickly the vegetation is recovering. The first set was taken in 1987 the last year cattle grazed in the river bottom and the second in 1992 after 4 years of rest.

A series of Point Intercept/Line Intercept Transects crossing the river were set up in 1988-89 and re-run in 1991-92 to quantify the changes occurring over time. 202 Points were sampled in the 11 transects to look at basal cover, bare ground and litter. After 3 years bare ground had decreased and litter had increased, exotic perennial grasses showed mixed results -some increase, some decrease, but native perennial grasses showed dramatic increases in all but 2 transects where they showed only slight decline. Mesquite and willow cover showed little change but cottonwood canopy cover increased dramatically particularly in the southern half of the NCA. Salt Cedar seems to be increasing slightly in the northern, non perennial portion of the NCA. Pace frequency transects have also been run in the uplands where there has been a steady increase in perennial grass cover in most of the transects run at three year intervals.

Shrub species have also shown a steady increase in the riparian zone. Although not favored as food by cattle, shrubs were probably held in check by compaction and scouring. The increase in these species has had multiple effects. The dramatic increase in understory obligate birds I'll get to later but equally important has been the moderating effect of these plants on flood waters.

Regeneration of cottonwood and willow is apparently an iffy process. Seeds produced in the late winter must fall on exposed sand and gravel bars- obviously plentiful in the before pictures. Then water levels must drop no faster than the roots can follow. Monsoon floods frequently scour out the new seedlings before they can become firmly established. Obviously, ideal conditions don't occur every year for bumper crops of new trees. When cattle are present they eat the new trees and will strip trees they can bend. When the cattle were removed there was some regeneration but the process proceeded slowly. Pole plantings were done in areas without trees and were generally successful.

During a tour of the Walnut Gulch Experimental Range the participants were at the NCA headquarters and we were discussing the vegetative recovery. One of the leaders disagreed with the premiss that the recovery was due exclusively to the removal of livestock. "Just wait until you get a big flood, you'll be right back where you started". The implication was that the floods would scour out the channel whether or not there was an understory.

Floods have had a major impact on the riparian corridor. The incision of the late 19th Century was the direct result of high water events following bad land management. Subsequent floods in the Summer of 1926 (28,000cfs), Oct. '26 (estimated at 98,000cfs), '38 (22.901cfs), and Summer of '78 (86,000cfs), had a tremendous effect on the San Pedro doubtlessly scouring out grasses, shrubs and even large trees. The river, normally a few feet wide and inches deep, would swell to half a mile or even a mile wide and 20 or more feet deep.

In January of 1993 unusual weather conditions caused a three week period of almost daily rain. The river at the beginning of the month was running at a roughly normal 9cfs. By January 20th the flow reached 11,500cfs or nearly 4 times the previous winter high of 3000cfs set in 1915. Arizonans will remember the floods of '93 , Coolidge Dam was at risk and Winkelman was partly under water leaving some parts of town permanently abandoned. Interstate 10 over the normally dry Gila River was briefly closed and the river ran a half mile wide for weeks. Along the lower Gila vast tracts of agricultural land were under water in an attempt to return to their riparian ancestry. As a side note I had Mallards swimming in a grassland transect a quarter mile from the river.

It was several weeks before we could get a thorough look at much of the NCA but even a superficial look presented a picture of what a healthy riparian system means during a major flood event. There was almost no loss of trees or for that matter of any vegetation. In areas where the water had been slow moving even the dead stalks of the sweet clover remained, acting as sediment rakes. The grass at the waters edge was still in place even though it had been under at least 15 feet of fast moving water. It wasn't quite all beneficial, there were areas where high banks were undercut and collapsed but in many cases this only served to change the bank from vertical to sloped. Many of these slopes remain nearly two years later and if they can stabilize before the next big flood some high cut-banks might be eliminated. We were left with the feeling we would like floods of this magnitude nearly every winter. It became apparent to anyone who was paying attention that flood control through engineering might ultimately be doomed to failure after great expense while flood buffering by natural means was not only inexpensive but it worked.

In addition, ideal conditions for cottonwood and willow regeneration occurred. The high water of winter insured that water remained through the Spring for the seedlings to take hold and the Summer Monsoons had no major pulses to scour out the young trees. Many of these trees are now 3 to 4 feet tall and flood resistant.

The general condition of the San Pedro channel at the time of acquisition was a broad, shallow streambed. Past flood events had caused major downcutting of the channel well below the original level (10-30 feet) and grazing and floods continued the process. With vegetative recovery there has been a steady tendency toward a narrower, deeper channel.

Where tributaries enter the river there is a damming effect from the sediment brought down. Behind many of these dams are ponds. At first there were only a few of these ponds but as the banks have stabilized there has been an increase in the number of ponds and in their length. After the 1993 floods the increase became almost dramatic, the perennial stretch from Hereford to Charleston is almost a continuous series of long pools alternating with riffles.

Any vegetation tends to armor the streambank, even the dead stalks of the sweet clover helped during the '93 floods, but perennial grasses and trees are particularly good at the armoring process. Cottonwoods and willows when undercut frequently pivoted like a hinge rather than being swept away.

During any high water event silt and sand are left in the lee of every obstruction. With a normal summer flood a quarter to half an inch of silt and sand are deposited. This is probably a good indication that the uplands are not in the best condition. During the 1`993 flood there were mounds of sand in the lee of tree groves 3 to 4 and even 5 feet thick. Composed of the topsoil of the eroding uplands, these mounds are nutrient rich and contribute to the continued increase of riparian vegetation. In addition there has been a tendency in some areas to fill downcuts.

At the shallow edges of the pools in slow stretches there is an increasing tendency for cattails and bulrushes to become established. Dense stands further slow the river and allow more silt deposition and therefore more of this marsh vegetation to become established ad infinitum. During the '93 flood sections of marsh vegetation tore loose and became established in new locations. As more of these marshy stretches become established flows will further slow and the bottom should rise leading to more slow moving marshy stretches.

These marshy stretches are what the river is thought to have been like before the changes brought on by Anglo settlement. Additionally, we hope to see beaver reintroduced into the perennial reaches. Beaver and fire are missing management tools that would help return the San Pedro to a natural, functioning ecosystem. It has been said "if you want to know what the land looked like before the coming of the white man, you must first, remember that is was inhabited by beaver". Few animals have such a dramatic impact on their surroundings. From the first trapping expeditions in the 1820s until their extirpation at the turn on the century tens of thousands of beaver were taken from the San Pedro. The river would likely have been a series of ponds from one end to the other.

Fire too would have shaped the river forest. Sacaton grass, adjacent to the riparian forest in some areas, when left alone, burns at fairly regular intervals, perhaps every 5 years or so. In 1990 an 80 acre fire in one such sacaton field killed cottonwoods along it's edge. The fire renews the sacaton and provides dead snags for birds and mammals. Avian transects in this areas consistently had the highest density and diversity of any grassland transect we ran.

One area where the outlook for recovery is not so bright is in native fisheries. Historic records show a much more diverse native fish population than exists today. Colorado Squawfish, Razorback Sucker, Flannelmouth Sucker, Round-tail Chub and Gila Chub were extirpated by the 1880s, Speckled Dace by 1904, Loach Minnow and Desert Pupfish and Spike Dace by the 60s and Sonoran Topminnow and Sonoran Sucker probably during the Cananea tailings spill in the late 70s. Currently only Long-fin Dace and Desert Sucker thrive in the San Pedro where there are large populations of aliens such as Carp, Green Sunfish, Gambusia, Bullhead, Channel Catfish and Largemouth Bass. We are looking at the possibilities for reintroduction of natives but with numerous aliens reintroduction opportunities are limited. AZ Dept of Game and Fish has done a suitability study of the river from Fairbank to the Mexican border and we have identified former quarry ponds as potential stocking areas.

The mammal and herp faunas seem to be doing well. There are healthy populations of white-tail, mule deer, and javelina and what has been described as the second most diverse mammalian fauna in the U.S. Ocelot has been taken and Jaguar is a possibility. Lesser Long-nosed and over 30 other species of bat are present but little is known about their abundance and distribution. The few herp species of concern are either not riparian species, Gila Monster and Desert Tortoise, or are rarely encountered. Other than a healthy riparian how do you manage for Mexican Gartersnake?

More and more the San Pedro is becoming known as a world class bird watching area. Each year tens of thousands of Bird Watchers make the pilgrimage to Southeastern Arizona to look for birds found no where else in the U.S. and each year more and more of them are including the San Pedro in their itinerary. During the Spring of 1992 an Ecotourism Study conducted by the University of Arizona's Department of Agriculture and Resource Economics found that visitation to the San Pedro and Ramsey Canyon contributed nearly 3 million dollars to the Sierra Vista economy during that year. Much of this increase must be due to the discoveries made over the past 9 years by the Avian Monitoring program conducted by BLM Biologists since the creation of the NCA. Beginning it's 10th year next month this is the largest avian data set in the Bureau. Currently we are running 6 transects on the San Pedro and another 5 on nearby Empire Ranch. A total of 23 transects have been run on the San Pedro sampling habitats ranging from Cottonwood gallery forest to burned Sacaton Grassland.

More important than number of transects is continuity. Continuity blunts the dips and spikes and because of this continuity trends become apparent. The most obvious trend has been the dramatic increase in the number of understory obligate species. It is obvious that species like Yellow-breasted Chat and Abert's Towhee which feed and nest near the ground would undergo population expansion as this habitat improves. Corresponding increases in canopy species such and Yellow Warbler and Summer Tanager are perhaps less obviously explained but a general improvement in the habitat likely accounts for this increase. Most dramatic are the increases in species of the lowest level of the understory and for obvious reasons. The habitat for Common Yellowthroat and Song Sparrow barely existed in the before pictures and has expanded tremendously by the second series of photos. Additionally, Common Yellowthroat, in normal years, uses the Sacaton as nesting habitat only to retreat into the riparian corridor in dry summers such as this year . Apparently the riparian corridor acts as a buffer for some species in years of drought allowing them some nesting to carry them over into years of plenty.

Northern Gray Hawk has experienced similar gains along the San Pedro. With perhaps 75% of the U.S. population found along the San Pedro and 40% within the NCA this is a species we have given special monitoring emphasis. Annual nest search and some monitoring have show increases comparable to other species. In 1986 11 pairs and 9 nests were located. By 1994 there were at least 22 territories occupied and 18 nests located, an increase of 100% in eight years. Some of this increase could be due to better search methods, some to protection, but the bulk must be due to improved habitat conditions.

My own favorite success story involves the Green Kingfisher. Before 1988 this species was considered an accidental winter visitor to Southeastern Arizona. During the summer of '88 a nest was discovered on the San Pedro north of Hwy 90. A second nest in 1990 was thought to have been abandoned due to disturbance by bird watchers. Then in 1993 adults were observed feeding 2 fledglings a mile south of the 1st nest and a second pair were observed entering a potential nest hole 6 miles to the north. During the previously mentioned fish habitat assessment by Arizona Game and Fish Department 15 Green Kingfishers were noted in the perennial stretch from Charleston to Hereford. That fall a bird was reported from Boquillas Ranch several miles north of Charleston and most impressively another was reported from Bingham Cienega 50-60 miles to the north. The pair that nested near Hwy 90 nested twice this summer, a second pair fledged young just to the south and another pair was seen carrying food on several occasions in the vicinity of the 1988 nest. Birds were observed again in the area of the nest hole 6 miles north, a pair was at the Hereford Bridge area where they have been observed in the past and multiple birds (perhaps as many as 6) were in an isolated area about midway from Hereford to Hwy 90. Clearly this species is undergoing a dramatic population explosion along the San Pedro. Green Kingfisher dives from low branches overhanging rivers and streams. Before BLM acquisition there was little vegetation overhanging the water. Although it is probable that these birds are expanding throughout Southeastern Arizona (they are also being seen in Patagonia the Nature Conservancy's Patagonia/ Sonoita Creek Preserve) it is likely the streambank vegetation recovery and stream profile changes together with improved conditions for small fish are having a very positive effect on this little kingfisher.

The San Pedro seems to be a river that is recovering, healing very quickly from the effects of a rapid population expansion during a period when people had little understanding of, and even less concern for the effects of their actions. But what of the future? The recovery process will continue to change the river. In an ideal world with no outside influences the changes we are seeing along the San Pedro today would ultimately lead to something close to pre-settlement conditions. The return of beaver would thin the cottonwoods, increase the numbers of pools and raise the water level. A raised water level would create more marsh areas and probably drown out many of the trees. The incised areas would re-fill creating a broad marshy bottomland with trees primarily along the edges. Cottonwood and Willow would give way to Ash and Walnut and scrub covered lower benches would give way to Mesquite Bosque.

But the 55,000 acres of the San Pedro NCA is only a little piece of the watershed, the ribbon of diversity along the bottom of the basin. Most of what happens to the river in the future will depend not just on the BLM but on all the watershed. On Sierra Vista, and all the smaller towns, on Fort Huachuca, Coronado National Forest and the State Land Department, on Mexico and the city of Cananea, and all the people who live in the watershed. The San Pedro Valley is once again experiencing a population boom. Sierra Vista is one of the fastest growing cities in a fast growing state. Can we be proactive enough to prevent a recurrence of disaster for the San Pedro?

The Research Program of the Southwest Watershed Research Center

Kenneth G. Renard and Leonard J. Lane[1]

Abstract.—The Southwest Watershed Research Center of the USDA Agricultural Research Service operates the Walnut Gulch Experimental Watershed located at Tombstone in southeastern Arizona. The semiarid lands which the watershed represents are characterized by extreme variability of precipitation, soils, vegetation, infiltration, runoff, and erosion and sediment yield. The results obtained from the research program of the Southwest Watershed Research Center describe and summarize this temporal and spatial variability and the impact of management decisions in altering the hydrologic and sedimentation cycles. Examples of publications pertaining to erosion control and water quality impacts that have been prepared by the staff of scientists and engineers are presented.

INTRODUCTION

The Southwest Watershed Research Center of the USDA Agricultural Research Service consists of a multidisciplinary staff of 10 scientists and engineers located in Tucson, Arizona. This staff operates the Walnut Gulch Experimental Watershed located at Tombstone in southeastern Arizona. The semiarid lands which the watershed represents are characterized by extreme variability of precipitation, soils, vegetation, infiltration, runoff, and erosion and sediment yield.

THE RESEARCH PROGRAM

The results obtained from the research program of the Southwest Watershed Research Center describe and summarize this temporal and spatial variability and the impact of management decisions in altering the hydrologic and sedimentation cycles. Potential impacts of global change on the natural resources of such semiarid lands are also reported. Specific results include frequency relationships for runoff amounts. Analytic simulation models such as CREAMS, RUSLE, WEPP, and KINEROS, developed using data collected on the Walnut Gulch Experimental Watershed, are described and used to illustrate the impact of land management practices on the hydrologic cycle in a semiarid environment. Data and research findings from Walnut Gulch are being used to develop new technology for natural resource modeling and management.

Examples of publications pertaining to erosion control and water quality impacts that have been prepared by the staff of scientists and engineers at the Southwest Watershed Research Center are listed below to illustrate the nature of their work.

1994

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1993

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Woolhiser, D. A., R. E. Smith, and D. C. Goodrich. 1990. KINEROS: A Kinematic Runoff and Erosion Model: Documentation and User Manual. USDA Agricultural Research Service, ARS-77, 130 pp.

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A Growth and Yield Model of Emory Oak: Applications on Watershed Lands in Southwestern United States

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Abstract.—Variable-density yield tables, in which stand density is used as an independent variable with stand age and site index to estimate growth and yield, have been developed for applications in even-aged stands on watershed lands in the oak woodlands of the southwestern United States. These tables are represented by a set of equations to estimate current and then future yields, with the difference between these two estimates being a prediction of growth for the period in consideration. The formulas representing these yield tables form a basis for the growth and yield model described in this paper. Applications and management implications of the model on watershed lands are also presented.

INTRODUCTION

Encinal woodlands, which encompass approximately 80,300 square kilometers, are found in largely in the Sierra Madre of Mexico, with northern most portions of its range in southeastern Arizona, southwestern New Mexico, and western Texas. Historically, the encinals have furnished fuel, foodstuffs, and building materials to local people (Ffolliott and Guertin 1987, Little 1968, Phillips 1912). With the introduction of livestock into the region, by the Spanish, the woodlands became important grazing lands and a source of posts and poles for fences and corrals. At the turn of the century, mining industries utilized large quantities of oak for charcoal smelting and fuelwood for steam boilers. From the late 1930s to the early 1970s, with the availability of fossil fuels and changes in mining techniques, the demand for wood declined (Bahre and Hutchinson 1985).

Demands for wood products from encinal woodlands are increasing. However, to meet required multiple use objectives in a framework of sustainability, plans for harvesting of wood must consider consequences of these actions on wildlife habitats, watershed protection, recreational opportunities, livestock production, and mineral interests. Development of techniques to estimate growth and yield, therefore, are a prerequisite to conservation and sustainable development, and multiple use management of encinal woodlands. This study focuses on this need.

DESCRIPTION OF THE STUDY

The purpose of this study was to develop a growth and yield model for applications in the encinal oak woodlands. A yield table approach to modeling was selected for this development. Yield tables present estimates of volume of even-aged stands characterized by age classes, site quality values, and stand-density (Avery and Burkhart 1994, Curtis 1972, Husch, Miller, and Beers 1982). Yield tables have been a basis to estimate growth and yield of forests and woodlands in Europe for over a century and in the United States since the early 1900s (Curtis 1972).

Study Area

Source data for development of the growth and yield model for encinal woodlands were collected on the Coronado National Forest, located in

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southeastern Arizona. Emory oak (*Quercus emoryi*) is the predominate species, with silverleaf (*Q. hypolevooides*), Arizona white (*Q. arizonica*), Mexican blue (*Q. oblongifolia*), netleaf (*Q. rugosa*), gray (*Q. grisea*), and shrub live (*Q. turbinella*) oaks intermixed. Measurements were collected only on Emory oak, however.

Emory oak is found at elevations from 1,5000 to 2,000 meters, on undulating topography of diverse aspects and topography. Soils are generally more than 150 centimeters deep, formed in old alluvium from mixed igneous and sedimentary rocks. Annual precipitation averages 300 to 500 milimeters. Most of the study area is located in the *Quercus emoryi/Bouteloua curtipendula* habitat (USDA Forest Service 1987).

Field Procedures

Measurements were obtained on 84 temporarily located .04 hectare sample plots randomly distributed in two strata representing past land use histories. Fifty-one plots were located in uncut stands and 33 plots in stands which had experienced partial wood harvesting. Individual tree measurements taken at each plot included dbh, total height, and crown position (dominant, co-dominant, intermediate, or suppressed). A total of 1,239 trees were measured. When present on a plot, a dominant or co-dominant tree was cored with an increment borer to estimate age. If such a tree was not found, a dominant or co-dominant tree off the plot was cored. Average age of the trees on each sample plot were determined from relations of dbh and total height to age, or from knowledge of prior wood harvesting.

Analytical Techniques

Yield tables are generally tabular presentations (Husch et al. 1982). With the use of computers, however, yield tables can also be presented as a set of equations, as they are in this study.

After collecting the source data, volume and basal area (the latter representing a measure of stand density) of the Emory oak trees on each sample plot were calculated. Site index values (an indicator of site quality) for the sample plots were also determined. Volume was estimated from equations presented by Chojnacky (1988). Because of the frequently encountered multi-stemmed nature of Emory oak, sample trees were differentiated into single stem and multiple stem, with the appropriate equation applied to each. Basal area was selected as the measure of stand density because it is determined easily in the field, it can be converted easily to other expressions of stand density, and many multiple use relationships in encinal oak woodlands have been developed with basal area as the independent variable. Site index was determined from tables prepared by Callison (1988).

Initial analysis indicated that data sets from the uncut and partially harvested sample plots were not significantly different in terms of the variables studied and, therefore, were pooled for subsequent analysis. A multiple regression approach to the development of equations for variable-density yield tables had been used in similar studies (Avery and Burkhart 1983, Clutter et al, 1983, Husch et al. 1982), with the model initially proposed by Schumacher (1939) most commonly used; this approach was also used in this study. A stepwise multiple regression analysis (Sokal and Rohlf 1981) was used to relate volume to age, site index, and basal area. Variable transformations were based on knowledge of processes being modeled and statistical fit of the data points (Little and Hills 1978). All examples are reported at a 95% confidence interval.

Synthesis of Model

The growth and yield model facilitates the estimation of current yield by solving the variable-density equation obtained for current stand conditions. Future yield is estimated by making appropriate adjustments in age and the basal area value, and then re-solving the variable-density yield equation. Site index is assumed to remain unchanged.

A set of equations to adjust basal area values to estimate future yields was developed. The data were grouped into three site index classes (high, average, and low), and within each class, grouped into basal area classes and age. Second-degree polynomials defining these relationships were differentiated to describe the rates of change in basal area with respect to age.

The variable-density yield equation developed for Emory oak is:

$$lnV = 1.25 + 1.01(lnBA) - 8.83(A^{-1}) + 0.565(lnSI)$$

$Sy.x = 0.186; r^2 = 0.951$

where:

V = volume in cubic feet per acre
BA = basal area in square feet per acre
A = age in years at dbh
SI = site index value (Callison 1988)
Sy.x = Standard error estimate
r2 = coefficient of determination

When solved for current stand conditions, equation (1), provides an estimate of current yield in cubic feet per acre. Age and basal area are adjusted to reflect future conditions to estimate future yield. Basal area values are adjusted by one of the following equations:

Site Class I

$$\frac{dBA}{dA} = 1.85 - 0.0318(A)$$

Site Class II

$$\frac{dBA}{dA} = 1.55 - 0.0276(A)$$

Site Class III

$$\frac{dBA}{dA} = 0.155 - 0.0023(A)$$

To solve equation (1) for future yield, the adjusted future basal area value is estimated by summing estimated annual changes in basal area from the current to future age for the appropriate site class; the total change in basal area is added to the current basal area value to obtain the estimate of basal area in the future. For example the adjustment for site class II is:

$$BA_f = BA_c + [\textstyle\sum_{A_{c+1}}^{A_f} \frac{dBA}{dA} = 1.55 - 0.0276A]$$

As mentioned above, the adjusted basal area value, along with the future age and site index value are inputs to equation (1) to estimate future yield. Change in yield between current and future stand conditions is defined as periodic growth.

APPLICATION OF MODEL: AN EXAMPLE

To determine the validity of the estimates of current yield, future yield, and growth obtained from the application of the growth and yield model, these estimates were compared with actual measurements from an uncut stand of Emory oak in southeastern Arizona not included as a study area. From inventory data, it was determined that the stand was 25 years old, site index was was 15, and current basal area was 3.65 square meters per hectare. Current yield was estimated by solving equation (1) in terms of these input variables. The estimated current yield for this uncut stand was 12.9 ± .10 cubic meters per hectare. Future yield at age 40, for example, was estimated by changing the age variable accordingly, using the site index value of 15, and adjusting the basal area value by solving equation (3), which represents Site Class II, for ages 26 through 40 and summing the annual estimates of change. These variables were used to solve equation (1) once again, this time to estimate future yield. In this example, future yield is 23.8 ± .10 cubic meters per hectare.

Growth is placed on an annual basis by dividing periodic growth by the number of years in the growth period, in this case, the period was 15 years. In this example, periodic annual growth was .73 ± .15 cubic meters per hectare. The estimate of current yield agreed with estimates of current yield obtained from Forest Inventory and Analysis (FIA) inventory data for oak woodlands in Arizona (Conner et.al. 1990). Estimates of future yield and growth were also similar to those obtain independently from a simulation model based on a stand projection method (Ffolliott et al. 1988). It was concluded, therefore, that the variable-density yield table is applicable to Emory oak stands in southeastern Arizona.

MANAGEMENT IMPLICATIONS

One way to attain a balance between conservation and sustainable development of the encinal woodlands id through a *watershed management approach,* which incorporates soil and water conservation and land use planning into a broader, logical framework of management (Ffolliott et al. 1993). Attaining this balance is a key to sustaining the encinal woodlands in the face of increasing pressures being placed on them. Estimates of current yield, future yield, and growth of the woodland overstories on watershed lands is prerequisite to this purpose. These estimates can be generated through application of the growth and yield model described in this paper.

Application of the growth and yield model to watershed lands comprised largely of Emory oak is relatively straightforward. The woodland overstories are initially grouped into strata representing even-aged stands. The minimum size of a stratum is set arbitrarily by the user, although the strata must be large enough to facilitate the implementation of subsequent management practices. The strata can be delineated from the ground or through the interpretation of airphotos.

Once the strata have been delineated, the growth and yield models is applied to each stratum to obtain the estimates of growth and yield importance. It is necessary that the specific age, basal area, and site index inputs be known for each stratum; if knowledge of these inputs is lacking, the statistical value of the stratification is reduced. The estimates of growth and yield obtained are representative of the strata delineated on the watershed lands and, consequently, must be "pooled" to obtain estimates of the watershed as an entity.

FUTURE DEVELOPMENT

Estimations of growth and yield for a wider range of stand conditions and longer periods of time, for example, over rotational cycles, must be validated. As relationships of the effects of management Emory Oak woodlands upon both water quantity and quality become known, it may be possible to link growth and yield model to water quanity and quality models, providing a predictive watershed-based tool for mangagers of Emory Oak Woodlands.

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Sky Island Aquatic Resources: Habitats and Refugia for Native Fishes

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Abstract.—The combination of topography and meteorology of the Sky Island geographic area in southern Arizona produces isolated, unique and invaluable aquatic habitats. Orographic rainfall and xeric climate combine with basin and range geology to produce: 1) disjunct perennial streams on mountain ranges and their bajadas and pediments, 2) isolated springs and spring runs on both mountains and in the inter-basin, valley areas, and 3) valley streams sustained by basin aquifers.

The extant native fish fauna of this area is un-diverse (13 species) but uniquely adapted to survive harsh, limited aquatic habitats. Current threats to the native fish fauna include: 1) pumping of aquifers 2) water diversions and 3) introduced species of fishes. The security of the native fish fauna of the southeastern "sky island" region of Arizona resides in 1) extensive public and key private land ownership, 2) jurisdiction of landscapes encompassing isolated aquatic habitats, 3) the official listing status of species, 4) vigilant monitoring and recovery activity, and 5) international cooperation.

INTRODUCTION

The Sky Islands of southeastern Arizona are at the northern limits of the Madrean Archipelago. The topographic features of this arid region combine with weather patterns (Green and Sellers 1964) to produce isolated aquatic habitats on mountain ranges, their bajadas and pediments, and in basin areas interdigitated between uplifted landscapes. Historically, an un-diverse fish fauna has sustained itself notwithstanding cycles of extreme drought and extensive flooding (Minckley 1973, Deacon and Minckley 1974, Rinne and Minckley 1991).

Anthropogenic factors have induced additional impacts on those naturally occurring (i.e drought, flooding, wildfire (Hastings 1959). Commencing in the late 1800's extensive livestock grazing was imposed on the landscape (Hendrickson and Minckley 1984). Escalation of agricultural development of floodplain areas commenced in the 1950s and placed further demand on surface water resources through water diversion and on aquifers through groundwater mining. Finally, increasing human population growth in the area was followed by introduction of nonnative species of fishes for sport and biological control. Despite the threats from habitat loss and introduced species, land ownership is perhaps the sole remaining securitor of aquatic habitats for native fishes.

The objectives of this paper are to: 1) introduce the geologic and climatic setting producing the varying types of aquatic habitats and their distributions across the landscape, 2) delineate land ownership as it relates to extant aquatic habitats, 3) introduce and discuss the historic and currently residing native fish fauna and its status, 4) address the threats to the native fishes, and 5) discuss the management guidelines to sustain these valuable aquatic resources and their native fishes.

THE SETTING

Topography—As stated by Green and Sellers (1964) "One of the most distinctive sections of Arizona lies in the southeast corner. Here desert plains, lush grasslands, and pine-topped moun-

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tains are profusely intermingled to produce a picture which suggests simultaneously both feast and famine." This region lies just to the east of the eastern margin of the Sonoran Desert (Jaeger 1957, Dunbier 1968). In southeastern Arizona, most mountain ranges rise to over 2200 m. Elevations over 2750 m occur (fig. 1). The Pinaleno Mountains containing Mt. Graham and Heliograph Peak surpass 3,000 m (3060 and 3270 m, respectively) and are the pinnacles of the Sky Islands in this region. However, Chiricahua Peak (2985 m), Mt. Wrightson (2875 m), and Miller Peak (2880 m) approach the 3,000 meter mark. Where roads occur, one can drive from hot desert environments to cool montane climate through several vegetational life zones (Lowe 1985) in less than a hour.

These topographic features are components of one of the three major geologic zones in Arizona, the Basin and Range Province (Nations and Stump 1981). Isolated block-faulted mountains of ancient (Precambrian, Paleozoic, Mesozoic and Cenozoic) materials flanked by interdigitated outwash plains and surrounded by continuous basins or troughs characterize the region. Generally coursing from northwest to southeast, these insular mountain ranges dictate the course of and feed into the broad alluvial valleys where major rivers are similarly aligned (fig. 1; and see below). These conspicuous, contiguous uplifted landforms are in near enough proximity that one range is most always in view from another.

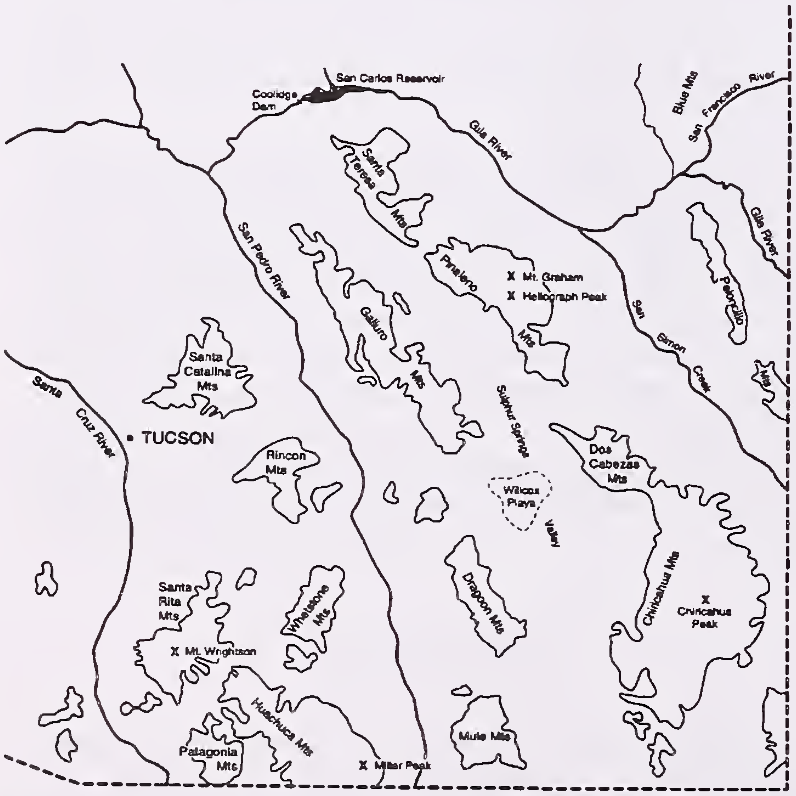

Figure 1.—Principal mountain ranges, peaks, and watercourses in southeastern region of Arizona. Map modified from Green and Sellers, 1964.

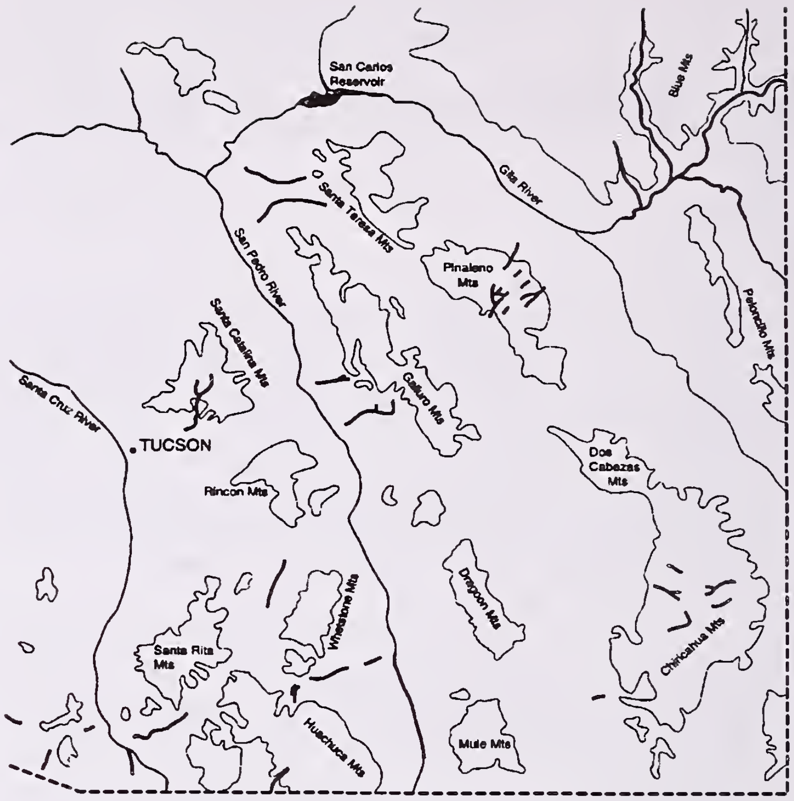

Figure 2.—Perennial waters in the southeastern region of Arizona relative to principal mountains ranges. Map modified from Brown, Carmony, and Turners' 1977 map of perennial streams and wetlands.

Four major river valleys or basins lies between the sky island topography (fig. 1). The San Pedro, San Simon and Santa Cruz rivers all flow north ultimately to the Gila River. In contrast to the above rivers, the Sulfur Springs Valley drains south into Mexico (fig. 2). In geologic time, the other four rivers flowed south into Mexico (Melton 1960, 1965; Rinne 1976).

The San Francisco and Gila rivers enter the region from the east in southwestern New Mexico and derive most of their water supply from the mountains of this region. These two rivers sustain surface flow more commonly than do the Santa Cruz, San Simon and San Pedro rivers. Except in times of high runoff and flood events that normally result from either summer convectional storms or winter storms from the Pacific, the San Pedro, Santa Cruz, and San Simon rivers flow subsurface and intermittently in alluvial materials than may reach depths of more than 500 m. Sustained surface flow in the one reach of the upper Santa Cruz results from sewage treatment effluent (fig. 2).

Numerous small perennial creeks are superimposed upon the mountain ranges and their adjoining slopes (fig. 2). Several streams are positioned upon uplifted land masses (e.g. Ash, Grant and Cave creeks) on the Pinaleno and Chiricahua ranges, respectively. Most perennial waters, however, are located on flanking mountain slopes (bajadas or pediment plains) before they become intermittent and ultimately consumed by evaporational loss and valley or basin alluvium as they make their way to valley floors (fig. 2). Base flows of most streams are mostly less than a cubic foot per second. These streams are frequently canyon-bound and may contain deep pools and large boulders intermixed with riparian vegetation. Aquatic habitats on flanking slopes are more permanent than the large rivers in the basins and provide more secure habitats for native fishes.

Springs and spring runs in the region occur frequently, at varying sizes, and differing elevations (Feth and Hem 1963). These aquatic habitats form when either a fracture or fissure in the earth's surface allow deep waters to emit to the surface or when subsurface accumulations of water at upper elevations on the mountain ranges gravitate through substrata to lower elevation bajadas and valley floors. Many are intermittent and seasonal. Others such as Monkey Springs are consistently perennial and are constant in temperature and water quality. Artesian springs occur in extreme southeastern Arizona on the U. S. Fish and Wildlife Service's San Bernadino National Wildlife Refuge and in the San Pedro valley in the vicinity of St. David, Arizona. These springs result from the interactions of permeable and impermeable layers of valley alluvium that result in water pressure buildup, which ultimately is released with considerable force at the surface.

Cienegas or wet meadows are the final natural-occurring aquatic habitat types. These wetland habitats were once much more widespread in southeastern Arizona than at present (Hendrickson and Minckley 1984). These are formed through the combined processes of water accumulation and vegetation propagation and succession. Because of the importance of these aquatic resources as both habitat for native fishes and for their functioning as "sponges" to supply water to downstream creeks and rivers in time of drought, attempts are being made to restore them on the USFWS's San Bernardino National Wildlife Refuge.

Climate—The southeastern portion of Arizona is not the most arid region in the state. Although roughly half of the state receives less than 25.4 cm of precipitation per year, the majority of that area is in the southwest and north east. The San Simon Valley does align with these areas of less than 25.4 cm of annual precipitation (fig. 3). The Chiricahua Mountains receive twice to 2.5 times the amount of precipitation as the nearby San Simon Valley. Most of the rainfall comes in the monsoon period July and August when atmospheric wind patterns issue from the Gulf of Mexico and Mexico to the south (Green and Sellers 1964). Summer convectional storms although isolated and short in duration, are often intense and occur, in part, as moisture laden air is thrust upward and cooled by the respective mountain ranges. They also result from rising moist air which create cells of low pressure. In winter, air flow from the West ushers in Pacific storms. Normally, May-June is the time of driest or drought conditions. In most simple terms, precipitation is controlled by moisture laden air, mountainous terrain, prevailing air flow or wind patterns and thermal heating. In turn, these factors are responsible for streamflow and aquifer recharge.

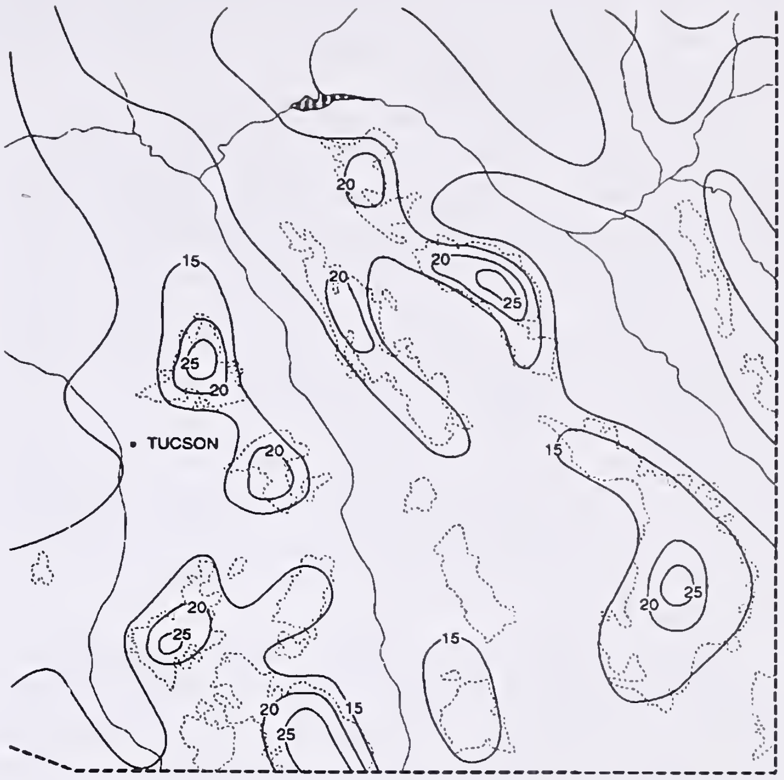

Figure 3.—Map of annual rainfall relative to sky islands in southeastern Arizona, modified from Green and Sellers (1964).

Vegetation—The vegetation of the Southeast is dictated by the climate of the region. Succession from desert vegetation on basin floors to evergreen forests on mountain tops occurs abruptly and distinctly (Lowe 1985, Brown and Lowe 1982). Riparian corridors of cottonwood (*Populus*), Sycamore (*Platanus*) and other hardwood riparian species (Brown and Lowe 1982, Minckley and Brown 1982, Szaro 1984) line creeks and rivers. Most of the area in the Southeast is categorized as

Semidesert Grassland. Madrean Evergreen Woodland and Chihuahuan Desertscrub comprise the majority of the remainder of the landscape (Brown and Lowe 1982.)

Land Ownership—Based on a 1977 State of Arizona map (Dept. of Economic Planning and Development), a large percentage (75%) of the landscape in the Southeast is under Federal (U. S. Forest Service [18%] and Bureau of Land Management [17%]) and State ownership (31%) and jurisdiction (fig. 4). The mountain ranges largely comprise the disjunct components of the Coronado National Forest. The U. S. Bureau of Land Management owns a large block of land in the San Simon and Gila River valleys. Equally important is BLM management of the San Pedro National Riparian Conservation Area and Aravaipa Creek Primitive Area.

United States Fish and Wildlife holdings are largely comprised of two National Wildlife Refuges and are very small relative to total landscape area (fig. 4). State lands are intermittently dispersed across the basins and river valleys. By comparison, the majority of the private ownership is in the basins and along river valleys. National parks and monuments and military reservations also comprise a small (<5%) proportion of the landscape. Private holdings by The Nature Conservancy (e.g. Canelo Hills and Sonoita Creek) are minute relative to the total landscape, however, similar to Fish and Wildlife lands, are disproportionately significant relative to their size by providing both key extant and potential aquatic habitats for the native fishes.

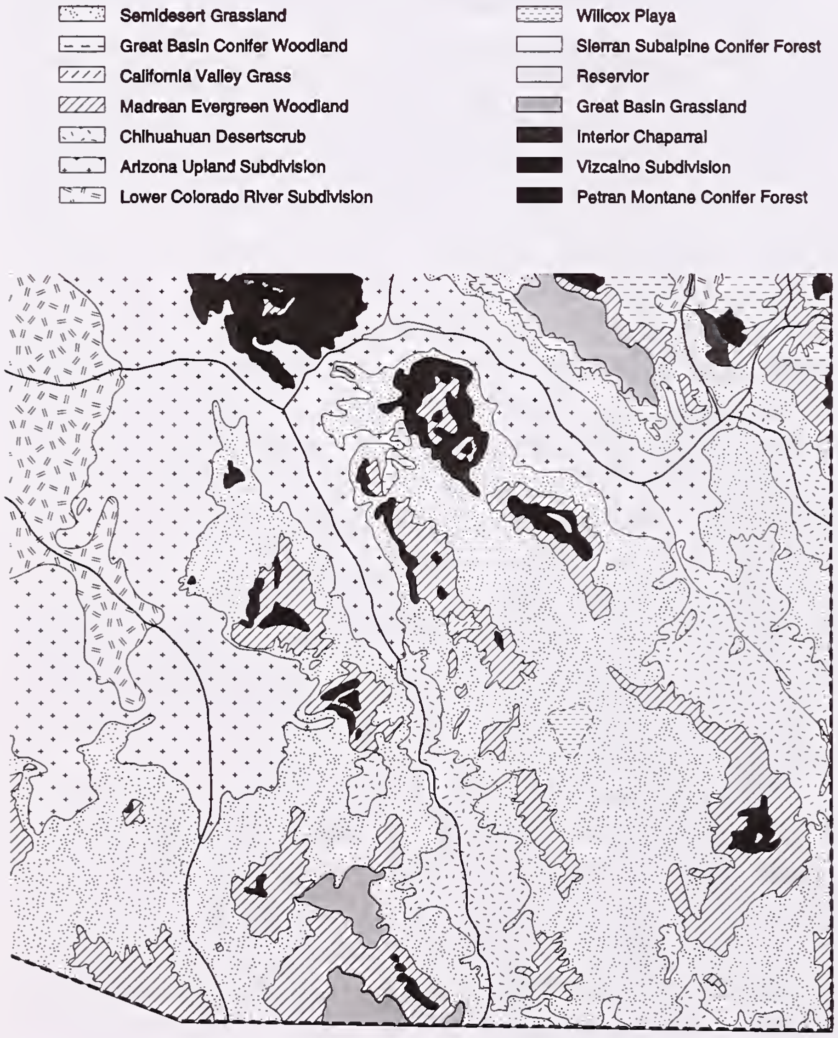

Figure 4.—Map indicating vegetation of southeastern Arizona. Map based on and modified from Brown and Lowe (1977).

THE FISHES

The extant naturally-occurring native fish fauna of the region is characteristically un-diverse (Minckley 1973, Rinne and Minckley 1991), currently numbering only thirteen species (Table 1). Most all are cypriniforms (i.e. minnows and suckers) which is characteristic of other desert regions in the United States and around the world (Rinne et al. in press). The remaining species, Gila topminnow (*Poeciliopsis occidentalis*) is the only extant, naturally-occurring cyprinodontiform taxa in the region (Minckley 1973, Minckley et al. 1977, Simons et al. 1989). A population of desert pupfish, *Cyprinodon macularius* persists in the Quitobaquito Springs, Organ Pipe Cactus National Monument, also in southern Arizona but to the west of the area under discussion.

This region is the center of distribution for the Gila chub (*Gila intermedia*) (Rinne and Minckley 1970, Minckley 1973, Rinne 1976) and Gila topminnow (Simons et al. 1989). Two congeners, the Yaqui (*G. purpurea*) and Sonora (*G. ditaenia*) chubs (Miller 1945, Minckley 1973) and the Mexican stoneroller (*Campostoma ornatum*) are restricted to south-flowing headwater streams of the Rios Yaqui and Magdalena and closed basins of northern Mexico (Hendrickson et al. 1980). The Sonora chub occurs in Arizona only in Sycamore Creek on the Coronado National Forest (Miller 1945, Carpenter and Maughan 1993.) The Yaqui chub occurs only as a result of removal from Astin spring in Blackwater Draw a tributary to San Bernardino Creek and introduction in Leslie Creek where they survive to present. Additional chubs were captured in the Rio Yaqui and introduced into the waters of the San Bernardino National Wildlife Refuge.

The remaining species, longfin dace (*Agosia chrysogaster*), desert (*Catostomus clarki*) and Sonora (*C. insignis*) suckers, and speckled dace (*Rhinichthys osculus*) are widespread and gener-

Table 1.—Aquatic habitats and associated native fishes of southeastern Arizona, 1994.

Habitat						Species							
	AC	CI	CC	GR	GI	GP	GD	RO	MF	RC	PO	CO	CF[1]
Creeks													
Arivaca	X												
Aravaipa	X	X	X	X				X	X	X			
Bass Can.	X	X	X					X					
Bonita	X	X	X					X					
Cave Can.								X					
Cienega	X				X						X		
Eagle	X	X	X		X			X	X				
Hardin C.	X	X	X					X					
Leslie	X					X					X		
Odonnell		X			X								
Redfield	X	X	X		X			X					
Redrock	X										X		
Rucker	X											X	
Sabino					X								
San Bernardino				X					X		X		
Sonoita	X	X	X					X			X		
Sycamore								X					
Turkey		X	X		X								
Rivers													
Gila	X	X	X	X				X	X	X			
San Fran.	X	X	X					X		X			
San Pedro	X	X		X									
Santa Cruz	X	X	X		X		X						
Babocomori	X				X								

[1] *AC = longfin dace, Agosia chrysogaster; CI = Sonora sucker, Catostomus insignis; CC = desert sucker, Catostomus clarki; GR = roundtail chub, Gila robusta; GI = Gila chub, Gila intermedia; GP = Yaqui chub, Gila purpurea; GD = Sonora chub, Gila ditaenia; RO = speckled dace, Rhinichthys osculus; MF = spikedace, Meda fulgida; TC = loach minnow, Rhinichthys cobitis; PO = Sonora topminnow, Poecilliopsis occidentalis; CO = Mexican stoneroller, Campostoma ornatum; and CF = beautiful shiner, Cyprinella formosus.*

ally abundant in the Gila River Basin to the north (Minckley 1973) and in the case of longfin dace in Mexico to the South (Hendrickson et al 1980). In contrast, the once widespread and abundant roundtail chub (Rinne and Minckley 1970, Minckley 1973, Rinne 1976), *Gila robusta*, is becoming increasingly more rare in the Gila Basin, now extant only in Eagle, Bonita, Aravaipa creeks and the upper Gila River. Both suckers and the three minnows are all candidate species; the speckled dace is a Forest Service Sensitive species.

Two federally threatened species, the spikedace (*Meda fulgida*) and loach minnow (*Rhinichthys cobitis*) occur in southeastern Arizona at the southern limits of their range. These two species occur naturally in the Gila River headwaters to the east and in the mainstream as it enters the state of Arizona (Rinne 1989, 1991, Propst et al. 1986, 1987, Hendrickson et al. 1994). Other populations of loach minnow are to the north in the Blue and San Francisco rivers tributaries of the Gila. The spikedace also occurs in the upper Verde River in the north-central part of the state. Sustaining populations of both species occur in Aravaipa Creek, Pinal County.

Eagle, Redfield and Sonoita creeks also sustain five native species at present. A half dozen other streams contain 3 or less species of native fishes, 3 contain only a single species (Table 1).

Several taxa of native fishes have been extirpated from the aquatic resources of the Southeast. Several large river species, the Colorado squawfish and flannelmouth and razorback suckers, once occurred in the Gila and San Pedro Rivers. The squawfish was formerly distributed as far upstream as Fort Thomas near Safford on the Gila River and Fairbank on the San Pedro River (Minckley 1973). The desert pupfish was once widely distributed in the Gila, San Pedro and Santa Cruz rivers. It is now absent from these waters.

An undescribed pupfish from Monkey Springs was formerly abundant in this remarkable spring and a downstream cienega. This high carbonate water spring formed an impressive (5+ meter) travertine structure which isolated the pupfish from downstream populations through time. Attempted modification by man in the 1960s breached the travertine seal and drained the cienega. The pupfish survived in abundance in the springhead until largemouth bass (*Micropterus salmoides*) were introduced for sport fishing in 1969. By 1971 this undescribed species was extinct (Miller et al. 1989).

To exacerbate the loss of the pupfish, an unusual form of Gila chub, perhaps different taxonomically due to isolated above the travertine dike, was also lost to predation by largemouth bass. The author recalls being involved personally in reintroducing probably the last living members of this perhaps unique fish from a stilling basin below the artificial pond following draining to remove the largemouth bass. Attempts were unsuccessful and this fish was rendered extinct by largemouth bass (Minckley 1973) that either survived attempted removal or were later reintroduced.

The beautiful shiner, *Cyprinella lutrensis*, once occurred in the San Bernardino Creek, headwaters of the Rio Yaqui of northern Mexico. It is now extirpated from Arizona waters. The Yaqui catfish, *Ictalurus pricei*, and Yaqui sucker (*Catostomus bernardini*) similar to the beautiful shiner occurred in extreme southeastern Arizona in headwaters of the Rio Yaqui.

Impacts and threats to the native fish fauna—Loss or alteration of aquatic habitats and introduction of non-native fishes are the primary threats to the native fishes (Miller 1961, Rinne 1990, 1993, Rinne and Minckley 1991). Extensive alteration and loss of aquatic habitats occurred in the late 1800s during initiation of a period of arroyo cutting (Hastings 1959, Hastings and Turner 1964, Hendrickson and Minckley 1984). Arroyo cutting has been attributed, in part, to excessive, uncontrolled livestock grazing and, in part to irrigation diversions in case of the San Simon. Creation of nick points or gradient changes then rapidly enlarged and moved upstream toward headwaters lowering water tables up to 5+ meters in some reaches of stream (fig. 5). Extensive loss of cienegas or wet meadows and once perennial reaches of major rivers such as the San Simon and

Figure 5.—Arroyo cutting as indicated here in Cienega Creek (A), Santa Cruz County, Arizona, commenced in 1890 and rapidly and markedly altered aquatic habitats in southeastern Arizona. Dark bands in incised bank (B) indicate former cienega or wet meadow habitat. Lowering of water tables to near or below root depths (C) have resulted in the loss of riparian vegetation.

San Pedro had a dramatic negative impact on native fishes.

No major dams are present in the Southeast, however irrigation diversions cumulatively have resulted in periodic loss of surface water, primarily in summer when not only quantity but quality of streamflow is critical to survival of fishes. These diversions combined with mining of river aquifers most probably caused the demise of the large river species such as Colorado squawfish and razorback sucker. Only the more hardy and adaptive species such as longfin dace, and desert and Sonora sucker have survived and persist in downstream, mainstem river channels such as the San Pedro and Santa Cruz (Table 1).

Superimposed on habitat loss and alteration have been the introduction of non-native species for sport and biological control (Simons et al 1989, Minckley, 1973, Rinne 1993, in press). Introduction of the introduced, highly competitive western mosquitofish, *Gambusia affinis* (Meyers 1965) for mosquito control has had major negative impact on the native Gila topminnow. The mosquitofish has been demonstrated to effect ively out compete the topminnow through direct predation (Schoenherr 1974, 1985; Meffe 1984, 1985). Cattle tank or stock pond introductions of species of centrarchids (sunfishes and basses) also have been detrimental to native species. For example, the green sunfish, *Lepomis cyanellus*, now occupies Sabino Creek where a population of the rare Gila chub is extant. The introduced species is gradually, but surely working its way to the headwaters, displacing the native chub as it goes (Dudley and Matter 1994). Although the mechanism of replacement is not clear, direct predation, as recorded for mosquitofish on topminnow, is very probably a contributing factor.

As part of an overall restoration effort for razorback sucker (Johnson 1985) attempts were made to restock the species into the Gila River east of Safford. Immediate predation by a large introduced, resident predator, flathead catfish, *Pylodictus olivaris*, had dramatic, negative impacts (Marsh and Brooks 1989). Removal of these predators is unfeasible, in part, because of size of habitat and, in part,undesirable because of potential impact on other species (see below).

Cessation of stocking of non-native species for both sport and bait will be essential for commencing to reduce this threat to the native fishes of southeastern Arizona. Barriers to prevent upstream invasion of non-natives from downstream rivers may be necessary in some instances. Stream renovations have been widely used in fisheries management in Arizona to remove undesirable species prior to restocking of target species (Rinne and Turner 1991, Meffe 1983). However, because of potential impacts on other aquatic species such as macroinvertebrates (Minckley and Mihalek 1981), which are relatively little studied in the southeastern Arizona, this management technique should be used as a last resort.

MANAGEMENT STRATEGIES

Land ownership—A key component to sustaining the native fish fauna of the Madrean Archipelago region in southeastern Arizona is land ownership, and in turn jurisdiction over aquatic habitats (Williams et al. 1989. Rinne 1993, Rinne and Janisch in press). Because the majority (75%) of the landscape is under federal or state jurisdiction and management, the aquatic habitats on which the native fishes depend can be more readily and assuredly conserved. The purchase by public agencies and private organizations of key private lands that encompass key aquatic resource areas than contain one or more native fish species is equally as important. The Nature Convervancy's Canelo Hills and Sonoita Creek Preserves are two invaluable examples. These two Preserves protect habitats for a half dozen native fish species.

The former San Bernardino Ranch on the United State Mexico Border is now under U. S. Fish and Wildlife Service ownership and management. The San Bernadino National Wildlife Refuge encompasses 2,309 acres and is now managed to sustain six species of native fishes of the Rio Yaqui, Mexico that once occurred in southeaster Arizona, but have been extirpated from the waters of the state (Hendrickson et al. 1980). The San Bernardino NWR was acquired by the U. S. Fish and Wildlife Service in 1982. A management plan for the Refuge (U. S. Fish & Wildlife Service 1986) states "The refuge was purchased in 1982 to provide habitat and refuge for 6 Rio Yaqui fishes." Currently, three (Yaqui chub and topminnow, and beautiful shiner) of a total of eight species native to the Rio Yaqui are being sustained at the Refuge. Plans include re-establishing the Yaqui catfish and sucker and ultimately the Mexican stoneroller, longfin dace and roundtail chub. In addition, the rare Chiricahua leopard frog also occurs in waters of the Refuge.

Similarly, the Buenos Aires National Wildlife Refuge, a 100,000+ acre parcel is managed for a number of endangered species. Similar to The San

Bernardino Refuge, a management plan exists for this Refuge. Ponds on this Refuge have been used to grow out the threatened razorback sucker and endangered humpback chub (*Gila cypha*) for restocking in historic range. Similar to the San Bernardino NWR , a population of the leopard frog also is extant as is the only population of masked bobwhite. Two plants on the refuge are also endangered.

A significant acquisition by the Bureau of Land Management on the San Pedro River affords protection to two native species (Table 1). The management plan for this valuable riparian corridor that encompasses over 100 km of the mainstream San Pedro. The San Pedro in the reach of this specially designated has "certified" instream flow designation.

Perhaps the jewel of the streams in the Southeast is Aravaipa Creek (fig. 4). It contains seven of the original 17 Gila River basin native fish species (Barber and Minckley 1966, Rinne 1993). Two of the seven species, spikedace and loach minnow, are federally threatened species. Three of the remaining four (desert and Sonora sucker and speckled dace) are candidates for listing. The speckled dace is also a U. F. Forest Service sensitive species. This Upper Sonoran Desert stream is within the Aravaipa Canyon Wilderness area. Instream flow rights are in "permitted status" for this creek thereby protecting the aquatic biota (Dept. Water Resource 1993).

Listing status—A important factor to sustaining the native fishes in southeastern Arizona is their official listing status (Table 2). By law, federal agencies cannot expend monies or conduct any activities which will negatively impact a listed species. The Forest Service and Bureau of Land Management own and are responsible for management of extensive portions of the landscape which encompasses aquatic habitats for native fishes. Accordingly, by status and the law these fishes are more secure relative to non- listed species. Notwithstanding the Endangered Species Act, the Forest Service, Southwest Region (R-3) has official documents (USDA Forest Service 1992, 1993) that are designed to sustain all native species, including fishes (Rinne and Medina in press).

Several species in the region are "candidate species" (Table 2). Although listing of species has been and will be necessary, it is not the bottomline. As stated over a decade ago by Johnson and Rinne (1982) we must move from listing (and thereby official protected status) to on-the-ground recovery activity. The Forest Service is currently in process of drafting "Conservation Assessments" for species that are candidates for listing in an effort to prevent their official listing. These management plans chart a strategy to sustain, enhance and recover species in lieu of their listing. Active, fully-funded and viable recovery plans are extant for probably less than a quarter of almost 900 listed species in the United States. For the threatened and endangered fish species listed in Table 2, few species have official recovery plans in place and functioning. Listed status provides protection, but recovery will only come with proactive, focused, and viligant effort.

Table 2.—The status of native fishes occurring in the southeastern region of Arizona. Status abbreviations are ACS, Arizona candidate species; ASE, Arizona state endangered; AST, Arizona state threatened; FSS, Forest Service sensitive; FT, Federally threatened; FE, Federally endangered; Candidate for listing; C.

Common Name	Scientific name	Status	Rec.Plan
Sonora Sucker	*Catostomus insignis*	C	
Desert Sucker	*Catostomus clarki*	C	
Yaqui sucker	*Catostomus bernardini*	ASE/C	
Speckled dace	*Rhinichthys osculus*	FSS	
Loach minnow	*Rhinichthys cobitis*	FT	Yes
Yaqui shiner	*Cyprinella formosa mearnsi*	FT	Draft
Gila chub	*Gila intermedia*	AST	
Roundtail chub	*Gila robusta*	AST/C	
Sonora chub	*Gila ditaenia*	FT	Yes
Yaqui chub	*Gila purpurea*	FE	Draft
Spikedace	*Meda fulgida*	FT	Yes
Mexican stoneroller	*Campostoma ornatum pricei*	ASE	
Desert pupfish	*Cyprinodon macularius*	FE	Yes
Gila topminnow	*Poeciliopsis o. occidentalis*	FE	Yes
Yaqui topminnow	*Poeciliopsis o. sonoriensis*	FE	Yes
Yaqui catfish	*Ictalurus pricei*	FT	Draft
Longfin dace	*Agosia chrysogaster*	C	

Monitoring—Periodic monitoring of fish species and communities in isolated, disjunct habitats is necessary to both monitor trends and facilitate early warning of impending threats to and loss of populations. Because of the extent of public lands in the area, responsibility lies with state and federal agencies to insure that their management activities do not negatively impact aquatic habitats and, in turn, native fishes. Although the two species of fishes rendered extinct in southeastern Arizona were in the same isolated habitat on private land, this could potentially happen on public lands if populations status and trends are not monitored.

International cooperation—Because about half of the fishes listed as currently occupying the waters of southeastern Arizona occur in northern

Mexico (Hendrick son et al 1990), international cooperative management will play an important role in sustaining these species. Although not a new concept to the U. S. Fish and Wildlife Service and to researchers in academia, the U. S. Forest Service recently enter into an MOU with Mexico designed to foster cooperation with sister agencies in Mexico. Researchers and land managers in the two countries should be ever viligant of opportunities to interact to insure the survival of these species.

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Status of Gila Topminnow and Results of Monitoring the Fish Community in Redrock Canyon, Coronado National Forest, 1979 — 1993

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Abstract.—Redrock Canyon, an intermittent tributary to Sonoita Creek in the Santa Cruz River basin near Patagonia, is one of eight sites in Arizona supporting a natural population of Gila topminnow *Poeciliopsis occidentalis occidentalis*, an endangered fish. The stream also contains nonnative western mosquitofish *Gambusia affinis* and largemouth bass *Micropterus salmoides*, predators with proven potential to eliminate Gila topminnow. In 1979, native Gila topminnow were throughout the stream, native longfin dace *Agosia chrysogaster* occurred low in the drainage, and western mosquitofish and largemouth bass in a stock tank in the headwaters. Currently, Gila topminnow remains present throughout Redrock Canyon, but western mosquitofish now predominate in the headwaters, in tributaries, and near the mouth. Whether this pattern reflects coexistence, or ongoing replacement of the native species is unknown. Longfin dace now occur throughout the stream, largemouth bass are established in the headwaters, and nonnative green sunfish *Lepomis cyanellus* and bluegill *Lepomis macrochirus* are occasionally found. A single desert sucker *Catostomus (Pantosteus) clarki* was collected in 1987.

Potential loss of Gila topminnow from Redrock Canyon, and establishment of several nonnative fishes will reduce aquatic biodiversity locally and in the National Forest System. Conservation efforts to preserve the aquatic biodiversity of Redrock Canyon have included fencing to exclude livestock and motorized vehicles, changes in livestock management, watershed stabilization structures, and constraints on placement of a recreation trail. Further efforts should include removal of nonnative species, continued surveillance of the fish community, and feedback mechanisms to direct management activities

INTRODUCTION

Gila topminnow (*Poeciliopsis occidentalis occidentalis*), termed "one of the commonest fishes in the southern part of the Colorado River drainage basin (Hubbs and Miller 1941)..." prior to about the 1940's, was nearly extinct in the United States by 1967 when it was listed as endangered (U.S. Fish and Wildlife Service [FWS] 1967). The rapid decline of this diminutive livebearer was attributed to loss of habitat from dams and diversion of water, habitat destruction from livestock grazing, stream channelization, roads and mining, and introduction of nonnative, competing fishes, principally western mosquitofish (*Gambusia affinis*) (Meffe et al. 1983). Gila topminnow now remains in eight natural sites in Arizona (Brown and Abarca 1992); only one, Redrock Canyon in Santa Cruz County, is on National Forest System (NFS) lands. Redrock Canyon, a tributary of Sonoita Creek in the Santa Cruz River drainage, is located within Coronado National Forest near Patagonia.

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Minckley et al. (1977) were not optimistic regarding the possibility of coexistence between topminnow and mosquitofish, concluding that mosquitofish will ultimately replace the native species. In most instances, Gila topminnow have not been able to coexist with western mosquitofish, often being eliminated within a few years after introduction of the nonnative (Minckley et al. 1977, Meffe 1984, 1985). In the few cases where the two species appear to coexist, no readily apparent answer is available to explain how the balance is maintained. However, it appears related to periodic flooding, complexity of habitat, and the presence of springhead refuges (Meffe et al. 1982, Meffe 1984, 1985, Minckley and Meffe, 1987).

Habitat requirements of Gila topminnow and western mosquitofish appear similar, thus artificial alteration of habitat to favor one species over the other appears problematic. Both prefer shallow, warm, and fairly quiet waters, but can adjust to a rather wide range, living in quiet to moderate currents, depths to one m, and water temperatures from constant 25°C springs to streams fluctuating from 6 to 37°C. A wide variety of water types, including springs, cienegas, marshes, permanent or interrupted streams, and edges of large rivers can provide habitat. Preferred habitat contains dense mats of algae and debris, usually along stream margins or below riffles, with sandy substrates sometimes covered with organic mud and debris. Both are livebearers and do not select spawning sites (Minckley 1973, Meffe et al. 1983, Forrest 1992).

Western mosquitofish has been reported from Redrock Canyon since the mid-1980's (Simons 1987), but its relative abundance compared to Gila topminnow has been variable in both space and time. Whether this pattern reflects coexistence of the two species, or slow replacement of the native species is unknown. Potential loss of Gila topminnow from the Redrock Canyon drainage, and establishment of nonnative species will reduce the native (naturally evolved) biotic diversity (see Angermeier 1994) of the area, and of the NFS.

The Forest and Rangeland Renewable Resources Planning Act of 1974 (RPA) directed that forest planning would provide for diversity of plant and animal communities based on the suitability and capability of the specific land area. Wildlife and fish goals in the Coronado National Forest Plan (USDA Forest Service 1992a) include provisions for ecosystem diversity by at least maintaining viable populations of all native and desirable nonnative wildlife, fish, and plant species. In neither case was diversity defined. Management plans for the Redrock Canyon area that address grazing and recreational trails have been prepared (USDA Forest Service 1990, 1992b). In both cases, the health and survival of the Gila topminnow were paramount considerations in the proposed actions.

The recovery plan for topminnow (FWS 1984) called for periodic and systematic monitoring of all native and reintroduced populations. Monitoring of the fish community in Redrock Canyon is especially important because of the presence of the nonnative predatory and competitive fishes in the system, including western mosquitofish. Personnel from Arizona Game and Fish Department (AGFD) sampled for Gila topminnow in Redrock Canyon biennially since 1985 (Brooks 1985, 1986, Simons 1987, Bagley et al. 1991, Brown and Abarca 1992). We systematically monitored the fish community annually since 1988. Data from sampling efforts were provided in agency reports, office memos, and field notes. Results of monitoring are ambiguous due to different sampling techniques, reporting methods, and description of sampling localities. This report will summarize results of monitoring from available sources, and describe management activities that were undertaken in order to maintain the natural diversity of the drainage.

STUDY AREA

Redrock Canyon flows westerly from the Canelo Hills approximately 21 km before entering Sonoita Creek in the village of Patagonia, Arizona (fig. 1). Stream elevations range from 1,240 m at the mouth to 1,524 m near Downunder Tank. Average annual precipitation is 45 cm/yr, but daily precipitation can be greater than 10 cm (Sellers, et al. 1985). Redrock Canyon is an interrupted stream (see Reid 1961) with permanent surface flow occurring only in three short reaches, Falls, Gate Spring, and an unnamed tributary below Cott Tank. The remainder of the drainage is intermittent and surface flow occurs only during periods of precipitation and overland runoff. Several stock tanks are in the upper watershed. Discharge in Redrock Canyon is not gaged; the nearest stream gaging station is in Sonoita Creek eight km downstream from Patagonia (Arizona Department of Water Resources station 09481500). The watershed of Redrock Canyon is about 8,100 ha, comprising approximately 15% of the drainage area above the Sonoita Creek gaging station.

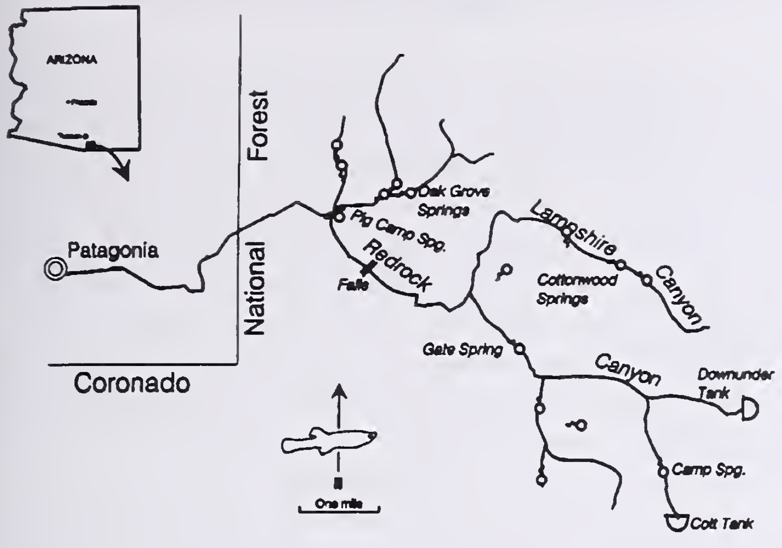

Figure 1. —Map of Redrock Canyon, Arizona, showing placenames mentioned in text.

Continual discharge at that station was recorded during the periods 1931-33 and 1936-72; peak flows have been recorded since 1972. A peak discharge of 453 m^3/s occurred in 1984, the highest recorded. Estimated two-year recurrence events have a discharge of 90 m^3/s, and a 10-year recurrence flood has an estimated discharge of 200 m^3/s (U.S. Geological Survey 1991). Aquatic biota of the Sonoita Creek basin was described by Minckley (1969a).

Aquatic habitat in Redrock Canyon was surveyed in late June 1989 (Stefferud 1989). Precipitation the previous few years was low, and extent of surface water in Redrock Canyon totaled 1,130 m. Surface water, a result of bedrock outcrops forcing subsurface flow to the surface, was noted 1.2 km above the Forest boundary, at Pig Camp Spring, Falls, Gate Spring, and in the Cott Tank drainage. Both Downunder and Cott tanks contained water.

Aquatic habitat types in Redrock Canyon typically were shallow pools formed by loose boulder and cobble berms and connected by shallow riffle/runs across bedrock or coarse sand. The predominant habitat type was shallow riffle/run with shifting sand/gravel substrate, often with watercress (*Rorippa nasturium-aquaticum*) or other aquatic emergent vegetation. Pools were mostly transitory as the berms were rearranged during flooding. Livestock grazing was intensive, with riparian herbaceous vegetation closely cropped and streambanks 100% chiseled by cattle hoof action. The overstory canopy was comprised of decadent Fremont cottonwood (*Populus fremontii*) and velvet ash (*Fraxinus velutina*) with limited reproduction; shrubs were predominately seep willow (*Baccharis salicifolia*). Vertical stucture of riparian vegetation was minimal.

In the drainage below Cott Tank, aquatic habitat consisted of discontinuous trench pools 0.5 to 1.5 m deep, 2 to 4 m wide, and up to 25 m long. The pools were intermittently connected by shallow runs with gravel substrate, or overland flow through grass or grass-like vegetation with no defined channel. Pools had vertical sides and afforded little cover for fish. Herbaceous vegetation was closely cropped by livestock, and there was little vegetation overhanging the pools. Seep willow was the predominate woody riparian species, and was sparse. A primitive road weaved back and forth across the narrow valley bottom and caused severe bank erosion and lateral migration of the channel.

Aquatic habitat in Redrock Canyon has remained essentially unchanged since 1989, although at least two floods of significant size have passed through the drainage. The only notable habitat change has been the deposition of sand in the system. Whereas in 1989, a considerable amount of bedrock was exposed at Gate Spring, a flood in 1990 deposited sand and raised the channel one m in height. Deflector devices installed in the mid-1980's functioned as designed and kept pools open at their bases. Reduction of livestock grazing at Gate Spring is allowing riparian vegetation to stabilize the sand and maintain the elevated streambed.

Although not as dramatic as at Gate Spring, sand deposition was evident throughout the remainder of the drainage. At Falls, a few pools that usually supported Gila topminnow were filled in with sand, and have not yet reestablished. In the Cott Tank drainage, flood debris indicated that the stream was out of its banks, but little channel damage or change was observed. Since 1992, exclusion of livestock grazing from the Cott Tank drainage has resulted in increased height of herbaceous vegetation and the length of grasses overhanging the pools.

The Cott Tank drainage was fenced in 1993 to exclude livestock and vehicles. Gate Spring was fenced in 1994, and Falls will be fenced in 1995.

METHODS

Survey methods to determine relative abundance and composition of the fish community in Redrock Canyon varied with the individual or agency performing the survey. A variety of equipment was used, including seines, backpack electrofishers, handheld dipnets of various sizes and meshes, and visual observation. Specific sites for sampling were inconsistently chosen or reported, and effort expended was variable. Verification of specimen identity, particularly for the poeciliids, ranged from identification of live specimens in the field to identification of preserved specimens under magnification.

We attempted to follow a protocol that delimits specific sites, sample methods, and timing of the survey to reduce the amount of variability inherent in field investigations. We sampled annually in late fall with 20 cm by 30 cm dipnets with 0.3 cm mesh at defined locations at Falls, Gate Spring, and Cott Tank drainage. Other sites in the drainage were irregularly sampled. We preserved a sub-sample of poeciliids from each site for verifiable identification, and later accession to a museum.

MONITORING RESULTS

Sampling by Rinne et al. 1980

Gila topminnow was first reported from Redrock Canyon in the early 1960's, but extent of the population was not determined until Rinne et al. (1980) reported their observations. In March 1979, they seined a headwater tank seven km above Gate Spring. During May of the same year, they examined Redrock Canyon near Redrock Ranch (Falls) and Gate Spring, several springs in and adjacent to Redrock Canyon, including Cottonwood Spring in Lampshire Canyon, and Camp Spring below Cott Tank. Gila topminnow were found above a two-m bedrock waterfall near Redrock Ranch (Falls) (table 1). At Gate Spring the total population of Gila topminnow was estimated at less than 100 fish. Adult longfin dace (*Agosia chrysogaster*) were found below the waterfall at Falls, and young-of-the-year longfin dace about six km downstream; none were found above Falls. Small (û mm) largemouth bass (*Micropterus salmoides*) were abundant in a headwater tank, and a single western mosquitofish was taken there. No fish were observed in the springs in Lampshire Canyon or at Camp Spring (Rinne et al. 1980).

Sampling by Arizona Game and Fish Department

Biennial surveys by AGFD began in July 1985. Brooks (1986) noted that Gila topminnow were rare at Gate Spring but became more abundant downstream. Largemouth bass were collected at Gate Spring. Western mosquitofish, but no Gila topminnow, were collected in Lampshire Canyon. The source of western mosquitofish was thought to be from an upstream stock tank that also contained green sunfish (*Lepomis cyanellus*) and bluegill (*L. macrochirus*). Other reaches of Redrock Canyon were not investigated.

Simons (1987) documented Gila topminnow and western mosquitofish distribution and relative abundance in Redrock Canyon. He assumed western mosquitofish had invaded Redrock Canyon from Cott and Downunder tanks. Western mosquitofish were abundant and Gila topminnow absent in reaches immediately below each tank. Western mosquitofish occurred to at least the vicinity of Gate Spring. Gila topminnow occurred from about 1.6 km below Cott Tank downstream to Falls. Largemouth bass and sunfish (*Lepomis* sp.), occurred in larger pools in the same areas as western mosquitofish. A third stock tank in a side tributary contained western mosquitofish and bluegill, but there were no fish and very little water in the tributary for four km downstream.

Gila topminnow and longfin dace were found in four isolated and previously unreported sites in Redrock Canyon in April or May 1987: two sites in tributaries to Oak Grove Spring drainage, at Pig Camp Spring, and in lower Lampshire Canyon. By July, 1987, the first three sites supported only longfin dace; the Lampshire Canyon site was not visited. A single desert sucker (*Pantosteus clarki*) was collected below Falls (Simons 1987).

An update of the composition of the fish community in Redrock Canyon was provided by Bagley et al. (1991). In 1989, they found solely Gila topminnow at Falls, Gate Spring and in Redrock Canyon below the entrance of the Cott Tank drainage. Western mosquitofish were found below Camp Spring. In 1990, they reported solely Gila topminnow at Gate Spring and in Redrock Canyon below the entrance of the Cott Tank drainage. Other sites were not visited in 1990.

Brown and Abarca (1992) reported that Gila topminnow were rare and no western mosquitofish were collected when they visited the

Table 1.—Record of monitoring of Gila topminnow at sites in Redrock Canyon drainage, 1979 to 1992. Results are grouped by sites, and site locations are arranged from downstream to upstream reaches.

Date of Sampling	Gila topminnow	Western mosquitofish	Source
Near USFS/pvt land boundary (T22S R16E Sec 03 NW)			
OCT 1990	0[1]	4	This study
Pig Camp Spring (T22S R16E Sec 11 NW)			
1987	Present	Absent	Simons 1987
JUL 1987	Absent	Absent	"
JUN 1989	Dry	Dry	Stefferud 1989
OCT 1991	Absent	Absent	This study
NOV 1992	Absent	Absent	"
Oak Grove Spring drainage (T21S R16E Sec 02 NW)			
1987	Present	Absent	Simons 1987
JUL 1987	Absent	Absent	"
OCT 1990	Absent	Present	This study
Unnamed Spring drainage (T22S R16E Sec 02 NW)			
1987	Present	Absent	Simons 1987
JUL 1987	Absent	Absent	"
OCT 1990	Absent	Absent	This study
Lampshire Canyon (T22S R17E Sec 06 S½)			
1985	Absent	Present	Brooks 1986
1987	Present	Absent	Simons 1987
NOV 1992	Absent	Absent	This study
Lampshire Canyon, Cottonwood Spring (T22S R17E Sec 05)			
MAY 1979	Absent	Absent	Rinne et al. 1980
NOV 1992	Absent	Absent	This study
Falls (T22S R16E Sec 11 NE)			
MAY 1979	Present	Absent	Rinne et al. 1980
JUN 1980	Present	Absent	Meffe and Hendrickson 1980
JUL 1985	Abundant	Absent	Brooks 1986
1987	100%	0%	Simons 1987
NOV 1988	53	0	This study
1989	100%	0%	Bagley et al. 1991
OCT 1989	22	0	This study
OCT 1990	4	0	"
OCT 1991	0	0	"
NOV 1992	161	4	"
Gate Spring (T22S R17E Sec 07 SE)			
MAY 1979	<100	0	Rinne et al. 1980
JUL 1985	Rare	Absent	Brooks 1986
1987	86%	14%	Simons 1987
NOV 1988	48	0	This study
1989	100%	0%	Bagley et al. 1991
OCT 1989	119	0	This study
1990	100%	0%	Bagley et al. 1991
OCT 1990	0	0	This study
OCT 1991	18	0	"
NOV 1992	85	4	"
Unnamed tank (T22S R17E Sec 21 Center)			
1987	Absent	Present	Simons 1987
Between Gate Spring and Red Bank well (T22S R17E Sec 07/17)			
1987	100%	0%	Simons 1987
JUN 1989	Dry	Dry	Stefferud 1989
100 m below windmill, immediately below stone house (T22S R17E Sec 16 SW¼ NE¼)			
1987	62%	38%	Simons 1987
1989	100%	0%	Bagley et al. 1991
1990	100%	0%	"
Lower Cott Tank drainage Silver Tank to Camp Spring (T22S R17E Sec 16 S½ and 21 N¼)			
MAY 1979	Absent	Absent	Rinne et al. 1980
1989	>99%	<1%	Bagley et al. 1991
OCT 1989	323	4	This study
1990	Rare	None	Brown and Abarca 1992
OCT 1990	54	1	This study
OCT 1991	50	20	"
NOV 1992	127	74	"
Upper Cott Tank drainage, Camp Spring to Cott Tank (T22S R17E Sec 21 N)			
1987	0%	100%	Simons 1987
1989	0%	100%	Bagley et al. 1991
OCT 1989	2	122	This study
OCT 1990	1	0	"
OCT 1991	0	23	"
NOV 1992	0	48	"

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[1] Values provided for Gila topminnow and western mosquitofish for this tudy are from specimens accessioned to the Museum of Fishes, Arizona State University.

drainage in August, 1990. They noted that their sampling came ten d after a strong summer monsoon had scoured the stream bed.

Sampling by Stefferud and Stefferud

We sampled sites in the Redrock Canyon drainage annually in the fall from 1988 to 1993. We consistently found Gila topminnow at Falls, Gate Spring, and lower Cott Tank drainage (fig. 2). At Falls and Gate Spring, western mosquitofish were collected in 1992. Actual numbers of Gila topminnow at both sites were reduced in 1990 and 1991 as a result of summer floods that scoured the stream channel.

Collections in Cott Tank drainage also reflected effects of the 1990 and 1991 floods on the abundance of poeciliids; actual numbers of fish were lower in 1990 and 1991 for both species. In lower Cott Tank drainage below Camp Spring, Gila topminnow were always predominant in the collections, although western mosquitofish has increased in relative abundance during the past three years. In upper Cott Tank drainage, western mosquitofish comprised 99% of total collections.

Fish collected in other areas of the Redrock Canyon drainage included western mosquitofish and longfin dace in the main stem near the Forest Service boundary, and western mosquitofish in Oak Grove Canyon in October 1990. Longfin dace were found below the tank in Lampshire Canyon in November 1992; fish were absent above the tank and at Cottonwood Springs. In July 1989, we removed 34 largemouth bass (3 to 25 cm total length [TL]) from pools in the drainage below Cott Tank. The number of young-of-the-year individuals in the sample indicated that reproduction had occurred. Poeciliids and longfin dace were noticeably absent from pools that contained largemouth bass. Due to high water conductivity (1,270 µmhos/cm at 25°C), the backpack electrofisher was ineffective in stunning fish, and not all largemouth bass were removed. Persistence of adult largemouth bass in the Cott Tank drainage was confirmed in November 1992. In October 1990, eleven bluegill (5 to 10 cm TL) were taken from a small isolated pool about one km below the confluence of Cott Tank drainage with Redrock Canyon.

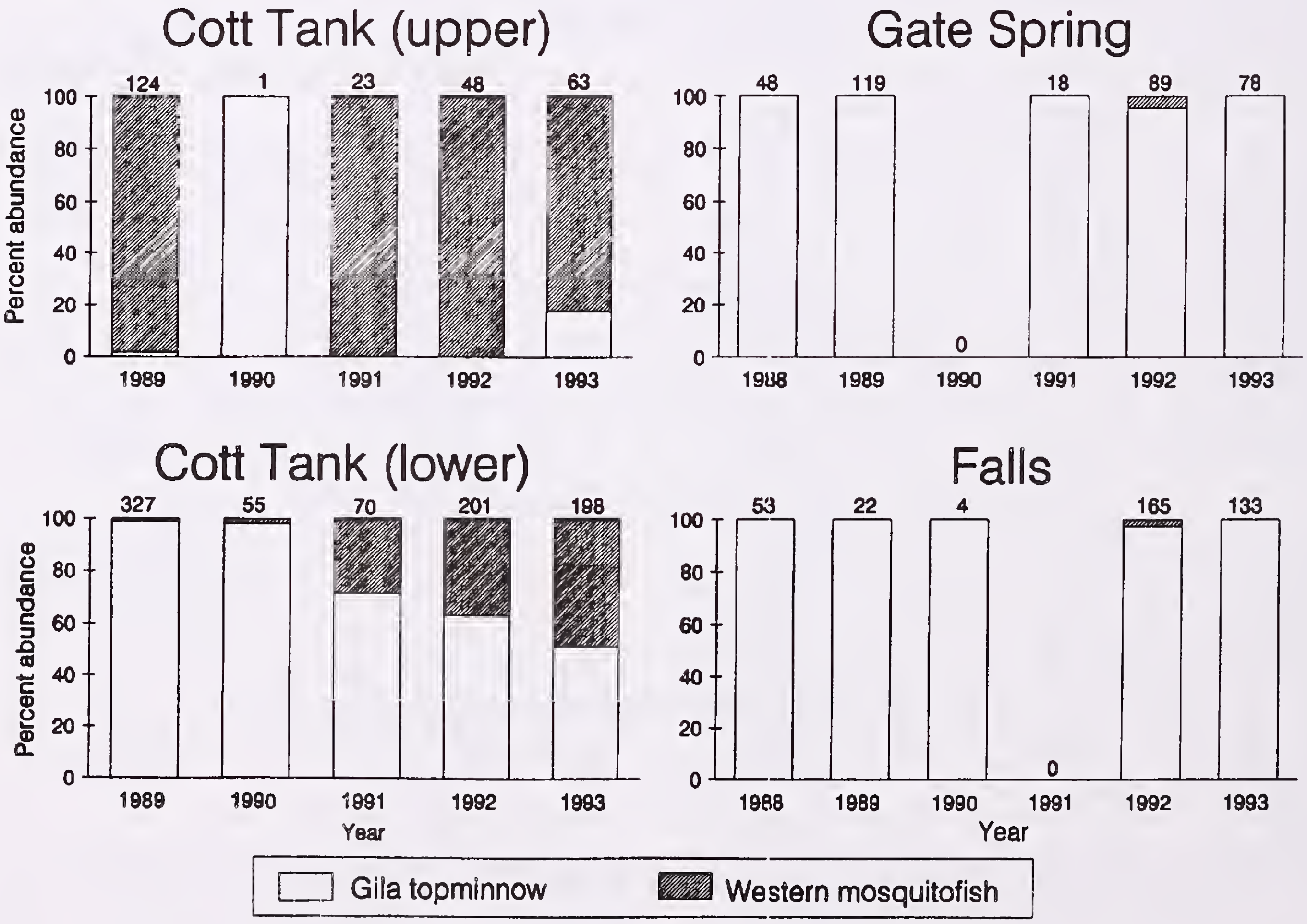

Figure 2.—Relative abundance of Gila topminnow and western mosquitofish at four sites in Redrock Canyon during 1988 to 1993, *N* is represented by numbers above columns. Data are from preserved specimens.

DISCUSSION

The pattern of relative abundance of Gila topminnow and western mosquitofish in Redrock Canyon has been western mosquitofish predominant in upper Cott and Downunder tanks drainages, Gila topminnow predominant in lower Cott Tank drainage, Gate Spring and downstream to Falls, and both species rare below Falls. Presence of any fish in the tributaries to lower Redrock Canyon seems ephemeral and dependent on surface water conditions. With few exceptions, Gila topminnow does not coexist with western mosquitofish (Minckley et al. 1977); the pattern of coexistence in Redrock Canyon is either an anomaly, or the onset of replacement of Gila topminnow. Gila topminnow apparently survive or rapidly recover from periodic floods in Redrock Canyon, and western mosquitofish are decimated, a pattern that has been observed in other streams (Meffe et al. 1982). However an extended period without floods could provide western mosquitofish the advantage needed to take over the system.

Continued survival of Gila topminnow in the wild appears dependent on natural sites that have the proven capability to provide long-term habitat (Hendrickson and Brooks 1991). Our understanding of natural systems, and technological capability to provide artificial habitats is vastly inadequate to let us construct, or even identify, waters that could provide the adaptive, self-sustaining biotic elements necessary for long-term survival of Gila topminnow. To illustrate this point, Gila topminnow was transplanted into ca. 200 springs, seeps, small streams, stock tanks and other artificial waters in southern Arizona during the past 25 years. With few exceptions, those introductions failed. Most failed for obvious reasons such as desiccation, but for a few there was no readily apparent explanation (Minckley 1969b, Minckley and Brooks 1985, Brown and Abarca 1992). Many of the sites were extremely limited in size, and probably could not support a large number of breeding individuals. It is possible that forcing a formerly widespread and riverine species into small and isolated habitats may have made them vulnerable to the special genetic and demographic problems of small populations (Minckley et al. 1991, Belovsky et al. 1994).

Maintenance of Gila topminnow in Redrock Canyon is vital to the survival of the species in the wild in Arizona. Gila topminnow remains in eight natural sites in the state; five contain western mosquitofish, thus their integrity is compromised. Several of the natural sites are restricted in size, have non-diverse habitat, and are highly vulnerable to extirpation from anthropogenic or natural events. Because Redrock Canyon is a relatively long and complex drainage subject to flooding, its channel morphology is diverse and provides a variety of habitats for Gila topminnow. Based on habitat alone, Redrock Canyon should provide for a large population of Gila topminnow at several locations, the abundance of each waxing and waning in accordance with the hydrograph and complex array of other biotic and abiotic conditions present in the natural system. Effects of floods in the upper drainage may be ameliorated by Cott Tank, thus allowing survival of western mosquitofish in the drainage. In addition, the extremely low numbers of Gila topminnow in the upper drainage may be below the minimum number necessary to establish a population, particularly in the presence of western mosquitofish.

Preservation of Gila topminnow in Redrock Canyon will sustain the natural biotic diversity of the NFS. If Gila topminnow is lost there, then both elements that reduce biotic diversity, extirpation and convergence, apply (Angermeier 1994). The natural biodiversity would be reduced through extirpation of the native species, and establishment of nonnative fishes common to other waters of the NFS would reduce biodiversity through convergence. Maintenance of the natural biodiversity in Redrock Canyon (and other natural sites) should be the focus of conservation efforts for Gila topminnow. The program of habitat restoration in Redrock Canyon should be continued, and expanded to include ecosystem recovery by actively eliminating nonnative fishes from the drainage.

RECOMMENDED CONSERVATION ACTIONS

Rinne et al. (1980) recommended management actions to both maintain and expand the population of Gila topminnow in Redrock Canyon. They recommended fencing of the stream at Falls and Gate Spring, protection from hard rock and water mining in the watershed, prohibition of vehicular travel to Gate Spring, and resurveys of the tanks and springs in the canyon to determine abundance and distribution of western mosquitofish. They also recommended removal of western mosquitofish from the drainage.

Many of the recommendations by Rinne et al. (1980) have been accomplished. Three concrete deflector devices were built at Gate Spring in the early 1980's to provide pool habitat for Gila topminnow. Fences have been constructed around the Cott Tank drainage, Gate Springs, Falls, and Pig Camp Spring. Vehicular traffic has been restricted in areas containing Gila topminnow. Annual surveys of perennial waters in the drainage are done. No attempt to remove western mosquitofish from the drainage has been made.

Monitoring of the fish community and aquatic habitat needs to be continued in order to track the well-being of Gila topminnow, and assess effects of anticipated changes in habitat conditions. Cott Tank is a constant source of contamination of nonnative fish to Redrock Canyon. Downunder Tank contains western mosquitofish, which also escape to the drainage immediately downstream. Other tanks in the drainage should be surveyed to determine presence or absence of nonnative species. Nonnative species should be removed from tanks to prevent continued contamination of Gila topminnow habitat in Redrock Canyon. With removal of western mosquitofish from tanks at the head of Redrock Canyon, it is possible that floods would eliminate or greatly reduce the nonnative in the rest of the drainage.

At this time, there is no immediate need for chemical removal of western mosquitofish from the Redrock Canyon drainage. The Desert Fishes Recovery Team have discussed this issue several times at their annual meetings, and concluded that so long as Gila topminnow predominate in much of the drainage, no removal attempts should be made. However, biannual monitoring must be continued to track the relative abundance of the two species. If it appears that western mosquitofish is gaining predominance in the drainage, then steps should be taken to immediately remove the nonnative.

Aquatic habitat in Oak Springs and Lampshire canyons appears suitable to support Gila topminnow, although these sites may desiccate during drought years. The surrounding riparian area in both canyons is intensely used by livestock, which may also restrict reestablishment of the fish. Aquatic and terrestrial riparian habitat in both canyons should be checked periodically to monitor effects of the revised grazing schemes, and assess suitability for establishment of Gila topminnow.

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Yaqui River Fishes Relevant to the Madrean Province: U.S.-Mexico Collaborations

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Abstract.—The native ichthyofauna of the Yaqui River system, Arizona, United States, and Sonora and Chihuahua, Mexico, includes 35 species two of which are undescribed. Approximately 50 per cent of the Yaqui River Basin is located within the Madrean Biogeographic Province, where 13 species of native fishes occur. Eight of these "Madrean" species historically were distributed in both the U.S. and Mexico. Detrimental land and water use practices and introduction of nonnative fishes resulted in the extirpation of four species of fishes historically found in the southeastern corner of Arizona. Binational efforts to reestablish the native Yaqui Basin fauna into Arizona, have resulted in the reintroduction of the beautiful shiner, *Cyprinella formosa*, into the San Bernardino/Leslie Canyon National Wildlife Refuge, and acquisition of Yaqui catfish, *Ictalurus pricei*, broodstock to be used in future reintroduction attempts in Arizona. Recovery actions for the species include development of a recovery plan for the Yaqui River fishes in the U.S. and a monitoring program to assess the status of fish populations in Sonora and Chihuahua. Additional studies of the biology and taxonomy of several native fishes, including the undescribed trout and pupfish in the Yaqui River Basin, as well as habitat protection and long-term monitoring, are badly needed to preserve this unique ichthyofauna from potentially negative effects of ongoing economic developments, proposed timber harvest projects, and introduction of nonnative species.

INTRODUCTION

The Yaqui River Basin is the most important aquatic system for the economy of the State of Sonora, Mexico. This watershed occupies 30% of the State territory with an area of approximately 73,000 km^2 and has an annual discharge of almost 2,800 ha^3, making it one of the major watersheds in the region (Blásquez 1959, Bojórquez et al. 1985). This complex drainage begins in western Chihuahua with the Rio Papigochic system, enters Sonora (as the rios Sirupa and Aros) to receive the Rio Bavispe, then trends southward after collecting the rios Moctezuma-Nacozari system to enter the Gulf of California near Ciudad Obregón, Sonora (Hendrickson et al. 1981). The native ichthyofauna of the Yaqui River includes 35 species, two of which are undescribed (Table 1). Approximately 50 per cent of the Yaqui River Basin is located within the Madrean Biogeographic Province, where 13 species of native fishes occur (Yaqui trout, *Oncorhynchus* sp.; Mexican stoneroller, *Campostoma ornatum*; Mesa del Norte chub, *Gila pulchra*; roundtail chub, *Gila robusta*; longfin dace, *Agosia chrysogaster*; ornate minnow, *Codoma ornata*; beautiful [Yaqui] shiner, *Cyprinella formosa*; Yaqui sucker, *Catostomus bernardini*; Bavispe sucker, *Catostomus leopoldi*; Cahita sucker, *Catostomus cahita*; Rio Grande mountain-sucker, *Pantosteus plebeius*; Yaqui catfish, *Ictalurus pricei*; and whitefin pupfish, *Cyprinodon* sp.) (Hendrickson et al. 1981). Most of the

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Yaqui River fishes, however, live at intermediate to lower elevations in springs, cienegas, and moderate-sized rivers and creeks. None is clearly a "big-river" fish in ecology (Rinne and Minckley 1991).

Of particular interest for the United States and Mexico is the Rio Bavispe sub-basin since its northernmost origin is located in Cochise County, Arizona and Hidalgo County, New Mexico, and it crosses the border to enter Sonora at Agua Prieta and San Bernardino (Figure 1). The small portion of the Rio Bavispe that lies within southwestern United States is believed to have harbored 8 native fish species (Mexican stoneroller, longfin dace, Yaqui topminnow [*Poeciliopsis occidentalis sonoriensis*], roundtail chub, Yaqui sucker, beautiful shiner [*Cyprinella formosa*], Yaqui chub [*Gila purpurea*] and Yaqui catfish). Longfin dace, roundtail chub and topminnow are also distributed in the Colorado River Basin, but the rest do not occur elsewhere in the United States (Hendrickson et al. 1981).

This paper summarizes information on conservation efforts between the United States and Mexico for native fishes of the Yaqui River Basin, and presents current status of the fish communities in the Río Bavispe above La Angostura Reservoir. Field activities were conducted during summer of 1994 under the auspices of the U.S.-Mexico Joint Committee for the Conservation of Flora and Fauna. Collection of fishes were made using seines, back-pack electrofishing, dip nets, and trammel/gill nets. A scientific research permit was granted by the Mexican government (SEDESOL, permit no. A00700[2] 00074).

CONSERVATION EFFORTS

The headwaters of the Yaqui River in southeastern Arizona once provided historic habitat for eight native species of fishes. Habitat degradation caused by diversion of water, overgrazing and subsequent erosion, aquifer pumping and introduction of exotic fishes, resulted in the extirpation of four of the native fishes (Yaqui sucker, Yaqui catfish, beautiful shiner, Yaqui form of roundtail chub), and the destruction or alteration of most fish habitat of the Yaqui River in the United States. Some of these species are now protected by the United States and/or Mexico (Table 2).

Table 1.—List of common and scientific names of native fishes in the Yaqui River Basin (Modified from Hendrickson et al. 1981). The list is presented as a sequence of families following Nelson (1994). * = Species historically found in Arizona. # = Species currently found in Arizona. † = Species found within the Madrean Province.

ELOPIDAE	
machete	*Elops affinis*
CLUPEIDAE	
herring	*Lile stolifera*
Pacific shad	*Dorosoma smithi*
CYPRINIDAE	
Mexican stoneroller	*Campostoma ornatum**#†
Yaqui chub	*Gila purpurea**#
Mesa del Norte chub	*Gila pulchra*†
Roundtail chub (Yaqui form)	*Gila robusta**†
Desert chub	*Gila eremica*
Longfin dace (Yaqui form)	*Agosia chrysogaster**#†
Ornate minnow	*Codoma ornata*†
Beautiful/Yaqui shiner	*Cyprinella formosa**#†
CATOSTOMIDAE	
Yaqui sucker	*Catostomus bernardini**†
Leopold sucker	*Catostomus leopoldi*†
Cahita sucker	*Catostomus cahita*†
Opata sucker	*Catostomus wigginsi*
Rio Grande mountain-sucker	*Pantosteous plebeius*†
ICTALURIDAE	
Yaqui catfish	*Ictalurus pricei**†
ARIIDAE	
none	*Arius caerulescens*
none	*Arius liropus*
SALMONIDAE	
Yaqui trout	*Salmo* sp.†
MUGILIDAE	
mountain mullet	*Agonostomus monticola*
white mullet	*Mugil curema*
POECILIIDAE	
Yaqui topminnow	*Poeciliopsis occidentalis sonorensis**#
none	*Poeciliopsis monacha-occidentalis*[1]
guatopote culiche	*Poeciliopsis prolifica*
CYPRINODONTIDAE	
Whitefin pupfish	*Cyprinodon* sp.†
CENTROPOMIDAE	
robalo prieto	*Centropomus nigrescens*
robalo de aleta amarilla	*Centropomus robalito*
LUTJANIDAE	
pargo amarillo	*Lutjanus novemfasciatus*
CICHLIDAE	
Sinaloan cihlid	*Cichalosma beani*
ELEOTRIDAE	
none	*Dormitator latriforms*
dormilón del Pacífico	*Eleotris picta*
dormilón manchado	*Gobiomorus maculatus*
GOBIIDAE	
none	*Awaous transandeanus*
SOLEIDAE	
sol	*Trinectes fonsecensis*

[1] = An all-female "species."

Although the uniqueness of the native fishes of the Yaqui River had long been known from reports by Meek (1904), De Buen (1940, 1947), Miller (1959, 1972), Branson et al. (1960), Needham and Gard (1964), Chernoff and Miller (1982), and McNatt (1974), it was not until the late 1970s that comprehensive surveys within the entire basin were conducted by Hendrickson et al. (1981). Approximately ten years later, personnel from the

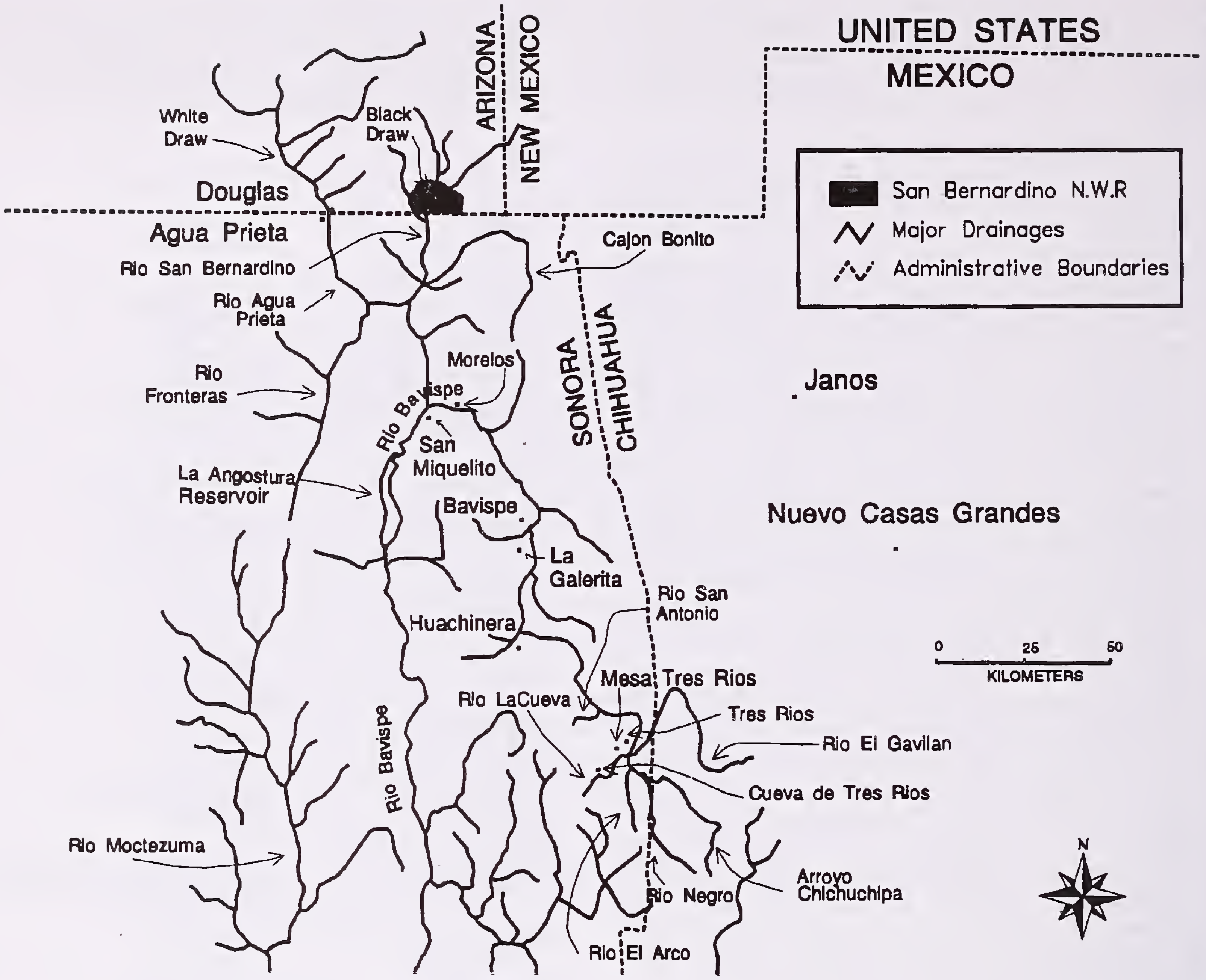

Figure 1.—Sketch map of the upper Yaqui River Basin, Arizona, United States, and Sonora, Mexico, showing major tributaries and place names used in text.

Centro Ecológico de Sonora (CES) conducted another major effort to determine the status of the Yaqui River fish communities (Campoy-Favela et al. 1989). Over the last few years, CES and the Arizona Game and Fish Department (AGFD) have collaborated in a long-term monitoring of native fishes in shared watersheds between Sonora and Arizona, including the Yaqui River.

Despite the documented efforts by Hendrickson et al. (1981) and Campoy-Favela et al. (1989), questions remain regarding the status and ecology of the Yaqui River native ichthyofauna. Hendrickson et al. (1981) recognized two undescribed species of *Catostomus* in northwestern Mexico. The first was found in the uppermost Río Bavispe drainage, at higher elevations (mostly greater than 2,000 m) in Arroyo Moctezuma, Arroyo de la Norteña, Río Negro and Arroyo San Antonio. In the former, the species is syntopic with Rio Grande mountain-sucker. The second form was located in southern and southeastern headwaters of the Yaqui River system, where it occurs widely between 1,500 and 2,135 m. Siebert and Minckley (1986) described these two catostomid fishes. The first taxa was named Bavispe sucker (*Catostomus leopoldi*), and the second Cahita sucker (*Catostomus cahita*). These authors concluded that the two suckers seem to be closely related.

DeMarais (1991) described a new species of cyprinid in northwestern Sonora, the desert chub (*Gila eremica*). This new chub was long confused with its nearest relative, the Yaqui chub. DeMarais

Table 2.—Fishes of the Yaqui River Basin listed as Endangered (E), Threatened (T), Rare (R), or of Special Concern (SC) by the U.S. Fish and Wildlife Service (FWS), under the Endangered Species Act (ESA) as ammended (50 CFR 17.11 and 17.12; August 29, 1992), by the Mexican government (Diario Oficial de la Federación, 1991, 1994), and by the American Fisheries Society (AFS) (Williams et al. 1989).

	ESA	MEX-1991	MEX-1994	AFS-1989
Yaqui trout (*Salmo* sp.)	NL	NL	NL	SC
Mexican stoneroller (*Campostoma ornatum*)	C2	E	E	SC
Rountail chub (*Gila robusta*)	C2	R	R	NL
Longfin dace (*Agosia chrysogaster*)	C2	R	T	NL
Beautiful shiner (*Cyprinella formosa*)	T	NL	T	SC
Yaqui sucker (*Catostomus bernardini*)	NL	NL	R	SC
Leopold sucker (*Catostomus leopoldi*)	NL	NL	R	SC
Cahita sucker (*Catostomus cahita*)	NL	NL	T	T
Opata sucker (*Catostomus wigginsi*)	NL	NL	NL	SC
Yaqui catfish (*Ictalurus pricei*)	T	R	R	SC
Yaqui topminnow (*Poeciliopsis occidentalis sonoriensis*)	E	R	T (1)	NL
Yaqui chub (*Gila purpurea*)	E	E	E	T

NL= Not Listed; (1)= Apparently includes both subspecies of Poeciliopsis occidentalis.

concluded that what was considered to be Yaqui chub in the Ríos Sonora, Matape, and Moctezuma-Nacozari is actually the desert chub. Only those chubs from the Río San Bernardino (Black Draw) correspond to the Yaqui chub. This finding suggests that the Yaqui chub has one of the most restricted distributions in the entire Yaqui River.

Other important studies conducted on Yaqui River fishes include phylogenetic relationships and genetic variability within the *Cyprinella formosa* species group by Mayden (1989) and Mayden and Wood (1992). DeMarais and Minckley (1993) examined effects of reintroduction efforts on the genetic and phenotypic structure of Yaqui chub populations. They found that genetic stability was indicated, with observed variations attributable to documented or inferred changes in population sizes. Morphology also remained uniform, both temporarily and spatially, with no evidence of changes attributable to recovery manipulations or ecophenotypic responses to novel environments. Presently, only Yaqui trout and whitefin pupfish remain as undescribed taxa in the Yaqui River system.

Major conservation measures to protect habitat and restore the native fish fauna of the Yaqui River in the United States took place in 1979 and 1988 when The Nature Conservancy (TNC) purchased the San Bernardino Ranch and Leslie Canyon, respectively. These lands were later sold to the U.S. Fish and Wildlife Service (USFWS) in 1982 and 1988, respectively, to establish what is known now as the San Bernardino/Leslie Creek National Wildlife Refuge (SB/LCNWR).

The Dexter National Fish Hatchery and Technology Center (DNFHTC), Dexter, New Mexico, has played a major role in the conservation of fishes of the SB/LCNWR. In 1969, drought conditions in southeastern Arizona almost extirpated the Yaqui chub. A handful of chubs were removed from Astin Spring, Cochise County, Arizona, and were placed into Leslie Creek by Dr. W.L. Minckley, Arizona State University (ASU). These fishes formed the basis for the Yaqui chub reintroductions in the years that followed. In 1976, stock from these fish were transferred to DNFHTC. The hatchery successfully produced enough chubs that were re-established on the SB/LCNWR in 1980. In addition to Leslie Creek, the species is also found in Black Draw and several ponds within SB/LCNWR. DeMarais and Minckley (1993) summarized the history of conservation efforts on this species including numerous transfers of fishes betweeen captive and wild stocks.

The Yaqui topminnow formerly occurred in the headwaters of the Yaqui River in the aquatic habitats of the Whitewater and Black draws. Topminnow populations declined coincident with the introduction of mosquitofish into the same habitats. In 1976, Yaqui topminnow were rescued from Astin Spring and placed in Leslie Creek where the species still exists. Also they were taken from San Bernardino Ranch in 1976 and 1980 to DNFHTC for "refugia purposes." Following eventual multiple site establishment on the new SBNWR, the stock at DNFHTC was pickled in May 1993. At present, topminnow also occur in Black Draw and several man-made ponds within SBNWR.

In 1987, a collaborative effort among CES, AGFD, USFWS, and ASU collected a broodstock of Yaqui catfish from Río Aros, Sonora. They were taken to DNFHTC for holding, genetic analysis and propagation for possible reintroduction into the SB/LCNWR. In 1990, a second collecting trip was conducted in Río Sirupa, Chihuahua, to obtain more broodstock. These fish were also taken to DNFHTC for holding and genetic analyses. Genetic analyses are completed, but captive propagation of Yaqui catfish has been particularly challenging with limited results. Once the propagation techniques are in place, Yaqui catfish are expected to be reintroduced into SB/LCNWR.

In 1989, under another U.S.-Mexico cooperative effort, beautiful shiners were collected from Arroyo Moctezuma (upper section of Río Gavilán, Chihuahua), and transported to DNFHTC for holding. In May of 1990, beautiful shiners were successfully transported from DNFHTC and stocked into Twin Pond on SB/LCNWR. Today, the species also occupies Oasis and Mesquite ponds within the refuge. Another form of beautiful shiner, the Guzmán beautiful shiner, native to the Mimbres River and Guzmán Basin in New Mexico, is being held at DNFHTC for future reintroduction efforts.

Recent conservation activities for Yaqui River fishes conducted in the United States include: a) nonnative renovations and control; b) genetic studies on Yaqui chub and Yaqui catfish; c) native fish habitat utilization studies; d) Leslie Creek instream flow rights acquisition, and; e) hydrologic studies and monitoring of wells.

In 1994, a recovery plan for the endangered and threatened fishes of the Yaqui River was drafted (USFWS 1994). Recovery objectives proposed in this draft plan are: 1) stabilize existing populations and downlist Yaqui chub and Yaqui topminnow, and 2) reintroduce Yaqui catfish and beautiful shiner into historic habitats in the United States and establish self-sustaining populations. Due to the limited habitat in the United States, these species cannot be delisted until there is sufficient protection in Mexico.

FISH COMMUNITIES OF THE RIO BAVISPE

The headwaters of the Río Bavispe are comprised of three distinct rivers, i.e., Río Gavilán, Río Negro and Río La Cueva, that all terminate in close proximity to form the Río Bavispe at a location naturally named "Tres Rios" (ca. 1,600 m) (fig. 1). The upper reach of the Río Gavilán (ca. 2,500 m) is called Arroyo Moctezuma. The Río Negro has one main tributary, Arroyo Chichuchipa, which enters the Negro at ca. 2,200 m elevation. The Río La Cueva, which drains the highest country in the Sierra Los Mojones, has no named primary tributaries. Just below Tres Rios, a small tributary named Arroyo San Antonio enters the Río Bavispe. From Tres Rios and the mouth of Arroyo San Antonio, the Bavispe flows northwesterly through the Sierra El Gato before opening to the broad Río Bavispe valley just above Huachinera, Bacerac and Bavispe. The Río Bavispe continues northward and then turns westward where it receives the Río San Bernardino at the town of Morelos before turning south where it flows into La Angostura Reservoir (Lázaro Cárdenas Dam). Below La Angostura the Bavispe flows south until meeting the Río Aros to form the Yaqui River.

The Tres Ríos area is characterized by encinal and pine-oak woodland (Brown 1982). The tributaries forming the Río Bavispe at Tres Ríos present an interesting assemblage of fishes with a native trout and three different suckers (Yaqui, Bavispe, and Rio Grande mountain suckers). Other native species of fishes encountered in this area (or just below) are Mexican stoneroller, roundtail chub, Yaqui catfish and longfin dace (Hendrickson et al. 1981). Our field surveys in this area were concentrated in the Río La Cueva, a previously unsurveyed tributary to our knowledge. Río La Cueva near Tres Ríos (1,490 m elevation), presented a continuous combination of riffle and run habitats and occasionally some backwaters and pools. However, no Yaqui trout were found in this locality (Table 3). Hendrickson et al. (1981) collected Yaqui trout in the middle Río Gavilán, Arroyo San Antonio, and Río Negro. Our surveys, in the lower Río Gavilán and Río Negro, failed to sample any trout, but local residents indicated that trout remain relatively abundant here and at higher elevations, particularly in the upper Río Negro. During the time of our visit to the upper Río Bavispe, sampling was difficult due to heavy rainfall. Río La Cueva at Rancho La Cueva contained Yaqui sucker, roundtail chub, longfin dace, beautiful shiner, and Mexican stoneroller. Yaqui catfish has been reported to be present at Tres Ríos, but our collection efforts did not produce any (Table 3). Particularly important was to observe black and yellow bullheads (*Ameirus melas* and *Ameirus natalis* respectively). This is the first time these predatory fishes have been reported in the Tres Ríos area, and their presence in the system represents a serious threat for the native ichthyofauna.

Table 3.—Relative abundance, in percent, of various fishes captured from the Río Bavispe, and its tributaries, Sonora, Mexico, during Summer of 1994. Locality information includes elevation in meters above the sea level. ONSP= *Oncorhynchus* sp. (Yaqui trout). CABE= (*Catostomus bernardini* (Yaqui sucker). PAPL= *Pantosteus plebeius* (Rio Grande sucker). CALE= *Catostomus leopoldi* (Bavispe sucker). GIRO= *Gila robusta* (roundtail chub). AGCH= *Agosia chrysogaster* (longfin dace). CYFO= *Cyprinella formosa* (beautiful shiner). CAOR= *Campostoma ornatum* (Mexican stoneroller). POOCSO= *Poeciliopsis occidentalis sonoriensis* (Yaqui topminnow). MISA= *Micropterus salmoides* (largemouth bass). LEMA= *Lepomis macrochirus* (bluegill). LECY= *Lepomis cyanellus* (green sunfish). AMME= *Ameiurus melas* (black bullhead). AMNA= *Ameiurus natalis* (yellow bullhead). CACAR= *Carpiodes carpio* (river carpsucker).

LOCALITY	SPECIES AND THEIR RELATIVE ABUNDANCE									
	ONSP	CABE	PAPL	CALE	GIRO	AGCH	CYFO	CAOR	POOCSO	OTHERS
1. Headwaters of Río Bavispe. Lower Río La Cueva at Rancho La Cueva (South of Tres Ríos). 1490 m.		8.4			70.0	1.6	9.5	10.0		AMNA 0.5
2. Río Negro (between mouth of La Cueva & mouth of Río Gavilán). 1630 m.		21.9			65.6		12.5			
3. Lower Río Gavilán. 1630 m.		6.1			10.6	6.1	54.5	10.6		LEMA 9.1 AMME 3.0
4. First small tributary of Río La Cueva at La Cueva de Tres Ríos (aka. "La Presita"). 1630 m.	15.3	14.5	8.9	5.6	25.8			29.8		
5. Second small tributary of Río La Cueva at La Cueva de Tres Ríos (at road crossing). 1700 m.		11.1			44.4	7.5		37.0		
6. Upper Río La Cueva at La Cueva de Tres Rios (ca. 1,000 m above road crossing). 1630 m.		5.4			33.9	3.6	8.9	48.2		
7. Río Bavispe at Huachinera (second road crossing on road to Bacerac). 1000 m.					0.8	2.8	5.1		91.0	LECY 0.3
8. Río Bavispe (ca. 1 mile South of La Galerita). 985 m.		16.2			13.4	0.5	56.9	6.1	2.3	CACAR 0.9 MISA 2.3 LECY 0.5 AMME 0.9
9. Río Bavispe North of Bavispe on road to San Miguelito. 915 m.		7.7			8.9	16.7	59.0	2.6		CACAR 1.3 MISA 0.4 LECY 1.7 AMME 1.7
10. Río Bavispe at San Miguelito. 900 m.		20.0			5.8	7.1	65.7		0.3	MISA 0.4 LECY 0.7
11. Río Bavispe at Morelos. 840 m.					38.0	1.1	46.7	1.1	10.9	MISA 1.1 LECY 1.1
12. Río San Bernardino at Rancho Cosuberachi.		2.7				62.4		2.7	32.2	

Hendrickson et al. (1981) indicated that Arroyo Moctezuma harbors the only Rio Grande mountain-sucker population known in the entire Yaqui River Basin. Other species found in this tributary are Mexican stoneroller, beautiful shiner, roundtail chub, and Bavispe sucker. No Yaqui trout has been reported in Arroyo Moctezuma, but the presence of rainbow trout (*Oncorhynchus mykiss*) may threaten native trout found at lower elevations (Hendrickson et al. 1981). Middle Río Gavilán contains Yaqui trout, Mexican stoneroller, roundtail chub, beautiful shiner, and the third sucker, Yaqui sucker. Arroyo Chuchichupa and Río Negro share three species, Mexican stoneroller, roundtail chub, and Bavispe sucker. Yaqui trout and Yaqui sucker are also found in Río Negro. Bluegill (*Lepomis macrochirus*) has been introduced into the upper Arroyo Chuchichupa (Hendrickson et al. 1981). Our sampling in the headwaters of the Río Bavispe indicates that bluegills may still be restricted to this area.

Our surveys in the Río La Cueva at La Cueva de Tres Ríos (1,630 m elevation) found the Yaqui trout to be locally abundant. This section of Río La Cueva presented deeper pools and more erosive conditions, characteristic of high elevation creeks. When present, small (cm total length) trout occupied slower waters in riffles. Largest individuals (14-23 cm total length) were found in deepest pools, near boulders, undercut banks, overhanging cliffs, or fallen trees as previously indicated by Hendrickson et al. (1981). Our collections at La

Presita, a small tributary of Río La Cueva, indicate that this is the only area in the entire Yaqui River system where the Yaqui, Rio Grande, and Bavispe suckers are sympatric. Other species inhabiting these waters were roundtail chub, and Mexican stoneroller (Table 3).

As noted earlier, the Río Bavispe enters a broad valley with extended flood plains after it emerges from the Sierra El Gato, upstream from Huachinera, Bacerac and Bavispe. Access to the river in this area is difficult due to extensive private farms along river banks. Through this reach of the Río Bavispe, roundtail chub, Mexican stoneroller, longfin dace, and beautiful shiner were generally found at each locality where we sampled (Table 3). Unfortunately, the same can be applied to green sunfish (*Lepomis cyanellus*), largemouth bass (*Micropterus salmoides*), and black bullheads. Juveniles (cm) river carpsucker (*Carpiodes carpio*) were observed in samples made in the Río Bavispe both upstream and downstream from the town of Bavispe. Hendrickson et al. (1981) reported common carp (*Cyprinus carpio*), ornate minnow, and Yaqui catfish in this area. None of these three fishes were observed during our sampling. Yaqui topminnow were particularly scarce in the Río Bavispe between Tres Rios and Morelos. Heavy rains just prior to our samplings may have displaced topminnow from the mainstem of the Río Bavispe.

The Mexican stoneroller seems to be widely distributed within the Río Bavispe, occupying waters from 800 to 1,700 m elevation. The species prefers shallow riffles and runs over gravel/cobble substrates. At lower elevations, stonerollers occupied runs and occasional pools with sandy bottoms. During collections, some large adults of about 15 cm total length displayed bright colors on body or fins, but no tubercles were present on the snout or head.

The roundtail chub is also widely distributed in the Yaqui River system, and is most abundant in rivers or in smaller streams that have well developed and permanent pools (Hendrickson et al. 1981). We found the species to be relatively abundant in the Río Bavispe, occupying open pools and rapids alike, with many being taken from eddies behind boulders. Most of the specimens observed were healthy with a small percentage (%) infected by *Lernaea* sp.

Hendrickson et al. (1981) reported the beautiful shiner to be relatively scarce throughout its wide range in the Yaqui River system. They also indicated that only in smaller streams, or in intermittent pools of creeks that have a high percentage of riffle habitat in wetter periods and occasionally in some ponds at lower elevations, the species was found to be abundant. In contrast, our surveys indicate that the shiner was relatively common in the mainstem of the Río Bavispe, comprising almost 50 per cent of our samples from Huachinera to Morelos (Table 3). The beautiful shiner would be particularly vulnerable to introduction of red shiner, *Cyprinella lutrensis* (Williams et al. 1985).

The Yaqui sucker enjoys one of the widest geographic and ecologic distributions of any fish species in the Yaqui River Basin. The species ranges from the lowest elevations (on and near the river's delta) to higher than 2,000 m in mountain streams. They resemble Sonora suckers both ecologically and morphologically, and may represent only a subspecies of that Gila River form (Hendrickson et al. 1981, Rinne and Minckley 1991). We collected Yaqui suckers in shallow and deeper pools from mountain creeks, as well as runs and riffles from desert creeks.

The native fish fauna in Río San Bernardino at Rancho Cosuberachi was dominated by longfin dace. Yaqui topminnow were second in abundance with a few Yaqui sucker and Mexican stoneroller also being taken. A similar composition was reported by Hendrickson et al. (1981).

The longfin dace is typically found in areas below 1,500 m elevation and most abundantly in desert and semi-desert streams where it is usually associated with topminnow in intermittent pools. However, we found this species as high as 1,700 m in the Río La Cueva at La Cueva de Tres Rios (Hendrickson et al. 1981).

DISCUSSION AND RECOMMENDATIONS

Detrimental land and water use practices and introduction of nonnative fishes throughout the Río Bavispe, above La Angostura Dam, are the most serious threats to the existence of its native fishes. Logging has long been a part of the economy of the Sierra Madre Occidental region, although with serious questions about the benefit to local communities. Over the last few years there have been plans to improve roads and increase logging throughout the region through financing by the World Bank. If ever implemented without careful ecological planning, this project could seriously deteriorate wildlife habitat and threaten several watersheds in northwestern Mexico, including the upper portions of the Río Bavispe and Ríos Papigochic, Sirupa and Aros.

Habitat degradation is an ever present threat to endemic trout populations (Rinne and Minckley 1991). Extensive montane logging has opened stream channels to direct sunlight, altered patterns of organic input, and increased erosion and sedimentation. Sawmill waste has been a major source of organic pollution in Mexico (Rinne and Minckley 1991). Regardless of the implementation of the proposed forestry project, logging activities continue in the region.

In addition to forestry projects, construction of a highway between Huachinera and Bavispe will likely increase the chances of economic growth of these cities and those between them. A similar situation could be expected for those towns between Tres Ríos and Nuevo Casas Grandes where another road has been recently constructed. Unless economic growth is conceived and carried out in a well planned and sustainable fashion, severe and irreparable damage to the aquatic ecosystems may result.

It is imperative to establish a binational recovery team and develop a comprehensive plan that includes conservation actions on both sides of the border in order to protect the unique native fish fauna of the Yaqui River Basin.

Recommended actions in the United States (some already indicated in the draft Yaqui Fishes Recovery Plan, USFWS 1994) are:

a)eradicate all nonnative species (particularly mosquitofish and bullfrogs) from SB/LCNWR and implement a program to prevent their reinvasion.
b)acquire broodstocks and develop culture techniques for Yaqui catfish and Yaqui sucker.
c)prevent erosion and loss of aquatic habitat.
d)protect critical habitat from detrimental human disturbances.
e)study water supplies to SB/LCNWR to better understand the effects of groundwater pumping.
f)secure and protect the San Bernardino aquifer so that all artesian well flows are maintained throughout the year.
g)secure and protect the Leslie Creek watershed to ensure adequate flows.
h)acquire and protect additional habitats and waters needed for the long-term existence of the Yaqui fishes.
i)monitor and manage the fish populations and their essential habitats.
j)implement educational programs on the plight of the Yaqui River native fishes.

Recommended conservation actions in Mexico include:

a)conduct an extensive and systematic resurvey of the basin (including initial surveys for those streams overlooked in past surveys). These surveys should be conducted by a binational team with a written protocol describing field methodologies. The surveys must secure permits to preserve voucher and research specimens.
b)secure additional broodstock for all listed Yaqui River fishes. Develop a protocol for broodstock acquisition and culture techniques (i.e. genetic integrity, production goals, handling and transport methodologies).
c)promote research on the life histories and ecologies of the Yaqui River native fishes.
d)determine the taxonomic and genetic status of the undescribed trout and whitefin pupfish, and clarify the relationship between the Yaqui forms of the roundtail chub and longfin dace with those in the Gila River.
e)determine the taxonomic and genetic status of all upper Río Bavispe drainage suckers with those in the Gila River, United States and the Guzmán Basin, United States and Mexico.
f)identify and establish refuges, preserves, and secure instream flows for those areas critical for native fishes.
g)conduct baseline water quality and hydrologic studies of the basin, including contaminants.
h)identify current and potential threats to the system due to detrimental land, water, construction or industrial practices.
i)evaluate the possibility of on the ground management (renovations, barriers, reintroductions, etc.).
j)monitor and manage the fish populations and their essential habitats.
k)implement educational programs on the plight of the Yaqui River native fishes.

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Conservation and Management of Madrean Populations of the Chiricahua Leopard Frog

Michael J. Sredl and Jeffrey M. Howland[1]

Abstract.—Surveys by Arizona Game and Fish Department and others have found apparently discrete metapopulations of Chiricahua leopard frogs (*Rana chiricahuensis*) associated with madrean mountain ranges and lower elevation permanent aquatic systems. These typically consist of a small group of subpopulations (<10) distributed within a few kilometers of each other in a single drainage or a small number of interconnected drainages. The few remaining metapopulations in Arizona are widely separated, with little potential for natural expansion or interchange. Persistence of historical populations may be greater at madrean sites (9 of 32 sites) than at lower elevations (3 of 21 sites). Subpopulation extinction rates are naturally high, and perhaps artificially elevated, and now surpass recolonization rates, which are probably depressed due to deterioration of dispersal corridors. We hope to enhance functioning metapopulations through relocation (facilitated dispersal) of frogs to appropriate, uninhabited sites within or around existing metapopulations. In some cases, we may create metapopulations around isolated sites by the same means. Renovation or rehabilitation of habitats and dispersal corridors will be important to the long-term success of such a conservation strategy. We recommend research on genetic structure of metapopulations for more thorough understanding of metapopulation dynamics. Before self-sustaining metapopulations can be restored to the madrean mountains, we must understand factors that influence rates of extinction (demographic, genetic, and environmental stochasticity) and recolonization (dispersal capabilities; physiological and ecological tolerances).

INTRODUCTION

Arizona's diverse herpetofauna includes seven native species of ranid frogs. Populations of most of these species have declined notably in the past 20 to thirty years (Clarkson and Rorabaugh 1989; Sredl 1993), as have other western ranids (Hayes and Jennings 1986; Jennings 1988). In the most dramatic case, the Tarahumara frog (*Rana tarahumarae*) disappeared from all known localities of occurrence in the state in the late 1970s and early 1980s and is now known to occur only in the madrean ranges of Mexico (Hale and May 1983; Hale and Jarchow 1988; Hale 1992). The relict leopard frog (*R. onca*), probably once native to Arizona, was thought to have gone extinct in the 1950s (see Platz 1984), though the species may recently have been rediscovered in Nevada (R. Jennings, pers. comm.). The northern leopard frog (*R. pipiens*), once widely distributed and abundant across the northern half of Arizona, is now known from just a few scattered localities. The plains leopard frog (*R. blairi*), which formerly inhabited aquatic sites throughout the Sulphur Springs Valley, is now known from a set of ash settling ponds at a large power plant, a few irrigation sumps, and a small number of sites along Whitewater Draw (Arizona Game and Fish Department (AGFD), unpubl. data; P. Rosen and C. Schwalbe, pers. comm.). The newly described Ramsey Canyon leopard frog (*R. subaquavocalis*) has been reduced to a handful of breeding colonies in two or three canyons of the Huachuca Mountains (Platz 1993). The Chiricahua leopard frog (*R. chiricahuensis*), while still known from

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several madrean mountain ranges in southeast Arizona, has disappeared from most large rivers and lakes, is difficult to find in its namesake, the Chiricahua Mountains, and has dwindled to just a few breeding populations in the White Mountains and along the Mogollon Rim, where it was common just 25 years ago (Platz and Mecham 1979). Only the lowland leopard frog (*R. yavapaiensis*) is still represented by large numbers of breeding populations, and even these are restricted to a portion of the former geographic range. Lowland leopard frogs have disappeared from New Mexico (C. Painter, pers. comm.) and California (Jennings and Hayes in press), and probably from Utah and Nevada, while status in Mexico is unknown. The central Arizona mountains, below the Mogollon Rim, are perhaps the species's final stronghold.

Based on differences in morphology and call, *R. chiricahuensis* was described as a distinct species relatively recently (Platz and Mecham 1979). Our present knowledge of its historical distribution is based largely on collections by James Platz and colleagues during their studies of the taxonomy and relationships of southwestern leopard frogs (Frost and Platz 1983; Platz 1976, 1984, 1993; Platz and Frost 1984; Platz and Mecham 1979; Platz and Platz 1973), with significant contributions by a few other workers (Rosen and Schwalbe 1988; Hale 1992). Documentation of declines began with Clarkson and Rorabaugh (1989) and has been continued by the Arizona Game and Fish Department (AGFD, unpubl. data) and others.

R. chiricahuensis, is highly aquatic relative to other leopard frogs, inhabiting backwaters or slowly flowing stretches of rivers, streams, and cienegas, and plunge pools, springs, and stock tanks. Elevational range extends from 1150-2200 m in southeast Arizona (substantially higher in northern Arizona). Adults are moderate in size compared to other southwestern leopard frogs, occasionally exceeding 100 g total body mass. Breeding may occur nearly any time of year, but is most commonly observed in spring and again during the summer monsoon. Larvae may overwinter and reproductive maturity is probably attained within a year after metamorphosis. Adults have been determined to reach ages of at least seven years in the wild (P. Fernandez, pers. comm.).

In this paper, we address specific aspects of historical distribution and abundance of *R. chiricahuensis*, discuss evidence and probable causes of declines, examine facets of population biology that influence present status and conservation strategies, and make preliminary recommendations on how stabilization and recovery of remaining populations may be realized. The Madrean Sky Islands, while important to several of Arizona's sensitive amphibian species, may be our only opportunity to maintain viable populations of the Chiricahua leopard frog in the United States, as the few remaining population centers in New Mexico and northern Arizona steadily decrease in number (R. D. Jennings pers. comm.; Sredl et al. 1994).

METHODS

We have incorporated information from two basic lines of inquiry, statewide surveys and mark-recapture studies, in order to determine present status and distribution of native ranid frogs in Arizona. We use this information in combination with basic principles of conservation biology to outline a conservation strategy for Chiricahua leopard frogs in southeastern Arizona.

For historical information on the distribution and abundance of Chiricahua leopard frogs, we gathered locality information from published and unpublished reports and the records of several museums with significant collections of Arizona amphibians. Unfortunately, the identity of leopard frog specimens in many collections has not been verified since the major revisions of the *R. pipiens* complex in the 1960s through 1990s. As a result, southwestern leopard frogs in many older collections are identified simply as *Rana pipiens*. We must be cautious in the use of museum records (M. Jennings, pers. comm.).

Beginning in 1990, we searched historical and potential sites of occurrence of *R. chiricahuensis* statewide. Sites were surveyed by recording visual encounters (*sensu* Crump and Scott 1994) as developed by Sredl et al. (1994). All data were recorded on standard observation forms and entered into the Nongame Amphibians and Reptiles Database for further analysis (dBASE IV®, see Waters et al. 1994).

To gain an understanding of the population biology of southwestern leopard frogs, we performed mark-recapture studies on lowland and Chiricahua leopard frogs at seven sites (AGFD unpubl. data). We visited sites three to four times per year and captured as many frogs as possible during each visit. Each frog was weighed and measured, given a unique mark (by toe-clipping), sexed, and released near point of capture. We analyzed capture data using program Jolly-age (Pollock et al. 1990), when possible, or by simple

Lincoln-Peterson estimation. Comparison across seasons and years allowed characterization of population dynamics (including some of the sources of population fluctuations). While most of our mark-recapture work has focused on *R. yavapaiensis*, our less extensive studies of *R. chiricahuensis* indicate substantial similarities between the two species.

RESULTS

Inventory Surveys

From 1990 to 1994, we surveyed over 265 potential sites for *R. chiricahuensis*, including 87 of the 114 known sites of historical occurrence in southeastern Arizona. Combining our results with those of Clarkson and Rorabaugh (1989) and other recent studies (since 1985), we determined recent presence of Chiricahua leopard frogs at 12 historical (pre-1985) sites and 51 previously unknown sites (fig. 1).

Of particular importance is the conspicuous absence of populations from large rivers, such as the Santa Cruz and San Pedro. In recent surveys at non-Madrean sites (low elevation, below the madrean evergreen forest and woodland, encinal and oak-pine, plant community of Brown, Lowe, and Pase 1979), Chiricahua leopard frogs were found at only 3 of 21 historical localities. At Madrean sites (high elevation, encinal and pine-oak woodland or higher), recent surveys confirmed extant populations at 9 of 32 historical sites. The distribution of persistent populations at historical sites between madrean and non-madrean localities is not significantly different from random (P> 0.05), but is in the direction expected if lower elevation sites have been subject to greater impacts. In fact, the three non-madrean sites with extant populations are among the last relatively pristine lowland areas in southeast Arizona. However, significant losses may have occurred in some madrean habitats as well. For example, there has been no recent verification of Chiricahua leopard frogs from the Pinaleno Mountains, where anecdotal reports suggest that leopard frogs were formerly common (e.g. Nickerson and Mays 1969; L. Vitt, pers. comm.).

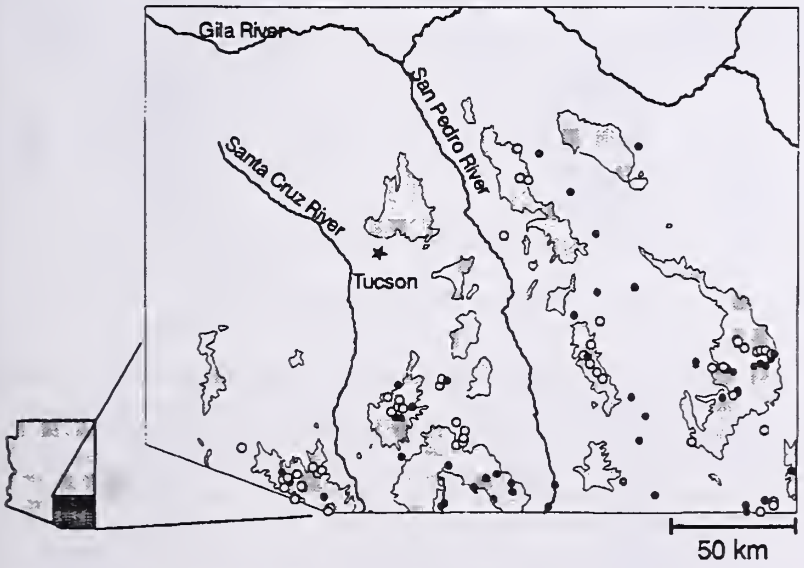

Figure 1.—Recent status of Chiricahua leopard frog populations in southeast Arizona. Open circles represent sites where frogs have been observed since 1985. Closed circles are sites of historical presence (pre-1985) where frogs were not observed in recent surveys or status is unknown. Stippled areas represent madrean habitats.

Mark-recapture Studies

Our mark-recapture studies showed considerable fluctuations in population size at individual sites. In only two years, each of five lowland leopard frog sites originally established in 1992 showed substantial mortality events, sometimes followed by recovery (Table 1; fig. 2). At Tule Creek, our largest site, the high winter rainfall of 1993 caused approximately 90% mortality. By the end of the 1993 activity season, however, numbers of frogs were nearly back to pre-flood levels, although age structure had shifted toward younger age classes.

At Big Springs, another relatively large site, a disease outbreak (*Aeromonas*, or red-leg) caused mortality rates of about 50-80% in late 1992 and early 1993. Adult animals were impacted to a lesser degree than juveniles. Reduction in total habitat area at this site, due to siltation of several important pools, preceded (and may have exacerbated) the die-off. Population recovery from the epidemic has been modest (fig. 2) and siltation continues to degrade remaining habitat.

At three smaller sites, declines were even more dramatic. Populations at Alamo Canyon and Thicket Springs apparently disappeared in 1992, the first year of the study. Recolonization has not occurred at Alamo Canyon, and frogs were seen at Thicket Springs in the summer of 1994 for the first time in two years. At Reed Springs, population size has dropped to only a few individuals, with some visits yielding sightings of nothing more than a few tadpoles.

In April 1994, a mark-recapture study of *R. chiricahuensis* was initiated at two ponds, about one mile apart, in Pinery Canyon (Chiricahua Mountains). Prior to our second mark-recapture visit in June, frogs began dying at one of the ponds. We sampled dead and moribund frogs and water. We concluded that disease was an unlikely cause, but levels of hydrogen sulfide in the water were high enough to be toxic to aquatic wildlife (Meyer and Barclay 1990). We suspect that a high detritus load in the pond, coupled with lowering of water level, high water temperature, and low concentrations of dissolved oxygen combined to form an anoxic environment suitable for proliferation of sulphur producing bacteria. This event reduced a population of 60-80 adult frogs to fewer than 10.

It is clear that leopard frog populations in the southwestern United States are vulnerable to large-scale mortality, on a frequent basis, at the hands of a variety of causative factors. Mortality may be density-independent (floods or sulphur toxicity) or density-dependent (red-leg). However, the different insults share a common result: potentially disastrous mortality with possible extinction of local populations.

DISCUSSION

Whether disappearance of local populations of leopard frogs is attributable to non-native invaders, pollution, dewatering, or some other cause is generally unknown, and may vary from one site to another. However, correlative evidence suggests that certain factors may be particularly important. For example, *R. chiricahuensis* is

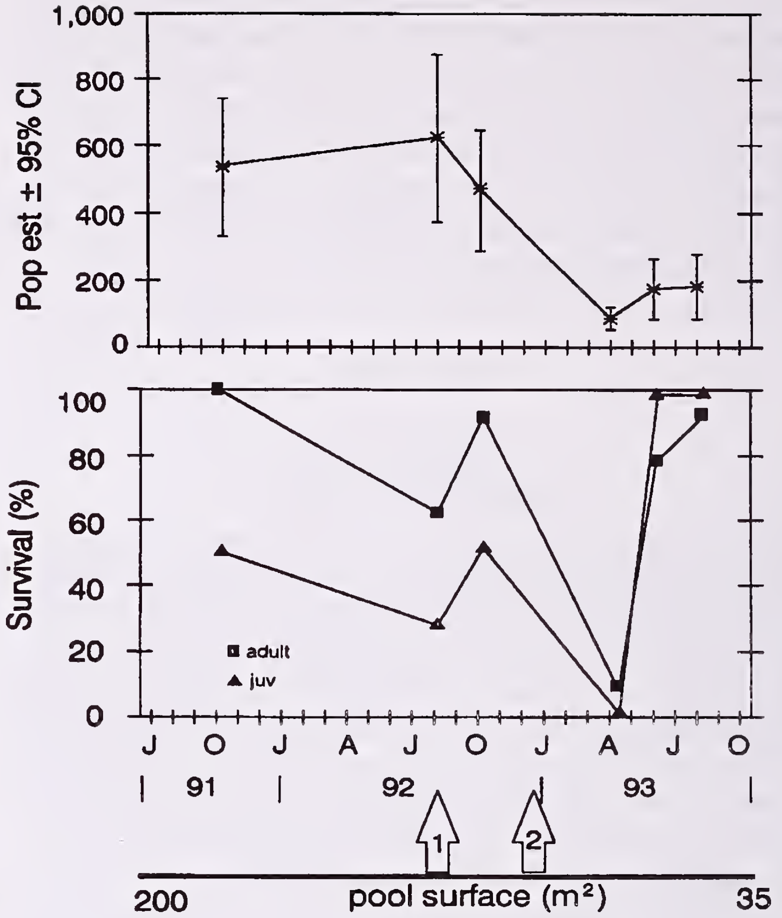

Figure 2.—Results of mark-recapture studies on lowland leopard frogs at Big Springs, Graham Co., Arizona, from 1991-1993. Arrow #1 marks the time of a flood event that resulted in an important reduction in total surface area of open water at the site through siltation of large pools. Arrow #2 marks a disease outbreak that caused mass mortality across all age classes of frogs.

Table 1. —Summary of results of AGFD mark-recapture studies. Surveys were performed during indicated years. The highest population estimate (Jolly-age or Lincoln-Peterson) obtained through the entire study period is noted for each site (ne - not estimable). Observed declines and their presumed causes are given by date of observation for each site.

Site	Years	Highest Pop. Est.	Date	Observation
Alamo Canyon, Pima Co.	1991-1993	149	4/93 6/93 10/93	no leopard frogs " "
Barnhardt Mesa Tanks, Gila Co.	1994	ne	7/94	main breeding tank dried - high mortality
Big Spring, Graham Co.	1991-1994	625	1/93	red-leg epidemic - high mortality; population estimated at 86 individuals
Reed Spring, Gila Co.	1991-1994	156	4/93 6/93 10/93	3 leopard frog tadpoles, no adults 4 " 11 metamorph leopard frogs
Thicket Spring, Gila Co.	1991-1994	121	9/92 4/93 6/93 10/93	1 leopard frog no leopard frogs " "
Tule Creek, Yavapai Co.	1991-1993	3284	1/93	catastrophic flash flood - high mortality; population estimated at 14 individuals
Pinery Canyon Tanks, Cochise Co.	1994	ne	ne	large die-off (hydrogen sulphide?)

nearly always absent from sites where bullfrogs and introduced predatory fishes are present, or where pollution or extensive human development (agricultural or urban) have occurred (AGFD, unpubl. data).

Extant populations tend to fall in clusters, rather than showing random spatial distribution (fig. 1). These clusters are commonly centered on remote, undisturbed drainages that have several discrete pockets of aquatic habitat (cattle tanks, plunge pools, areas of perennially flowing stream). Even within a cluster of populations in a given system/drainage, most aquatic sites are uninhabited by leopard frogs. We suspect that these remaining clusters are remnants of former populations. Historically, these were either continuously distributed along larger perennial aquatic systems (which are now contracted, see Hendrickson and Minckley 1984) or they were peripheral subpopulations in a metapopulation that included a large aquatic system as the central source population (fig. 3).

Our observations of leopard frog populations lead us to believe that patches of aquatic habitat, connected by drainages that can be traveled by dispersing leopard frogs, at least intermittently, form the microgeographic basis for development of metapopulations. Furthermore, the life history of Southwest leopard frogs predisposes them to high rates of local extinction and recolonization. Rates of reproduction and recruitment are highly variable and dependant upon rainfall and other environmental influences. Leopard frogs are strongly aquatic and are therefore vulnerable to desiccation, especially as larvae. Stimuli such as sudden cold snaps commonly result in devastating disease outbreaks, especially at local sites where overcrowding occurs (due to high recent reproductive success, or habitat contraction from drought or sedimentation of pools). Leopard frogs are mobile, so dispersal should occur between isolated perennial aquatic sites using intermittent or ephemeral aquatic corridors. We suspect that population declines among southwestern leopard frogs can, at least in part, be attributed to disruption of normal metapopulation dynamics (see Sjogren 1991 on the importance of uninhabited sites, proximity of subpopulations, and connectivity for proper functioning of aquatic ranid frog metapopulations). Various human disturbances lead to increased rates of extinction accompanied by decreased rates of recolonization, changing basic metapopulation structure (fig. 3).

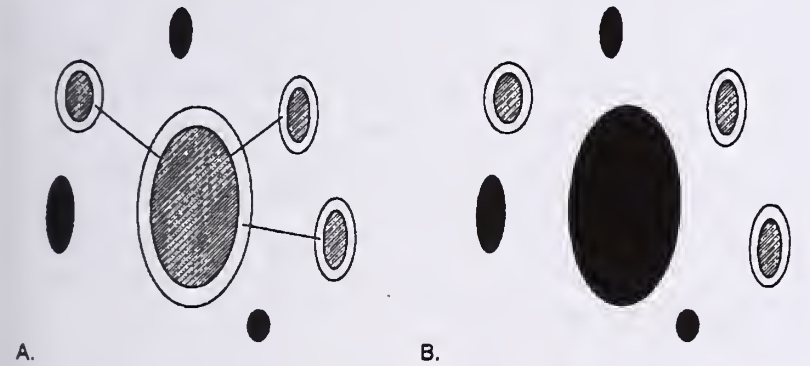

Figure 3.—Schematic representations of suspected historical (A.) and present (B.) metapopulation structure of *R. chiricahuensis* in southeast Arizona. Solid areas are uninhabited aquatic sites, cross-hatched areas are inhabited, and connecting lines indicate dispersal. Following Harrison (1991): A.) source-sink metapopulation; large, stable core population from which dispersers establish satellite populations; historically, large rivers and cienegas probably hosted source populations with smaller streams, ponds, and springs hosting unstable satellite populations. B.) non-equilibrium metapopulation; source population extinct, many sites (including source site) uninhabitable, and dispersal corridors unusable; remaining small populations vulnerable to extinction and recolonization unlikely.

Habitat has been reduced to small pockets that are capable of supporting only small, unstable populations of leopard frogs. Big rivers, with dams and introduced predators and competitors, no longer provide suitable habitat for large populations. Ground water pumping has dried many springs, cienegas, streams and other wetlands, further reducing habitat availability. Dispersal corridors have suffered the same fate. They are impassable due to lack of water or, in the case of perennially flowing corridors, the presence of large populations of bullfrogs and non-native predatory fishes.

Small populations of leopard frogs, subjected to various forms of human disturbance, are far more likely to suffer local extinction than larger, undisturbed populations that inhabited Arizona just several decades ago. When leopard frogs disappear from a site, whether by natural or anthropogenic design, the probability of recolonization is far lower than in former times because of interrupted dispersal corridors and the lack of large riverine populations to serve as sources of dispersing frogs.

In the short-term, we propose to develop management strategies to address some of the observed problems and, through time, restore functioning metapopulations to many areas where leopard frogs are on the verge of disappearing. Strategies may include habitat creation and renovation, removal of non-native predators, and facilitated dispersal (relocation) of leopard frogs to uninhabited sites within distances that could realistically be covered by the frogs themselves, given passable routes of dispersal.

Habitat renovation may be as complex as cienega restoration, such as that underway at Black Draw, San Bernardino National Wildlife Refuge, Cochise Co., Arizona. Livestock grazing has been eliminated and structures are in place for stabilizing banks and preventing further downward or outward erosion in the stream channel. As vegetation recovers, the eroded channel will slowly fill with sediments and eventually form a new cienega. In other cases, simple repair of berms on eroded stock tanks may be adequate. For bare, mud-banked tanks, enhancement of aquatic habitat heterogeneity through addition of brush or other structural materials might increase resistance to predation and competition and provide better oviposition sites.

Predator removal is a rather daunting task when viewed from a statewide perspective, but may be feasible in local areas. Bullfrog removal has begun at two *R. chiricahuensis* sites and has had a notable effect on resident bullfrog populations (C. Schwalbe, pers. comm.; AGFD, unpubl. data). We have begun removal of non-native crayfish from another site, but are unable to evaluate the efficacy of the project at this time. Removal of non-native predatory fishes may be the most difficult job. For large-scale success, cooperation within AGFD and with other resource management agencies will be essential.

Facilitated dispersal of wild "surplus" or captive bred frogs to uninhabited sites might be the primary means of restoring functioning metapopulations to many areas that have been reduced to inviable numbers of small breeding populations. At breeding ponds where adult populations are near carrying capacity, survival and recruitment rates of juveniles are low. Perhaps a portion of the eggs, tadpoles, and metamorph frogs could be considered for short-distance translocation to uninhabited but favorable sites. Ideally, these should be sites that were previously inhabited and are linked to the source population by dispersal corridors that remain functional or are restorable. In cases where sufficient numbers of wild surplus animals do not exist, a small number of wild frogs could be used to found captive breeding colonies (the feasibility of which has already been established, P. Fernandez, pers. comm.) where stock for relocation could be produced.

Many sites are presently vulnerable to stochastic extinction due to the small numbers of frogs hosted. Furthermore, many such sites are not linked by usable dispersal corridors to sites that can serve as sources for reinvasion. The combination of habitat renovation (of both breeding habitat and dispersal corridors), natural dispersal, and facilitated dispersal will hopefully result in reconstitution of functioning metapopulations in areas where frogs are destined for extirpation in the absence of active conservation management.

In order to design conservation strategies that will have a good chance for success, we need additional information in several areas. Genetic structure of leopard frog metapopulations (and constituent subpopulations) is unknown. For example, knowledge of levels of heterozygosity and genetic exchange within and among metapopulations would influence management goals concerning numbers and proximity of breeding populations that need to be established and/or maintained in order for metapopulations to continue or resume functioning. Dispersal capability of leopard frogs is also unknown. This information is important in identifying characteristics of dispersal corridors that will be necessary for establishment or maintenance of functioning metapopulations.

It is now critical that conservation strategies for the Chiricahua leopard frog be designed and implemented if we are to assure its continued existence as a member of Arizona's rich fauna.

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Fire Management in the Sky Islands

Larry S. Allen[1]

Fire has historically been a significant ecological factor in all ecosystems of Southeastern Arizona. Archeological evidence would indicate that man-caused fires were present in the sky islands long before the arrival of Europeans. The original Americans used fire as a tool and also experienced accidental fire escapes.

Many scientists attending this conference have helped to document the historical role of fire and its ecological effects. It is well established that ecological changes have occurred in the Borderlands and that these changes continue. Such change was accelerated with the arrival of Europeans. The causes of these changes are complex and varied and much debated among experts. However, there is general agreement that fire is one significant factor.

Fire has been essentially excluded from many Southern Arizona ecosystems for about 90 years. This exclusion results from two primary factors - fire suppression by federal and state agencies, and modification of fuels by grazing and other causes. The Forest Service began the attempt to suppress all fires about 1904. Early day suppression was hampered by limited access and manpower and not particularly effective. These humble beginnings evolved into today's highly effective interagency firefighting capability. Currently the vast majority of wildfires are stopped at one acre or less.

The apparent result of 90 years of suppression and fuel modification at low and intermediate elevations is a significant increase in woody vegetation. Mesquites, junipers, pinyons, and various shrubs and half shrubs are increasing in density in the semi desert grassland. Savannahs are evolving into dense woodlands. At higher elevations, coniferous forests are changing from open grown ponderosa pine to dense stands of mixed conifers. Current fuel loading and plant communities are far from "natural conditions".

POLICIES REVISITED

An unusually severe fire season in the Western United States this year is causing many citizens to call for a reevaluation of the policy of suppressing all wildfires. Newspaper editorials are challenging the Forest Service and other agencies to consider a new paradigm in fire management. Agency personnel, as well as the general public, are beginning to take a new look at the policy. Many people, including the author, advocate a "more natural" role of fire in the ecosystem. Some are unrealistic about needed changes, and see the problem as one of just ceasing to suppress fires. They equate the agency's need to change to the currently popular "Just say no to drugs" slogan. Other citizens have constructed homes and cabins in dangerous fuel situations and they advocate suppressing every fire immediately.

1994 FIRE SEASON

A review of the 1994 fire season in the Southeast Zone of Arizona will illustrate the challenges. '94 was an unusually severe season, with 589 fires burning in excess of 84,000 acres. The first fire occurred on January 2, and fires continue to burn. Some experts at this conference are predicting that next year might be worse. Following are selected examples of fire situations.

Arson

One or more arsonists started 26 fires, in and around the Santa Rita Mountains, in the spring and early summer. An individual was caught by Forest Service law enforcement about June 1, and the arson problem ceased. Most of these fires were in the semi desert grasslands, and little resource damage resulted. Some threatened to spread to heavier fuels in the Santa Ritas and Huachucas. One of these arson fires overran a crew on the Santa Rita Experimental Range, necessitating deployment of protective shelters - an omen of things to come.

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Miller Fire

The first damaging fire of the year occurred in Miller Canyon, of the Huachuca Mountains, in early June. An escaped campfire burned about 3,000 acres in very steep terrain on the east slope of the mountain. Severe watershed damage occurred and, in spite of rehabilitation efforts, soil loss and downstream damage continues to occur.

Proposed Baker Prescribed Burn

A prescribed fire was planned for June, in Baker Canyon, of the Peloncillo Mountains. This proposal involved National Forest, Bureau of Land Management, and private lands in Arizona and New Mexico. After an 8 month planning and coordination effort, approval was obtained to burn in June. A hot prescription was needed, because target species included mesquite, juniper, and other difficult to kill species. The burn was planned for early summer in an attempt to mimic natural fire.

By mid-June the plan was approved and ignition was eminent, when fires in New Mexico usurped needed resources. It seemed that another "window of opportunity" would occur as fire resources returned from New Mexico following light rainfall. However, the New Mexico storm moved into the area and Baker Canyon received about one inch of rain. Grass in the area greened up and it was necessary to postpone the burn, due to excessive moisture in the fine fuels.

Several lightning fires occurred within the prescription area over a two week period and all were monitored, but total burned acreage was less than 100 acres. The Baker Prescribed Burn is currently scheduled for the spring of 1995.

Sycamore, Peloncillo, and Cottonwood Fires

Meanwhile, lightning ignited two fires just north of the Baker drainage. Current policy requires suppression of all fires, but allows for judgment in the selection of a cost effective strategy. Potential ecological impacts are not a consideration in these judgments. All fires in the Peloncillos were assigned low priority for suppression and a "confine, contain" strategy was adopted. The Sycamore Fire burned on BLM, State, and National Forest Land and affected about 24,000 acres. At one point it burned to the perimeter of the proposed Baker Burn and stopped. The Peloncillo Fire burned about 200 acres of National Forest and went out. Another low priority fire occurred at the same time in Cottonwood Canyon of the Santa Teresa Mountains. This fire was confined, by one crew, to natural barriers and burned 12,000 acres, with a total suppression cost of $24,000. All of these wildfires created mosaic vegetation patterns and accomplished the objectives outlined in the Baker Burn Plan.

Oracle Fire

Arizona State Land Department was also experiencing numerous fires. One of the most challenging was in the vicinity of the town of Oracle. Oracle is built in some significant fuels and many houses are in danger from any nearby wildfire. This fire was especially significant; because it was east of town in the heaviest fuels with an easterly wind, an unusual situation. Because the Oracle Fire threatened to burn through the town, an aggressive suppression effort was undertaken. The Southeast Zone Overhead Team was dispatched, with significant resources, and the fire was turned away from the improvements, with extensive use of aerial retardant.

Pima Fire

While the Oracle Fire was burning on the North side of the Catalinas, the lightning-caused Pima fire started on the South side of the mountain. This fire burned about 500 acres in a place that was highly visible from the city of Tucson. The burned area was all in desert bighorn habitat, and significant ecological benefits occurred; but there was a perceived threat to high value homes at the urban interface. Sonoran Desert plants such as saguaros and palo verdes apparently evolved in the absence of frequent fire and they are particularly susceptible to fire. These plants are highly valued by the people of Tucson and they were plentiful in the vicinity of the fire. In the late stages of the Pima Fire a helicopter crashed while on a mission to take supplies to firefighters in a narrow, rocky canyon. The pilot was severely burned and experienced internal injuries, and the cost in human suffering was great.

Rattlesnake Fire

At about the same time, a lightning storm moved across the Peloncillo and Chiricahua Mountains. The Owl fire in the Peloncillos was assigned a low priority, while two ignitions in the Chiricahuas were aggressively attacked. One was suppressed. The Rattlesnake Fire escaped initial attack and eventually burned 27,500 acres. This escape was at least partially due to the fact that the Oracle Fire received priority for air support, because of the threat to life and property.

The Rattlesnake Fire burned in a typical mosaic pattern, with interspersed hot burns, light burns, and intermediate intensities. Severe damage to timber and watersheds occurred on a significant acreage. Structures at Rustler Park, Methodist Camp, and in Cave Creek Canyon were threatened, but a valiant effort by firefighters saved all but one outhouse. This fire was a classic example of the effects of 90 years of fuel accumulation in a conifer forest. Fuel loading exceeded 200 tons per acre in many places, compared with a "natural loading" of 60 tons or less. Extremely heavy fuels and rugged terrain made it unsafe to place personnel in the path of the fire, and it was not controllable with available resources. Cost of this suppression effort was 6.5 million dollars. Current conditions on the Penaleno Mountains to the north are thought to be even more explosive and challenging.

Rincon - Reddington Fires

Lightning started a complex of fires in the Rincon Mountains, which include both Saguaro National Monument, and Coronado National Forest. These fires started as the Pima and Oracle Fires were winding down and the Rattlesnake was beginning. By this time over 100 fires were burning in the Southwestern Region and no rain was predicted.

The National Park Service's Rincon Fire was initially allowed to burn under a prescribed natural fire prescription. The Forest Service was consulted in this decision and it was agreed that this was a proper approach under a previous agreement to allow fire to assume a more natural role in this wilderness area, and due to severely limited resources. The Forest Service brought in a Class 2 overhead team from the Coconino National Forest and attacked the Reddington Fire. After about a week, it was decided to declare the Rincon a wildfire and aggressive suppression of both fires was pursued. This decision was based on worsening fire danger and continued lack of resource availability. There was a concern that the Rincon Fire might endanger firefighters on the nearby Reddington Fire. The Rincon Fire burned 2,400 acres, and the Reddington burned 4,000 acres. Suppression of the complex cost about 6.5 to 7 million dollars.

Maverick - Cloverdale Fires

It was decided to return to a more aggressive suppression posture in the Peloncillo Mountains, due to limited resources and the total commitment of Douglas District personnel to the Rattlesnake suppression effort. This decision had little actual effect on burned acreage, due to other priorities for very limited resources. The Maverick Fire burned 900 acres and the Cloverdale was 800. Neither caused significant resource damage.

Lessons Learned

The 1994 fire season is not over at the time of this writing, and all involved agencies are still in the process of evaluating policy. The following opinions are personal observations and do not reflect agency direction:

- Putting out all small fires is not a good idea.
- It is not feasible to "just say no to suppression".
- More prescribed burning is needed.
- The current process for approving burning is much too complex and time consuming.
- Agencies must find a way to incorporate ecological factors into suppression decisions.
    - This will require a new paradigm in fire management.
    - It will require public trust of decision makers.
    - Scientists can help with public education.
    - Environmental groups can help with public perceptions.

THE FUTURE

Current public discussions of fire policy are healthy and welcomed. The media are asking the right questions in a constructive fashion. Federal and state agencies are on the right track. This is evidenced by Forest Service Chief, Jack Ward Thomas' recent congressional testimony on the "Forest Health" issue, where he advocated more use of fire as a management tool. All agencies are beginning to advocate an ecosystem approach to natural resource management. This will involve a new look at the role of fire in the ecosystem and it is the hope of the future.

We have a long way to go to return fire to its proper role in western ecosystems, but recent trends are encouraging. Participants in this conference are urged to continue encouragement of administrators in the Forest Service, National Park Service, Bureau of Land Management, and State Land Departments.

Fire and Vegetation in a Madrean Oak Woodland, Santa Catalina Mountains, Southeastern Arizona

Anthony C. Caprio[1] and Malcolm J. Zwolinski[2]

Abstract.—The presence and effects of fire in Madrean oak woodland have often been noted but have been poorly studied, even though fire may play a significant role in the dynamics and structure of the vegetation. To provide information about how fire affects some of the major species in this community, we examined both the immediate effects and the postfire response of individual species following a June burn. Plant composition and biomass data were collected in burned and unburned areas on north, east, and south aspects, permitting several levels of comparison. Our findings indicated significant changes in species composition were caused by the fire, with varying postfire species responses. Woody species were reduced with limited recovery, while forb and graminoid species, which were initially reduced, had greater cover in burned than in unburned areas by 2½ years postfire. Recovery was rapid on the south-facing slope, dominated by graminoids, and more limited on the north slope, where woody species and *Selaginella* were important preburn.

Species favored by burning included *Artemisia ludoviciana*, *Gnaphalium wrightii*, *Aristida orcuttiana*, *A. adscensionis*, *Bouteloua curtipendula* and *Eragrostis intermedia*, while intolerant species included *Arctostaphylos pungens*, *Agave schottii*, *Haplopappus laricifolius*, *Trachypogon secundus* and *Selaginella rupincola*. Comparison of the two major tree species showed both resprouted well after injury, but indicated *Quercus oblongifolia*, with less top-kill, was more tolerant of fire than *Q. emoryi*, although both species suffered about 15% mortality. This information about tolerances and responses of woodland species to fire suggested that fire was an importance process in the shaping and maintenance Madrean oak woodlands in the past. Total herbaceous and litter biomass (fine fuels) 2½ years postfire varied between 272-622 g • m^{-2} at unburned and 253-370 g • m^{-2} at burned sites. Rapid accumulation of fine fuels, particularly on south aspects, could enable the occurrence of short intervals between fires (1-2 years), though accumulations may be influenced by precipitation. Rapid postfire fine-fuel accumulations indicated oak woodland may have supported frequent burns and could have been an important connection for fire spread between semi-desert grassland and higher elevation vegetation.

INTRODUCTION

The occurrence and prevalence of fire in southwestern plant communities have been recognized since the late 19th century (Holsinger 1902; Rothkugel 1909; Blumer 1910; Leopold 1924; Pearson 1931). While fire's role has been investigated within several biotic communities in the area: semi-desert grassland, interior chaparral, and ponderosa pine forest, there is currently a lack of adequate information on its effects, and plant species response to its occurrence in Madrean evergreen woodland. However, fire's presence within the woodland has often been noted (Leopold 1924; Gentry 1942; Whittaker and Niering 1964) which suggests that fire plays an important role in determining community compo-

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sition and diversity, natural selection processes, population dynamics, and species distributions. Furthermore, it remains unclear how the various attributes of fire might affect these variables over both differing spatial and short and long-term time scales.

Within the Madrean evergreen woodland there is evidence of vegetation changes having taken place during the last 100 years, with fire control suggested as a primary reason. The ecological consequences of the decisions about fire suppression made 80 to 90 years ago have had dramatic effects on the dynamics and structure of many ecosystems throughout western North America (Dodge 1972; Vankat 1977; Parsons and DeBennedetti 1979). Because of this the Forest Service, National Park Service, and private organizations, such as the Nature Conservancy, have begun or are planning prescribed burns in the woodland. Prerequisite for a wide-spread and fine-tuned burning program is a better understanding and knowledge about the physical and ecological effects of fire (Kickert et al. 1976; Trabaud 1987; USDA 1993) that goes beyond a simple knowledge of how an area or organism will be affected and respond to the postfire environment. It is becoming increasingly apparent that multiple postfire outcomes are possible, given the varied burning conditions and species compositions of an area. Understanding both the role and history of fire in an ecosystem is important in management planning and in identifying whether fire effects and responses are beneficial or detrimental to a resource given a desired management objective. The ultimate biological ramifications from both fire suppression and prescribed burning have still not been concluded and are leading to an unpredictable future, a future that may have multiple outcomes for the ecosystems which cannot presently be predicted. Even if we do initiate changes in management practices today the residual effects of past policies will carry forward into the future due to persistence and longevity of many organisms within an ecosystem.

This study focused on fire effects and postfire response of vegetation in a Madrean oak woodland community that burned during a late June wildfire. We attempted to answer some of these questions by comparing vegetation and associated changes caused by fire in burned areas relative to associated unburned areas. Quantitative results were sought to permit judgments to be made about the ecological role of fire and predictions about fire effects and plant responses. This included the identification and description of changes in species composition and establishment patterns in the woodland in relation to fire. Quantification of such fire effects in relation to ecological patterns and processes responsible for oak woodland dynamics and composition is of particular importance in providing guidance for ecosystem management planning.

STUDY AREA

Madrean oak woodland in the United States is common in southeastern Arizona and adjacent New Mexico at intermediate elevations between lower, more xeric, semi-desert grasslands and higher, more mesic, oak-pine woodlands (fig. 1). The area we sampled was located in Molino Basin on the south slope of the Santa Catalina Mountains at elevations between 1475 m and 1525 m (fig. 2). The Santa Catalina Mountains rise from the Santa Cruz valley floor at about 700 m up to the summit of Mt. Lemmon at 2775 m. This elevational change creates strong physical and biotic gradients from lower to upper elevations. Precipitation increases with elevation while temperature and evaporation generally decrease with increasing elevation (Whittaker and Niering 1964). Precipitation has a distinctly bimodal distribution with wet winters and summers (Pearson 1922; Jurwitz 1953).

Figure 1.—Regional distribution of oak woodlands and the location of the Molino Basin study area in the Santa Catalina Mountains.

Vegetation in Molino Basin forms a transition between semi-desert grassland on south facing slopes to moderately dense oak woodland on north facing slopes. It has components of typical open oak woodland plus some derived from interior chaparral found in central Arizona. The open or "savannah like" woodland shares many species with lower elevation semi-desert grasslands. Plant distribution patterns in the Santa Catalinas have been the subject of several classic studies (Shreve 1915; Whittaker and Niering 1964, 1965, 1968a, 1968b, 1975; Whittaker et al. 1968; Niering and Lowe 1984). Much of the basin burned during a fire from June 28 -30, 1983. Although the fire was human caused it burned during the foresummer dry season when natural fires are most common (Pearson 1922; Swetnam et al. 1989) and thus fire effects should be similar to those resulting from natural wildfire. Approximately 259 ha burned by the time suppression was successful (fig. 2) with about 200 ha burning the day ignition occurred prior to initiation of suppression activities. Containment of the burn was achieved by back-burning and guiding the fire into natural barriers. The three sites selected for study represented: 1) very open woodland on the south facing slope, 2) "open woodland" (Whittaker and Niering 1965) or "lower encinal" (Shreve 1915) on a southeast facing slope and 3) a relatively dense woodland on a north facing slope, characteristic of "pygmy conifer-oak woodland" (Whittaker and Niering 1965).

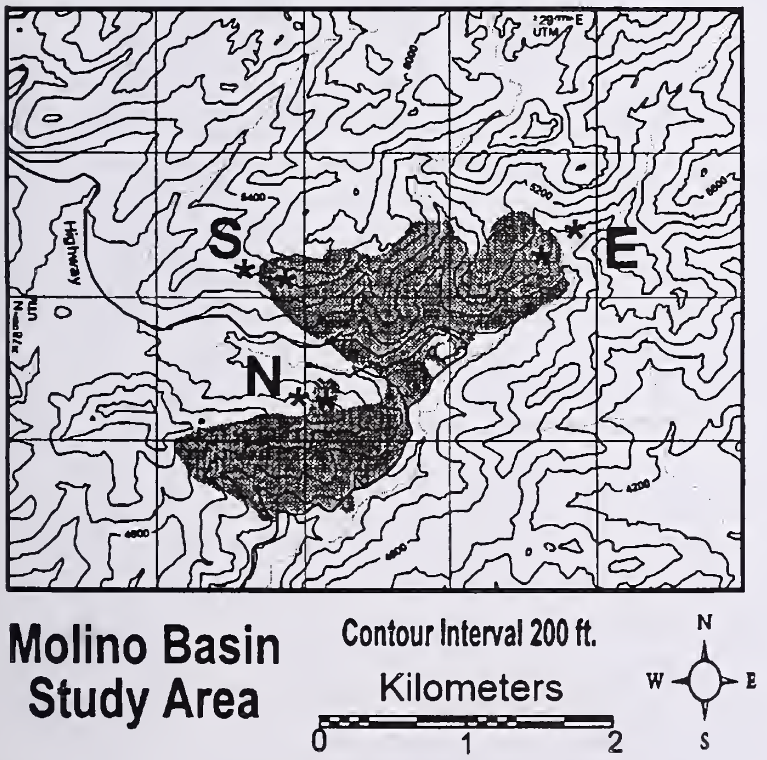

Figure 2.—Location of the paired burned and unburned sites on the three aspects and the approximate boundaries of the 1983 burn (shaded area).

METHODS

Sampling was designed to test for differences in vegetation at three sites of differing aspect, each with a burned and unburned area. This choice of sites allowed us to examine a range of fire effects since vegetation structure varied with aspect. We sampled vegetation using permanently placed plots in vegetatively similar areas at each site. Subsites were sampled using three randomly placed plots (15 x 30 m) established on adjacent burned and unburned areas. Individual plots consisted of line intercept transects and nested quadrats. Three quadrat sizes were used to sample each of the three life-form strata: herbaceous (20 x 50 cm), subshrub (3 x 5 m), and shrub-trees (5 x 30 m). Sampling was conducted to detect vegetation differences in cover, frequency, density, and biomass between site and burn factors. Cover of each herbaceous species in a microplot was recorded using modified Daubenmire cover classes (Daubenmire 1968b, Mueller-Dombois and Ellenberg 1974). Cover of woody species was sampled by measuring canopy interception along five 30 m transects. Frequency and density were sampled in each of the nested quadrats. Additionally, we took three random one-meter square herbaceous biomass samples (fine fuels) immediately adjacent to each permanent plot. Sampling was begun 10 months postburn and was conducted biannually for two years in April/May and September/October at the end of the winter/spring and summer growing seasons. This permitted us to measure the immediate fire effects and some longer term postburn vegetation responses. An additional larger sample of *Quercus oblongifolia* and *Q. emoryi* was taken during the summer of 1985, two years postburn as Plumb (1963; 1980) recommends, to account for delayed mortality. Individuals trees were recorded as resisting the burn (those trees in which the crown survived alive), topkilled but sprouting from the root crown, or as dead. Specific details of this sampling are given in Caprio and Zwolinski (1982).

The analysis focused on three areas; 1) description of species patterns and physical characteristics of the three sites, which provided baseline information important for the interpretation of the fire effects and postfire plant response, 2) comparison of differences in cover between burned and unburned areas for individual species (nomenclature followed Kearney and Peebles (1951 [Supplement 1960]) and in cover and biomass using broader life-form groupings of species.

RESULTS

The dominant tree species in the study area were *Quercus oblongifolia* (Mexican blue oak) and *Q. emoryi* (Emory oak or bellota) in addition to scattered *Q. arizonica* (Arizona white oak), *Pinus cembroides* (border piñon pine), and *Juniperus deppeana* (alligator juniper). Important shrubs were *Arctostaphylos pungens* (point-leaf manzanita) and *Garrya wrightii* (Wright silk-tassel) and common subshrubs were *Agave schottii* (amole or shin-dagger), *Calliandra eriophylla* (fairy-duster), *Dasylirion wheeleri* (sotal), *Haplopappus laricifolius* (turpentine bush), *Desmodium cinerascens* (tick-clover), *Nolina microcarpa* (beargrass), *Gossypium thurberi* (wild cotton or algodoncilla), *Brickellia californica,* and *Selloa glutinosa.* Wet or warm season graminoids dominated the herbaceous vegetation with important species being *Eragrostis intermedia* (plains lovegrass), *Muhlenbergia emersleyi* (bull grass), *Bouteloua curtipendula* (side-oats grama), *B. hirsuta* (hairy grama), *Andropogon cirratus* (Texas bluestem), *Lycurus phleoides* (wolftail), *Koelaria cristata* (mountain Junegrass), *Aristida adscensionis* (six-weeks three-awn), *Trachypogon secundus* (crinkle-awn) and *Heteropogon contortus* (tangle-head). Important forbs included *Gnaphalium wrightii, Artemisia ludoviciana* (sagebrush or groundsel), *Agastache breviflora,* and *Lotus rigidus* (deer-vetch). The non-flowering species: *Selaginella rupincola* (club moss) and *Cheilanthes wootoni* (beaded lip-fern) were also major cover constituents on the east and north slopes. Overall composition and dominance of species varied among the three sites sampled: graminoids were important on the south slope and woody species on the north slope, with the east slope being intermediate. The south slope had characteristics of an oak savannah while the north slope had some characteristics of interior chaparral.

We found that cover of woody species showed distinctive effects and responses among the three sites both in unburned and burned areas (**fig. 3**). Cover of woody species in unburned areas was greatest on the north slope and lowest on the south slope. The difference in cover between burned and unburned plots was greatest on the north slope (13.8% burned versus 59.6% unburned, average of all four sample periods) and least on the south slope (17.6% burned versus 37.9% unburned) when each of the three paired burned and unburned areas were compared. By 2½ years postburn, differences between burned and unburned areas were minimal, with burned areas having slightly higher percent cover.

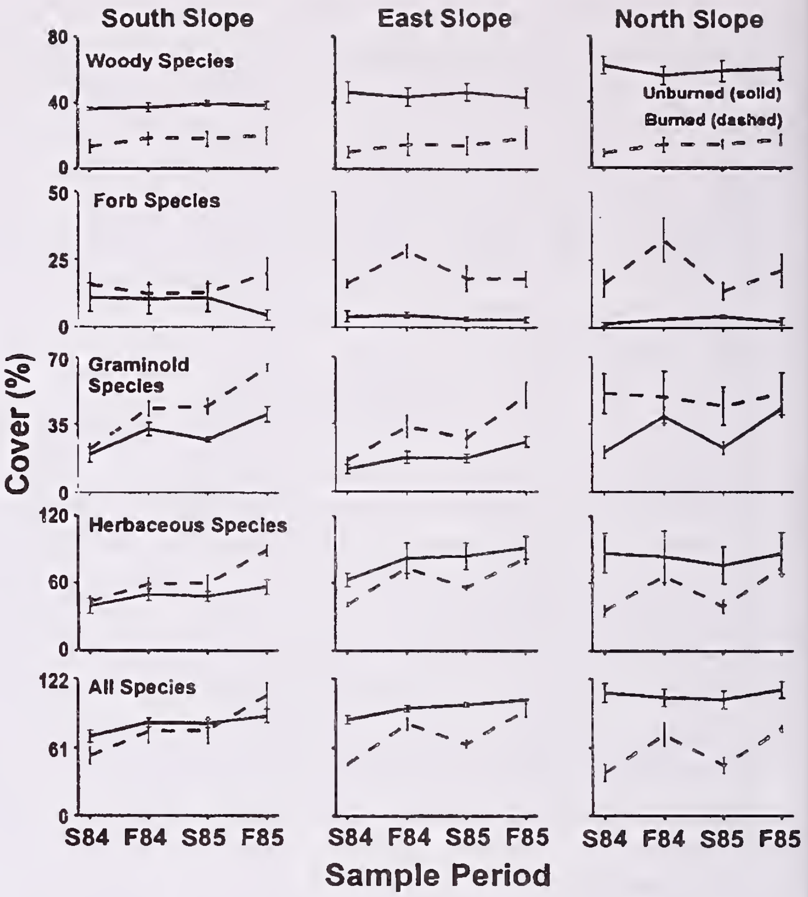

Figure 3.—Fire impacts and responses of vegetation at the three burned areas (dashed lines) compared to paired unburned areas (solid lines). Graphs show percent cover (±1SE) for species data summed into major life-form groups during each of the four samples at each of the three aspects.

Comparisons of forb and graminoid cover also showed specific site differences and postburn fire effects and responses. Forb cover was greatest in unburned areas on the south slope with low values for both the east and north slopes (fig. 3). Graminoid cover was greater than forb cover at all sites with cover on the south and north slope slightly exceeding the east slope (a large portion of the graminoid cover on the north slope was composed of summer annual species, particularly *Aristida adscensionis*). Overall, the burn produced a very rapid and positive response in forb and graminoid covert. By 10 months postburn, when sampling began, cover was greater in all burned areas compared to unburned areas. Postburn forb response was greatest on the north and east slopes, while graminoid cover increased substantially at all sites. The apparent rapid increase of graminoid cover on the north slope, that was then followed by fairly constant values, was a result of the immediate establishment of annual species. In contrast, increasing graminoid cover on the south and east slopes was due to growth or establishment of perennial species. Seasonal trends in cover data for forbs were obvious and most striking on the north slope, resulting from increases in summer annuals, particularly the first summer postburn.

Total herbaceous species cover (forbs, graminoids, and non-flowering species combined) showed consistent patterns among the three unburned sites, with cover greatest on the north slope and least on the south (fig. 3). This pattern (as contrasted with the cover values for forbs and graminoids alone) was largely due to the dominance of *Selaginella rupincola* on north and east slopes. Following the burn, this pattern shifted so that during the first postburn sample, cover was nearly equivalent among the three sites. This indicated that cover of herbaceous vegetation on the south slope was the least impacted by the burn while a greater impact occurred on the north slope. Longer-term postburn responses also varied among the sites. On the south slope average cover in burned plots exceeded that in unburned plots by 10 months postfire (42.9% burned versus 39.3% unburned) but only approached this point on the east and north slope by 2½ years postfire (82.8% east and 73.9% north burned versus 91.8% east and 87.0% north unburned). We found consistent cover increases on the south slope following the burn while the east and north slopes showed stronger seasonal trends reflecting the growth and dieback of annuals during a year. The differing postburn response of the south slope relative to the east and north slopes was primarily a result of a high proportion of sprouting perennial species on the south slope and the high cover values for

Table 1—Percent cover in unburned areas (clear) and burned areas (shaded) during the spring 1984 and fall 1985 sampling for the 21 common species.

	Spring 1984 Samples						Fall 1985 Samples					
Species	Unburned			Burned			Unburned			Burned		
	S	E	N	S	E	N	S	E	N	S	E	N
Quercus emoryi	0.68	9.12	3.59	0.47	0.47	0.51	0.72	8.49	3.67	0.36	0.85	1.08
Quercus oblongifolia	10.25	6.33	0.00	3.22	5.49	0.00	9.80	5.47	0.19	4.02	4.93	0.21
Arctostaphylos pungens	5.64	5.33	4.26	0.00	0.30	0.91	6.27	5.66	4.06	0.00	0.62	0.93
Garrya wrightii	0.27	3.61	24.53	0.13	0.03	1.82	0.23	2.96	22.57	0.30	0.52	3.12
Agave schottii	2.64	8.31	0.00	0.32	0.21	0.00	3.13	8.08	0.00	0.74	0.39	0.00
Dasylirion wheeleri	5.13	5.71	0.82	0.65	1.31	0.05	5.21	6.23	1.48	0.34	1.92	0.41
Haplopappus laricifolius	1.18	2.90	0.56	0.00	0.08	0.00	1.99	1.62	0.71	0.00	0.05	0.25
Nolina microcarpa	3.50	1.32	14.40	1.39	0.00	1.44	3.18	0.78	14.31	3.78	0.00	1.80
Artemisia ludoviciana	4.12	0.72	0.67	1.89	2.85	1.96	2.89	0.62	1.07	6.82	5.83	7.63
Gnaphalium wrightii	0.03	0.51	0.00	0.51	3.97	7.77	0.12	0.12	0.02	0.70	0.30	0.53
Lotus rigidus	4.25	0.78	0.05	0.81	1.19	0.80	0.51	0.87	0.00	7.47	0.28	0.00
Andropogon cirratus	1.80	3.74	0.91	0.12	1.13	0.58	1.80	7.52	1.86	0.43	5.37	3.81
Aristida orcuttiana	0.89	1.68	0.00	0.00	1.65	0.15	1.60	2.28	0.25	0.84	2.61	0.54
Bouteloua curtipendula	2.21	0.41	0.62	6.01	1.96	0.30	6.11	1.82	2.08	17.28	4.87	1.71
Eragrostis intermedia	0.38	0.00	0.00	2.60	3.49	1.51	1.46	0.64	0.84	17.53	5.89	4.20
Heteropogon contortus	0.13	0.58	0.00	0.36	2.21	0.00	0.30	2.08	0.00	1.89	6.62	0.00
Muhlenbergia emersleyi	9.99	5.52	1.22	3.44	3.41	2.81	20.37	4.95	1.63	5.59	16.05	7.94
Trachypogon secundus	1.66	2.42	0.00	0.00	1.09	0.00	2.82	4.76	0.00	0.81	4.54	0.00
*Aristida adscensionis**	0.03	0.33	2.18	1.99	0.31	3.78	0.00	0.46	1.49	0.00	0.15	3.63
Cheilanthes wootoni	2.15	2.48	3.82	0.97	1.84	1.66	2.00	3.39	1.96	0.74	2.97	2.41
Selaginella rupincola	1.06	20.81	25.92	0.00	1.87	3.09	1.04	27.04	24.32	0.00	2.94	4.31

*Fall sample in 1984, species is a summer annual.

Selaginella rupincola (see Table 1) on the east and north slopes which was severely reduced by the burn and showed no postburn recovery.

The combined cover data for all species presented the clearest overview of conditions at unburned sites, fire impacts, and postburn responses of vegetation in this oak woodland. Total cover in unburned plots was greatest on the north slope and in burned plots on the south slope, reflecting the greater burn impact on woody vegetation on the north slope versus the rapid recovery of the perennial herbaceous vegetation on the south slope (**fig. 3**). The reduction of cover on the east and north slope is primarily a result of the reduction of woody species and *Selaginella rupincola*. Total cover was greatest on the north slope in unburned areas (107.9% average for all four samples, SD=3.9) and on the south slope in burned areas (107.1% fall 1985 sample). The greatest difference in total cover between burned and unburned areas was measured on the north slope (112.5% versus 78.4%). On the south slope, total cover was only slightly less (relative to unburned) one year postburn (71.4% versus 54.1%), but it exceeded cover in unburned areas by 2½ years postburn (89.2% versus 107.1%).

Fire effects and responses of many of the major species following the burn were consistent among the three sites indicating that aspect did not dominate specific species fire effects. Fire effects and the subsequent response of species by 2½ years postburn resulted in an apparent cover decrease in all eight major woody species relative to unburned areas, a general increase in four herbaceous species, and no significant impact on the others (Table 1). Most woody species (*Quercus oblongifolia, Q. emoryi, Arctostaphylos pungens, Garrya wrightii, Agave schottii, Dasylirion wheeleri, Haplopappus laricifolius, eolina microcarpa*) did not show significant postburn recovery (relative to unburned) during the period of this study, however, several less common subshrubs (*Calliandra eriophylla, Gossypium thurberi, Brickellia californica*) did respond rapidly. In some burned areas cover of these subshrubs exceeded that in unburned areas. Forbs that showed a strong positive response following the burn were *Gnaphalium wrightii, Artemisia ludoviciana*. The response of *G. wrightii* was short-lived with high cover values the second year following the burn followed by a decline the third. *A. ludoviciana* showed a prolonged response with cover continuing to increase three years postburn. *Lotus rigidus* displayed little evidence of change due to the burn. The only graminoids exhibiting an obvious decline in cover when compared to paired plots was *Trachypogon secundus*. Graminoid species that increased following the burn, relative to paired unburned areas, included *Bouteloua curtipendula, Eragrostis intermedia, Muhlenbergia emersleyi,* and *Aristida adscensionis*. The burn had little impact on *Aristida orcuttiana, Andropogan cirratus,* and *Heteropogon contortus*. The two important non-flowering species in the study area, *Cheilanthes wootoni* and *Selaginella rupincola,* showed moderate to severe reductions in cover. While *C. wootoni* showed evidence of recovery by 2½ years postburn, cover of *S. rupincola* remained low.

We observed differing fire impacts on the two main oak species in the study area (fig. 4). *Quercus oblongifolia* showed greater resistance to either topkill or mortality than did *Q. emoryi* (average of 40.5% versus 61.6% at the three sites), but each species had about an equal proportion (14.1% vs 14.9%) of individuals being killed (or surviving, either with crown alive of via sprouting after being topkilled, 85.9% versus 85.1%). The most pronounced difference between the two species was the lower proportion of *Q. oblongifolia* topkilled relative to *Q. emoryi* (46.8% vs 26.4%).

Total herbaceous and litter biomass as a measure of fine fuels available to carry a fire had a higher degree of variability within a site than other measures due to each value being an average of only three subsamples (fig. 5). Biomass was greatest in unburned areas, with the largest values found on the south slope and smallest on the north (average of all four samples was 482.7 g•m^{-2} south, 373.4 g•m^{-2} east, and 246.2 g•m^{-2} north). At 10 months postburn, biomass in burned areas was 107.5 g•m^{-2}, 150.0 g•m^{-2}, 136.1 g•m^{-2} respectively on the south, east, and north slopes and by 2½ years postburn these values had increased to 253.2 g•m^{-2}, 370.5 g•m^{-2}, 253.7 g•m^{-2}. In contrast to biomass, litter cover showed more consistent patterns within burned and unburned areas (fig. 5). Litter cover was nearly constant through time and approximately equal at all unburned areas (averaging 33.0% for the four samples) while data from burned areas indicated reductions due to the burn were followed by consistent increases. In burned plots at 10 months postburn, cover was lowest on the north slope (12.4%) and greatest on the south slope (22.2%), while at 2½ years postburn litter cover had increased to 30.3% and 39.6% respectively at the two sites. Differences between burned and unburned areas declined rapidly following the burn. By 2½ years postburn, litter cover on the south and east slopes exceeded that in paired unburned plots (39.6% burned versus 30.1% on the unburned south slope and 34.8% burned versus 32.1% on the unburned east slope).

DISCUSSION

The 1983 burn during the region's dry fore-summer period had differing impacts on vegetation at each of the three sites, although impacts and responses of individual species among sites were often similar. Site differences were largely a result of interacting influences of varying species compositions and fuel loads. The fire had the least overall impact on the south and east slopes which responded rapidly following the burn. A more severe impact and a slower post-burn response occurred on the north slope. Reduced impacts on the south and east slope were apparently a result of the dominance of perennial graminoids that responded rapidly following the burn, often reaching preburn size within one year. Some of these species, such as *E. intermedia,* also exhibited increased vigor and establishment following the burn. The effects on the north slope were due to the fire's impact on woody species, such as *Arctostaphylos pungens* and *Selaginella rupincola,* that responded slowly following the burn. On this slope, woody species composed a larger proportion of the vegetation, with a greater dominance of species that were killed or topkilled by the fire, while many woody species on the south slope were subshrubs that recovered rapidly (*Acacia angustissima, Calliandra eriophylla*). Overall, species on the south slope generally exhibited greater resilience than species on the north slope. The north slope species were also impacted by fire of greater severity as a result of more woody fuels.

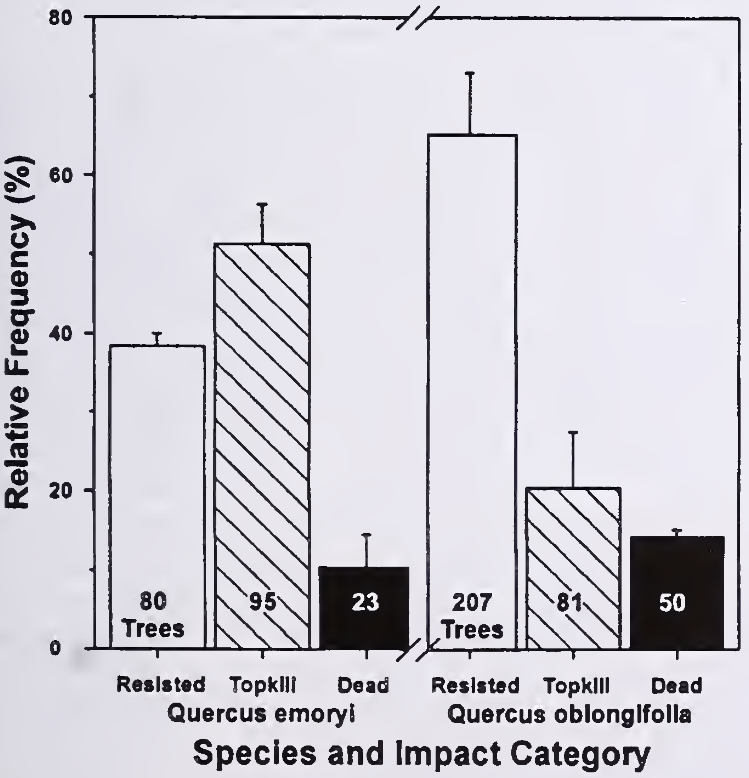

Figure 4.—Relative fire impacts on *Quercus oblongifolia* and *Q. emoryi* showing the proportion of trees that resisted the burn with their crown alive, or were topkilled, or died following the burn.

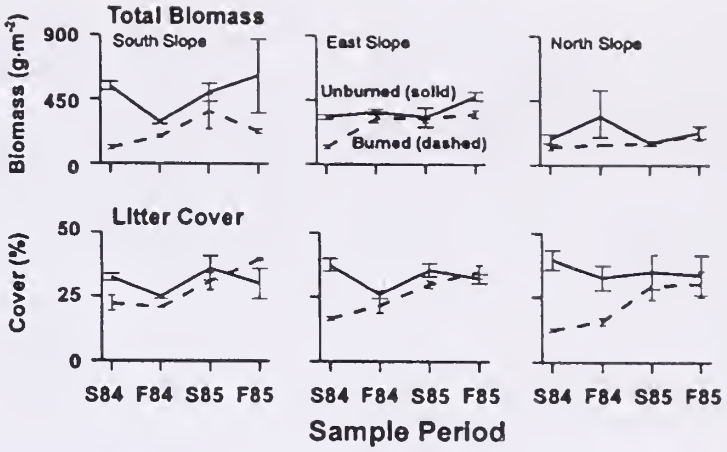

Figure 5.—Fire impacts and responses of biomass less-than one-centimeter diameter at the three burned areas (dashed lines) compared to paired unburned areas (solid lines). Graphs show fine fuels biomass (±1SE) for during each of the four samples at each of the three aspects.

The greater resistance of *Quercus oblongifolia* relative to *Q. emoryi* may be a function of differing bark characteristics, such as thickness, structure, composition, and moisture content that affect its ability to insulate the tree from fire (Plumb 1980, 1983). However, the lower resistance of *Q. emoryi* relative to *Q. oblongifolia* appears to be compensated by a more vigorous postfire sprouting response when the two oak species are compared (Caprio and Zwolinski 1992; Caprio 1994). These differences in resistance and survival may have important implications for the establishment and persistence of these species at specific sites in relation to fire occurrence and to the broader distributional patterns over the landscape. Over the long-term, depending on specific fire regime characteristics (such as frequency or severity), one species may be more strongly favored than the other. Such varying effects and responses of individual species to fire may have important influences on the distributional patterns of many species at differing scales throughout the region.

Our data showed that *Quercus emoryi* and *Q. oblongifolia* had a strong postburn response relative to two other less common tree species in lower oak woodlands (*Juniperus deppeana* and *Pinus discolor*). Although alligator juniper is known as a postfire sprouter (Carmichael et al.

1978), it only sprouted to a limited extent and suffered considerable mortality following this burn, while border piñon pine exhibited extreme sensitivity to fire with all individuals present within the burn perimeter killed (Caprio 1994). Like the two oaks, these differences in tolerance to fire may help explain some distributional patterns of these species within southwestern ecosystems that may not be apparent now that fire suppression is prevalent. With reduced fire occurrence over the last 100 years these species may be expanding their range locally and increasing in density at sites where they were formerly more restricted. Such changes in many species (most obviously woody taxa) at many locations may be a result of the combined effects of fire suppression, intensive grazing, and climatic variation.

Of the eight woody species (trees, shrubs, and subshrubs) intensively sampled as major species, four (50%) were not tolerant of fire while the remaining species were tolerant, although all were reduced by fire (Table 2). We only considered one (6.7%) of the 13 herbaceous species intensively sampled to be intolerant of fire, while eight (60.4%) were tolerant, and four (30.8%) strongly favored. The tolerant species were resilient, with good sprouting ability, while favored species were usually resilient species that also increased via seedling establishment. However, some favored species, such as *Gnaphalium wrightii* and *Aristida adscensionis,* were able to increase without resprouting, at least temporarily, from seed sources that appeared to be derived from seed banks. These differing survival and regeneration strategies are important in understanding long-term dynamics and interactions of vegetation and fire in oak woodlands.

Table 2.—Fire tolerance of the 21 major species sampled. Criteria for determining tolerance follow Wright (1980).

Species Name	*Tolerance Rating*
Quercus emoryi	*Tolerant*
Quercus oblongifolia	*Very Tolerant*
Arctostaphylos pungens	*Not Tolerant*
Garrya wrightii	*Tolerant*
Agave schottii	*Not Tolerant*
Dasylirion wheeleri	*Mod./Not Tolerant*
Haplopappus laricifolius	*Not Tolerant*
Nolina microcarpa	*Tolerant*
Artemisia ludoviciana	*Favored*
Gnaphalium wrightii	*Favored*
Lotus rigidus	*Tolerant*
Andropogon cirratus	*Tolerant*
Aristida orcuttiana	*Tolerant*
Bouteloua curtipendula	*Very Tolerant*
Eragrostis intermedia	*Favored*
Heteropogon contortus	*Moderately Tolerant*
Muhlenbergia emersleyi	*Tolerant*
Trachypogon secundus	*Not Tolerant*
Aristida adscensionis *	*Favored*
Cheilanthes wootoni	*Moderately Tolerant*
Selaginella rupincola	*Not Tolerant*

* *Based on fall 1984 samples because the species is a summer annual.*

Biomass samples (all plant material less-than one-centimeter diameter) showed predictable responses following the burn (fig. 5). Recovery was strongest on the south and east slopes and less pronounced on the north slope where fewer sprouting herbaceous species existed. Fine fuel accumulation rates indicated some lower elevation woodlands may be able to sustain a second burn within one or two years. For example, the lower portion of the study area in semi-desert grassland that burned in 1983 reburned in 1985. One of the most pronounced effects of the burn was its tendency to change fuel characteristics from one of spatially discontinuous fuels to one dominated by more evenly distributed fine fuels (variance in fuel samples was generally less following the burn, particularly on the north slope). This rapid recovery and more even distribution of fine flashy fuels may be important in understanding past fire frequencies in southeastern Arizona, New Mexico, and Mexico because it suggests low intensity surface fires, spreading over large areas, could have occurred frequently. Removal of these fuels from lower elevations during the period of severe overgrazing in the late 1800s (Bahre 1991), rather than changes in higher elevation fuels in pine-forests, may have been one of the more important factors causing fire frequency reductions in mountainous coniferous forests in the Southwest. In the past, both semi-desert grasslands and higher elevation mixed conifer areas appear to have been interconnected by fire spread, often through oak woodlands. Fuel conditions, species compositions, and fire history data from low elevation sites provide strong evidence that fires were burning these areas at relatively high frequencies. Additional evidence (Blumer 1910; Bahre 1991; Caprio 1994) indicates these fires were often of very large size and that fires at lower elevation may have been an important source for fire spread into higher elevations. An analogous situation also appears to have occurred on the west slope of the Sierra Nevada (Caprio and Swetnam in press).

The overall effect of the burn in Molino Basin was to cause shifts in species dominance between burned and unburned areas, with the north slope sustaining the greatest change. However, species that were present in unburned areas were also usually present in burned areas and not eliminated. Persistent sprouting species were responsible for rapid vegetation recovery on the south slope which had an open savanna character. The fire increased the dominance of herbaceous species, particularly graminoids, at the expense of woody species and *Selaginella*. The fire effects and postburn species responses observed during this study indicated that fire exclusion or greatly reduced frequencies since about 1880 have had a very strong influence on the patterns of vegetation change that have taken place in southeastern Arizona during this interval. In the past, fire in oak woodland undoubtedly played an important role in species distributions, at least on the local scale, although its effects were probably subject to the influence and interactions of such factors as climate, topography, moisture, temperature, and soils. The ramifications of past and continued fire suppression in oak woodland have been an increase in the dominance of woody species, a decreased cover of herbaceous species (graminoids and forbs), and a fuel matrix of variable heavy and light fuels that may be more susceptible to lower frequency burns but burns of greater intensity and severity.

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Fire History in the Pinaleño Mountains of Southeastern Arizona: Effects of Human-Related Disturbances

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Abstract.—We reconstructed the history of fire at two sites in the mixed-conifer forests of the Pinaleño Mountains of southern Arizona from 90 fire-scarred living and dead southwestern white pine (*Pinus strobiformis*) and ponderosa pine (*Pinus ponderosa*) trees. We used dendroecological techniques to date nearly 2000 fire scars to their exact year of formation, and obtained age structure information from over 600 increment cores and cross-sections collected from Engelmann spruce (*Picea engelmannii*) and corkbark fir (*Abies lasiocarpa*). We compared the age structure data with the reconstruction of past fires to determine which fires may have had an effect on the higher-elevation forests. During the pre-settlement period (prior to 1880), low-intensity surface fires occurred once every four to six years, based on the median probability interval derived using the Weibull distribution. The age structure of the spruce-fir forest suggests that the forest established after a stand-replacement fire that occurred in 1685, considered one of the most widespread and intense of any reconstructed fire event. Fires had occurred predominantly in the early portion of the growing season (May and June) similar to current dominant season of fire activity. The cessation of episodic fires after 1893 can be attributed to a combination of human-related disturbances, especially grazing and fire exclusion. The absence of ecologically-significant fires during the last 100 years in the Pinaleño Mountains should be considered when developing land and fire management plans for this environmentally sensitive area.

INTRODUCTION

With few exceptions, most Southwestern U.S. fire history studies have been conducted in ponderosa pine-dominated habitat types (Swetnam 1990). Hence, little is known about the frequency and scale of fire events in Southwestern mixed-conifer and spruce-fir forests prior to the Euro-American settlement era (ranging from the late 1500s to late 1800s in different areas of the Southern Rockies). However, fire regimes in mixed-conifer habitat types are generally thought to be a mixture of moderate frequency, low-intensity, surface fires and infrequent, stand-replacing crown fires, while fire regimes in spruce-fir forests generally consist of infrequent, intense, stand-replacing crown fires. Research into the fire history and fire ecology of these habitat types in the Southwestern U.S. will therefore provide valuable information that can be used by land management agencies for initiating programs that satisfy mandate requirements of the Ecosystem Management policy.

The purpose of this study was to reconstruct the history of fire in mixed-conifer/spruce-fir forests in the vicinity of Mount Graham in the Pinaleño Mountains of southeastern Arizona (fig. 1) from fire scars dated using well-established dendrochronological techniques. We also incorporated information about the current age structure of the adjacent spruce-fir forest to analyze the history and/or possible effects fire may have had upon these higher-elevation forests. Our historical study of pre-settlement fires offers both a long-term perspective of past forest dynamics as well

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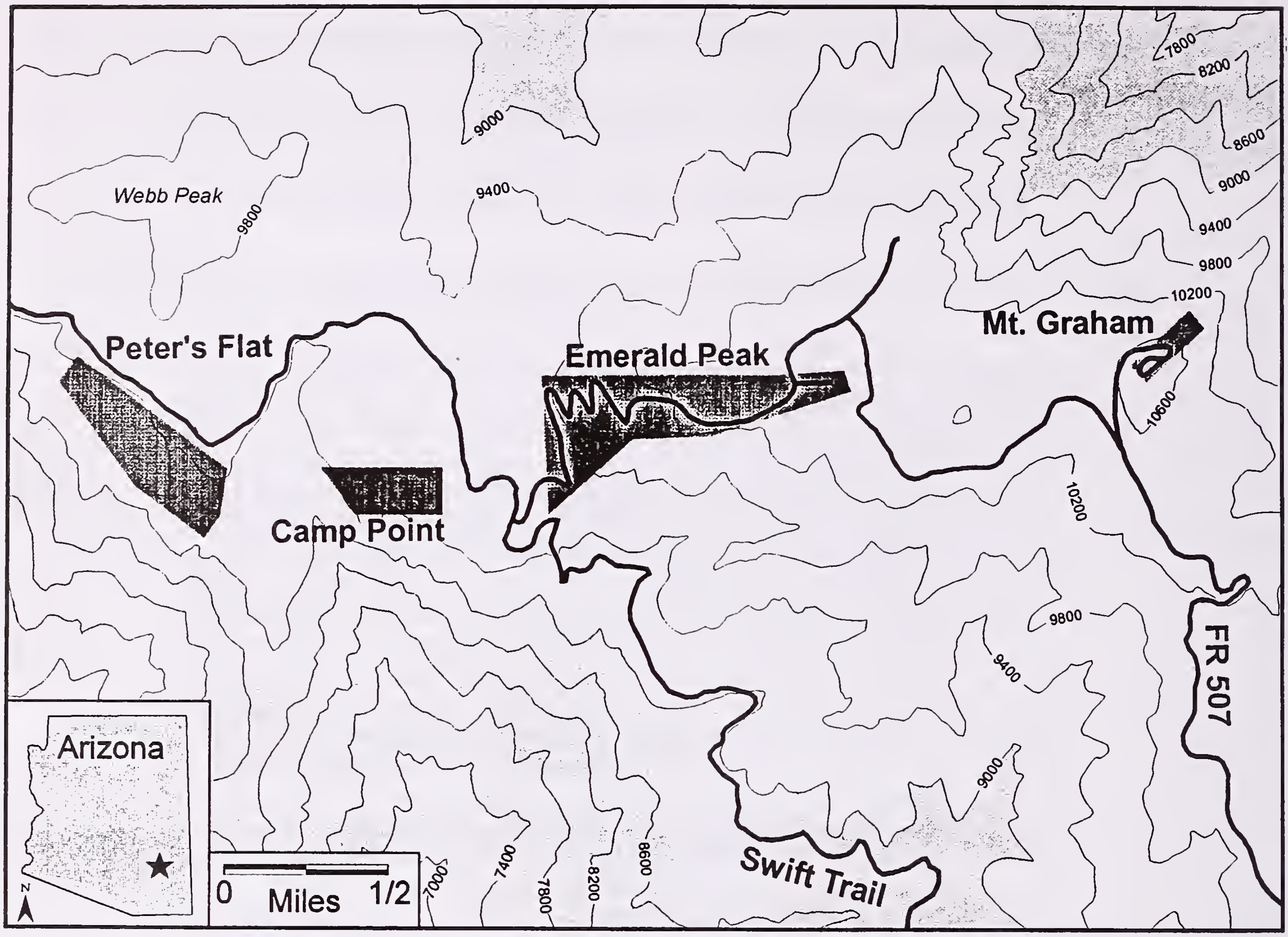

Figure 1.—Locations of the Peter's Flat (A), Camp Point (B), and Emerald Peak (C) fire history and age structure sites. The shaded area represents areas below 9000 ft (2750 m) emphasizing the semiplateau area in the higher elevations of the Pinaleño Mountains.

as a specific warning about the possible future trajectory of fire regimes and forests in the Pinaleño Mountains, with particular reference on potential impacts to the endangered Mount Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*).

STUDY AREA

The Pinaleño Mountains are the highest and steepest range in southeastern Arizona, reaching elevations of 10,400 ft at Heliograph Peak in the center of the range and 10,717 ft at Mount Graham. The Pinaleños rise precipitously, especially on the southwest and north east flanks, until approximately 9,000 ft where the range becomes a "semiplateau" dotted by several high peaks (Martin and Fletcher 1943). We chose two sites for fire history analyses, Peter's Flat and Camp Point, and collected samples for age structure analyses along anelevational gradient that culminated at Emerald Peak (fig. 1). The two fire history sites are located near the edge of the semiplateau area in the mixed-conifer forest and mixed-conifer/spruce-fir transition zone at elevations ranging from 9,200 to 9,700 ft. Slope at these sites varies from zero to 60%. Both sites are classified as mixed-conifer forest. This forest type covers approximately 11,100 ac in the upper elevations of the Pinaleño Mountains (USDA Forest Service 1988b). The Emerald Peak area is predominantly spruce-fir forest, which covers approximately 500-600 ac in the Pinaleños (USDA Forest Service 1988b). The spruce-fir forests of the Pinaleños represent the southernmost extent of this forest type in North America (Pase and Brown 1982; Johnson 1988; Stromberg and Patten 1991).

METHODS

We used a chainsaw to obtain entire and partial cross-sections from fire-scarred logs, remnant pieces of wood, snags, and living trees (Arno and Sneck 1977). We collected 40 samples from the Peter's Flat site and 36 samples from the Camp Point site. During construction of the access road leading to the astrophysical complex, 14 fire-scarred samples were collected in the spruce-fir transition zone to provide information on fires that possibly impacted the highest elevation forests. Most samples were collected from southwestern white pine (*Pinus strobiformis* Engelm.) and ponderosa (or Arizona) pine (*Pinus ponderosa* Lawson var. *arizonica* (Engelm.) Shaw). To provide information on the age structure of the spruce-fir forest, we collected cross-sections and increment cores from 168 Engelmann spruce (*Picea engelmannii* Parry) and 123 corkbark fir (*Abies lasiocarpa* (Hook.) Nutt. var. *arizonica* (Merriam) Lemmon) trees felled during construction of an access road and sites to be used by an international astrophysical complex (fig. 1, site C). All sections and cores were obtained as near to ground level as possible for maximum age determination.

In the laboratory, we sanded all surfaces with a 4" X 24" belt sander beginning with a coarse grit size (usually 40 grit) to plane the surface, then progressively used finer sandpaper until eventually using a 320 grit. This technique produces a surface on which the cellular structure of the wood is readily visible under 20-30X magnification. All cross-sections and increment cores were then crossdated, assigning each tree ring to its exact year of formation (Stokes and Smiley 1968; Swetnam *et al.* 1985), after which each fire scar was dated (Dieterich and Swetnam 1984).

To compare the seasonality of past fires with our current knowledge on the seasonality of fire activity, the season of fire occurrence was determined by noting the position of the fire scar within the annual ring (Dieterich and Swetnam 1984; Baisan and Swetnam 1990). We determined the dominant season of fire occurrence by compiling and graphically displaying the frequency distribution of the intra-annual positions of all dated fire scars. Fire scar positions and their seasonal designations followed Baisan and Swetnam (1990) and Swetnam et al. (1992) with minor modifications for the higher elevations of the Pinaleños. Fire scars were noted as occurring in: the dormant season (D) between the latewood of the previous year and earlywood of the current year; the early one-third portion of the earlywood (EE); the middle one-third of the earlywood (ME); the late one-third portion of the earlywood (LE); and, the latewood portion of the annual ring (L).

We combined data from the Peter's Flat and Camp Point sites to provide a comprehensive overview of fire occurrence in mixed-confer forests of the Pinaleños over a broader spatial scale than is provided by each individual site. We used the FHX2 fire history analysis computer program (Grissino-Mayer 1994) to provide a quantitative description of the combined fire regime based on the distribution of fire intervals. We used the Weibull distribution to model fire interval data because this distribution can model a variety of negatively and positively skewed distributions, and often provides a superior fit to fire interval data than does the normal distribution (Clark 1989; Johnson 1992; Baker 1992). We used FHX2 to calculate the fire interval associated with the 50% level of exceedance probability, termed the Weibull Median Probability Interval (WMPI), analogous to the Mean Fire Interval calculated for fire interval distributions based on the assumption of normality. We conducted two sets of analyses, the first based on *all* fire scars, regardless of the number of trees scarred in any fire year, and the second based on those fire years in which at least 10% of the trees at either site were scarred. This 10% cutoff emphasized widespread and/or more intense fires while de-emphasizing fires that affected only a very trees (Swetnam 1990; Grissino-Mayer and Swetnam, in press).

Ages for all individual spruce and fir trees from the transition zone and true spruce-fir forest determined from the crossdated pith dates obtained at ground level were input into a spreadsheet sorted by species. Age distributions in 20-year age classes were plotted to investigate changes in tree populations over time due to differences in life history strategies between the two species or due to disturbance events. Dates of past fires that occurred in the spruce-fir transition zone were compared with age distributions to investigate possible impacts these fires may have had on the spruce-fir forests.

RESULTS

We crossdated nearly 2000 fire scars that yielded 629 fire events from the 90 samples collected at Peter's Flat and Camp Point, and dated an additional 88 injuries possibly related to fire (table 1). In the combined record for both sites, 79 fire years (12.8%) occurred during the period 1376 to 1993. All statistical analyses were conducted beginning in 1584 because this was the first year in our collection in which fire scarred multiple samples at either site. The pre-settlement period was designated as ending in 1880 because human-related disturbances (especially grazing) began to significantly affect the environment during the period 1875 to 1885 (Bahre 1991).

The WMPI values for both scarred classes (4.23 yrs based on all trees scarred, and 5.23 yrs based on at least 10% trees scarred) were lower than MFI values derived from the simple arithmetic mean (table 2) because the Weibull is better able to model positively skewed distributions, making the WMPI a more robust estimator of central tendency in the fire interval distributions. The WMPI for both scarred classes increased dramatically when the full period (1584 to 1993) was analyzed compared to the pre-settlement period (1584-1880) (table 2) as the 20th century fire regime is characterized by unusually long fire-free periods. Based on exceedance probabilities during the pre-settlement period, significantly long fire intervals exceeding the 95% confidence level were 10.6 yrs for all trees scarred and 12.4 yrs for the 10% scarred class (table 3). These long intervals were rarely exceeded during the pre-settlement period, but have been greatly exceeded during the 20th century (figs. 2 and 3).

Seasonality of fires was determined on 468 of the 629 fire scars (74%) from samples in the Pinaleños. The dominant season of past fire occurrence was early in the growing season (44% of all scars), or approximately from early May to mid-June (fig. 4). In general, almost all fires (94%) occurred from just prior to the beginning of the growing season (dormant season scars) until midway through the growing season (middle earlywood scars). This percentage corresponds well with the seasonality of pre-settlement fires for the Rincon Mountains determined by Baisan and Swetnam (1990) in which they confirm a late spring through mid-summer fire season. In addition, Barrows (1978) noted that 60% of the annual total of area burned during the period 1960 - 1974 in the Southwest occurred during June despite the fact that the highest rate of ignitions occurred in July just before the height of the monsoon season (Baisan and Swetnam 1990).

Table 1.—Summary information for the Peter's Flat and Camp Point Fire History Sites.

	Peter's Flat	Camp Point
Beginning year	1376	1534
Last year	1993	1993
Chronology length (years)	618	460
Total number of samples at site	40	50
Total number of fire scars	363	266
Total number of all indicators	424	293
Total number of years with fire	65	44
Percentage of years with fire	10.5	9.6
Percentage of years without fire	89.5	90.4

Table 2.—Descriptive statistics for fire interval data in the Pinaleño Mountains during the pre-settlement period 1575 - 1880 and the full period 1575 to 1993, based on all fire years and on those years in which at least 10% of all trees sampled were scarred.

	Pre-settlement		Full Period	
	All	10%	All	10%
Total Intervals :	59	46	67	48
Mean Fire Interval :	4.86	6.24	6.10	8.52
Weibull MPI (WMPI) :	4.23	5.77	4.84	6.47
Median Fire Interval:	4.00	5.00	4.00	5.50
Standard Deviation :	3.29	3.65	6.65	14.13
Coef of Variation :	0.68	0.58	1.09	1.66
Skewness :	0.71	1.02	3.87	5.77
Kurtosis :	-0.40	1.47	19.73	34.38
Minimum Interval :	1	1	1	1
Maximum Interval :	13	19	47	100

Table 3.—Exceedance probabilities from the Weibull function for fire interval data in the Pinaleño Mountains during the pre-settlement period 1575 - 1880 and the full period 1575 to 1993, based on all fire years and years in which at least 10% of all trees sampled were scarred. Exceedance probabilities (X 100) are equivalent to percentages. The WMPI is associated with the 50% exceedance level.

Exceedance Probability	Pre-settlement Intervals		Full Period Intervals	
	All	10%	All	10%
0.999	0.07	0.19	0.05	0.11
0.990	0.30	0.64	0.26	0.45
0.975	0.53	1.03	0.50	0.81
0.950	0.83	1.49	0.81	1.26
0.900	1.30	2.16	1.33	1.98
0.800	2.08	3.20	2.22	3.17
0.750	2.44	3.65	2.65	3.72
0.667	3.02	4.36	3.35	4.62
0.600	3.49	4.92	3.92	5.34
0.500	4.23	5.77	4.84	6.47
0.400	5.04	6.67	5.86	7.71
0.333	5.64	7.34	6.64	8.64
0.250	6.53	8.28	7.79	10.01
0.200	7.17	8.95	8.63	10.99
0.100	8.97	10.79	11.04	13.77
0.050	10.58	12.37	13.22	16.24
0.025	12.06	13.79	15.25	18.52
0.010	13.86	15.48	17.76	21.29
0.001	17.87	19.12	23.47	27.47

The oldest trees sampled in the spruce-fir dominated forests were consistently Engelmann spruce. The age distribution of all spruce and fir trees collected revealed that many more old-aged

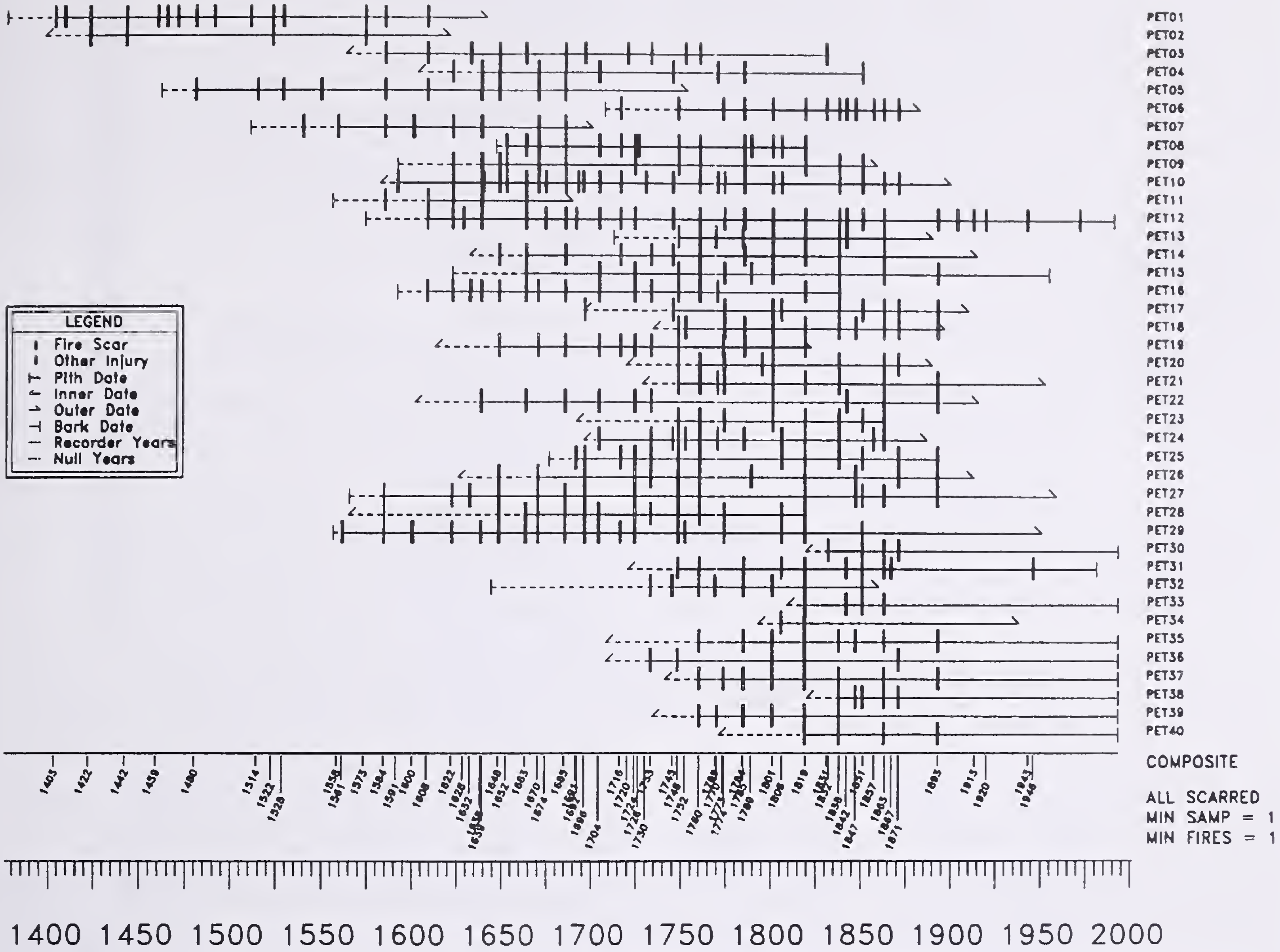

Figure 2.—The Peter's Flat fire history master chart. The horizontal lines represent individual trees with sample ID's given to the right of each line. Fire scar dates are indicated with solid vertical bars, while other injuries possibly associated with fires are indicated by open vertical bars.

Engelmann spruce are present in the Pinaleños than corkbark fir (fig. 5). This suggests that corkbark fir was a minor component of the initial spruce-fir forest or that corkbark fir is not as long-lived as Engelmann spruce. Both spruce and fir are able to colonize areas cleared after disturbance, but Engelmann spruce is the dominant colonizer because it is better able to withstand environmental extremes that arise after disturbance (Peet 1988; Stromberg and Patten 1991). The age distribution for corkbark fir shows that this species was present in the post-disturbance forest from the onset (fig. 5), similar to the findings of Aplet *et al.* (1988) in Colorado subalpine forests. The lack of individual spruce and fir trees exceeding 300 years of age suggests that a catastrophic disturbance, most likely fire, may have occurred between 300 and 400 years ago within the study areas. We hypothesize that this event was the 1685 fire. Nearly all fire-scarred samples collected in the mixed-conifer and transition zone sites that extended prior to 1690 clearly showed that the 1685 fire was the most intense based on the amount of cambial surface killed on survivor trees. Furthermore, surviving Douglas-fir trees in the mixed-conifer/spruce-fir transition zone showed evidence of serious injury and canopy loss in this year documented as a dramatic and rapid reduction in growth beginning in 1685, often with several missing rings, relative to Douglas-fir trees collected at a control site that could not have been affected by this fire. Douglas-fir is considered a very fire-tolerant species because of its thick bark (Wright and Bailey 1982),

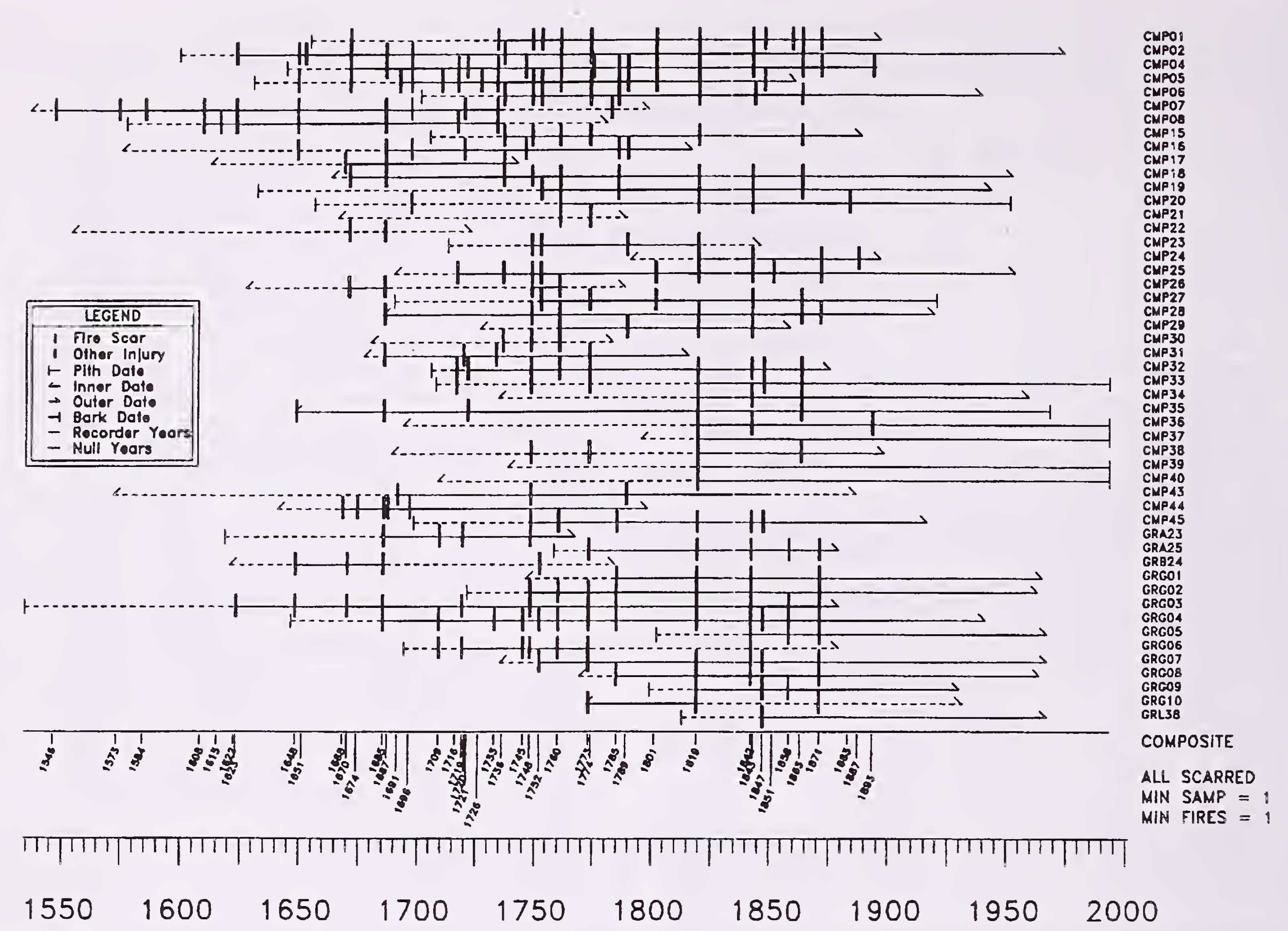

Figure 3.— The Camp Point fire history master chart. Samples GRA 23 through GRL 38 were collected within the transition zone along the access road leading up to the astrophysical complex within area (C) in figure 1.

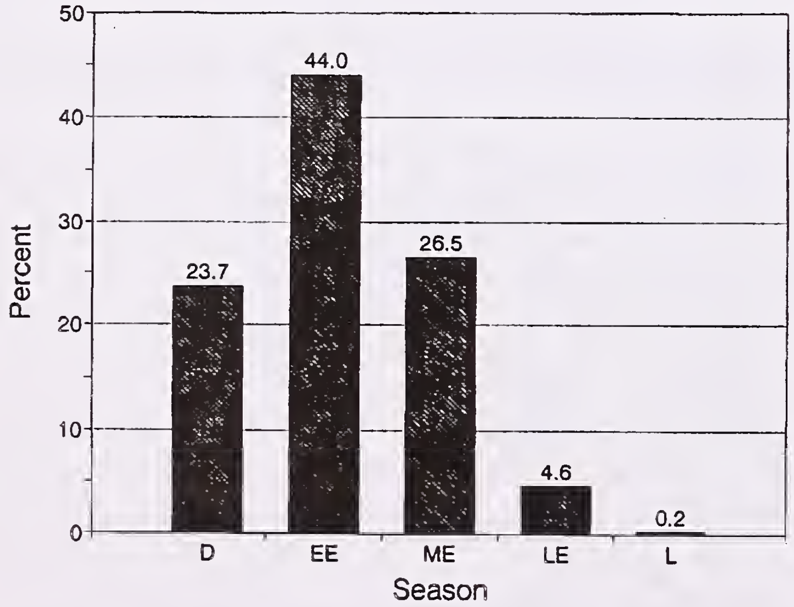

Figure 4. —The seasonal distribution of fire scars from 468 individual fire scar dates from 90 individual specimens, verifying an early spring to late summer fire season with the majority of fires occurring in the early portion of the growing season, from approximately early May to mid-June.

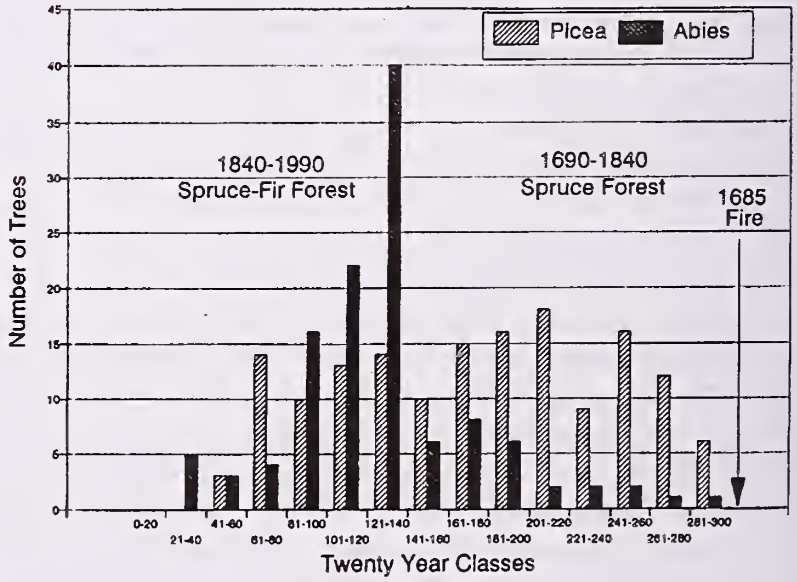

Figure 5.—Age distribution in 20-year age classes for Engelmann spruce and corkbark fir trees collected for this study. Corkbark fir was present in the post-disturbance area, but in low numbers.

yet individuals in the transition forest clearly were affected by the 1685 fire, confirming the high intensity and large areal extent of this fire. Whether or not a single catastrophic fire occurring in 1685 was responsible for resetting the successional pattern at the highest elevations, the age structure of the spruce-fir forests of the Pinaleños suggests a fire return interval of approximately 300-400 years.

DISCUSSION

Our results suggest that pre-settlement mixed-conifer forests in the Pinaleños burned as frequently (WMPI = 4.2 yrs) as some Southwestern ponderosa pine forests at lower elevations. The WMPI obtained for the mixed-conifer forests of the Pinaleños is considerably lower than the MFI obtained in previous studies in mixed-conifer forests of the southern and central Rockies. Dieterich (1983) determined that the MFI for widespread fires (20% scarred) for mixed-conifer forests in the White Mountains of eastern Arizona was 22 yrs (compared with the MFI of 11 yrs derived for our 20% scarred class). Ahlstrand (1980) estimated major fires had occurred once every 17 yrs in the Guadalupe Mountains National Park in southwestern Texas. Baisan and Swetnam (1990) derived a MFI of 9.9 yrs for mixed-conifer forests in the Rincon Mountains of southeastern Arizona. The short-interval regime in the mixed-conifer forests of the Pinaleños during the pre-settlement period suggests these forests were very open, characterized by relatively rapid fuel accumulation. Thus, the mixed-conifer fire regime suggests a forest structure similar to ponderosa pine forests at lower elevations but populated by mixed species.

Furthermore, we hypothesize that the relatively open canopy, pre-settlement mixed-conifer forest in the semiplateau area of the Pinaleños, characterized by heterogeneous forest composition, age structure, and fuel components, acted as a "buffer zone" around the spruce-fir forest. It seems likely that many fires that burned in the mixed-conifer forest on the semiplateau originated on the plateau or on the steep slopes below. These fires typically burned on the forest floor throughout the mixed-conifer stands, but did not spread into the spruce-fir forest zone because of the cooler, moister conditions that exist there. Only during the severest droughts did stand-replacement fires spread into the canopies of spruce-fir forests. We therefore hypothesize that the high frequency of fires and heterogeneous nature within the mixed-conifer forest "buffer zone" served to promote the long-term stability within the spruce-fir forest. Therefore, alterations to the fire regime and heterogeneity of the mixed-conifer forest buffer are likely to have significant effects upon the spruce-fir forest as well.

The dissimilarity between the mixed-conifer and spruce-fir fire regimes in the Pinaleños reveals an important characteristic not previously reported for Southwestern forests. Fire regimes in the mixed-conifer study sites were characterized by a WMPI of 4.2 yrs. However, fire return intervals in the spruce-fir study area located less than two miles away (between Peter's Flat and Mount Graham) range between 300-400 yrs based on the last fire known to have occurred in the spruce-fir forest. This extreme difference in fire return intervals between adjacent habitat types suggests an extremely steep gradient in fire frequency can occur in areas separated by very short distances.

CONCLUSIONS

Our reconstruction of fire history for the Pinaleño Mountains emphasizes the long-term stability and resilience of the pre-settlement mixed-conifer and spruce-fir forests. During the pre-settlement period, wildfires were commonplace in the Pinaleño Mountains for at least 8,000 yrs (Anderson and Shafer 1991) and should therefore be considered a "natural" component of this forest community. The mixed-conifer fire regime of the past four or five centuries suggests that this community was relatively stable and highly resilient to the changes induced by fires. The frequent, low-intensity surface fires were probably important in maintaining a substantial component of pine within the stands, since they are generally more resistant and tolerant of this type of fire regime than Douglas-fir or true firs (Wright and Bailey 1982). Furthermore, this relatively high frequency fire regime was similar to pre-settlement ponderosa pine fire regimes reconstructed elsewhere in the Southwest. This finding suggests that, like pre-settlement ponderosa pine forest structure (*e.g.* Covington and Moore 1994), the pre-settlement Pinaleño mixed-conifer stand densities were probably lower and more spatially heterogeneous than todays stands, possibly with an important understory component of grasses. The cessation of spreading fires with the rise of the livestock industry support the interpretation that grasses were important in the climate-fuel-fire dynamics of mixed-conifer forests.

High fuel loadings have increased the fire hazard in an area in which fire will con tinue to be actively suppressed due to its status as Fire Management Zone 1 (USDA Forest Service 1988a). The forest structure now favors the occurrence of high-intensity, stand-replacing fires in contrast to the low-intensity, stand-maintenance fires that occurred prior to Euro-American settlement (USDA Forest Service 1993). This hazard is further increased by the high flammability of Engelmann spruce and corkbark fir trees (Wright and Bailey 1982, p. 319) that exist upslope from the mixed-conifer study sites.

In the long-term, management of these forests should emphasize the restoration of greater stability and resiliency of the ecosystem (including both tree and squirrel populations) by reducing live and dead fuel loadings, particularly in the mixed-conifer zone. Re-introduction of fire by carefully planned and executed prescribed burning is one alternative for accomplishing this objective. However, the capriciousness of fire and weather will always add an element of hazard to this approach. The benefits of fire to ecosystems long adapted and dependent to some degree upon fire must be weighed against the hazards of prescribed fires "escaping" and becoming wildfires. These same hazards must also be weighed against the existing and perhaps increasing hazard of catastrophic fire sweeping across very large areas of both the mixed-conifer and spruce-fir forests of the Pinaleños. Not only is the red squirrel potentially endangered by high-intensity crown fires, but so is the astrophysical complex nestled among the spruces on the summit. In our opinion, with a continuation of current forest structures and increasing use of the mountain by recreationists and scientists, it is not a matter of "if" such fires will occur, but "when."

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Changes in Fire Regimes and Forest Structures of Unharvested Petran and Madrean Pine Forests

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Abstract.—In both Petran montane forests of the southwestern US and Madrean montane forests of northern Mexico, similar ecological processes of frequent, low-intensity fires maintained relatively open forests of large trees in the past. A comparison of examples from an unharvested ponderosa pine forest of northern Arizona, USA, with over 100 years of fire exclusion, and an unharvested mixed-species pine forest of northwestern Durango, Mexico, with approximately 50 years of fire exclusion, show that tree populations have irrupted, small trees are densely aggregated in clumped stands, and fuel loading and vertical continuity have increased, raising the susceptibility of these sites to high-intensity crown fires. In contrast, a reconstruction of the pre-fire-exclusion structure of the Arizona site as well as data from another Durango site currently under a frequent fire regime both share open forest structures with low fuel loads and little vertical fuel continuity. These ecological similarities suggest that Mexican forest managers may benefit from studying the deleterious effects of long-term fire exclusion in the US, while both US and Mexican managers could make use of unharvested, frequent-fire sites in Mexico as benchmarks of ecosystem process and structure.

INTRODUCTION

Fire is a common and powerful disturbance in forested ecosystems of northern Mexico and the southwestern United States. The paper focuses on the fire ecology of Petran (Rocky Mountain) and Madrean montane pine forests (Pase and Brown 1982). From an island biogeography perspective, the land masses of the Colorado Plateau and Rocky Mountains to the north and the Sierra Madre Occidental to the south, function as the ecological and evolutionary mainlands for the smaller montane islands of the Madrean archipelago. Similar ecological processes of frequent, low-intensity fires maintained relatively open forests of large trees in the past in both regions. However, fire exclusion in the last 50 to 120 years has led to substantial change in forest structure both in most southwestern US forests and in some regions of northern Mexico.

In the initial section of this paper, the role of fire and the effects of extended fire exclusion will be reviewed with an example from an unharvested southwestern US site. Next, data from unharvested forest sites in the Sierra Madre Occidental will show that fire is an important ecological force affecting forest structure, fuels, and regeneration, and that disruption of the frequent fire regime in Madrean forests leads to changes similar to those observed in fire-excluded US forests. Finally, we will compare the implications of current and potential patterns of forest structure, fuel loading, and fire behavior, with respect to the US and Mexican forests.

FIRE EXCLUSION IN A PETRAN PINE FOREST

The ecological role of fire has been described in several studies in Arizona and New Mexico.

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Mean fire intervals (MFIs) prior to European-American settlement of this region ranged from 2 to 10 years in forests of ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) until the 1870's to 1880's, when frequent, low-intensity fires ceased in the majority of southwestern US forests (review by Swetnam 1990). The exclusion of fires through a combination of active fire suppression and livestock grazing of grass fuels has been implicated as a key factor in the development of dense, stagnated forests, high fuel loading, reduced herbaceous production, and increased soil erosion throughout the western US (Weaver 1951; Cooper 1960; Bahre 1991; Savage 1991; Covington and Moore 1994; Covington et al. 1994). Over a century of fire exclusion in ponderosa pine forests has led to increased incidence of crown fires in Arizona (Cooper 1960; Swetnam 1990) as well as further north in Idaho (Steele et al. 1986), and even the so-called "collapse" of the Blue Mountain ponderosa pine ecosystem in Oregon (Mutch et al. 1993).

A specific example from the Petran ponderosa pine forest of northern Arizona illustrates many of these ecosystem changes. The Gus Pearson Natural Area was set aside within the Fort Valley Experimental Forest, the oldest experimental forest in the National Forest System, to serve as a virgin forest "standard of comparison for other managed, utilized, and artificial ecosystems" (Avery et al. 1976). However, as part of normal management policy, fire continued to be excluded from the region, where in presettlement times fires occurred every 2 to 4 years until the final presettlement fire in 1876 (Dieterich 1980). Between 1920 and the late 1980's, the forest density and fuel loading in the Pearson Area increased to such high levels that forest administrators became concerned about protecting the adjacent historic Fort Valley buildings from a catastrophic wildfire. A three-hectare portion of forest (fig. 1) was officially decommissioned from the Natural Area in 1987 to create a defensible firebreak. It has since become the site of an intensive research effort to restore the structural and functional characteristics of the presettlement forest (Covington and Moore 1994, Covington and others *in preparation*).

Table 1.—Forest structural characteristics at the Gus Pearson Natural Area restoration site. The last fire occurred in this region in 1876 (Dieterich 1980). The 1876 reconstruction is based on subtracting the measured growth increment of trees between 1876 and 1992, as well as estimating the 1876 characteristics of measured dead trees (reconstruction methods described in Covington and Moore 1994).

	1992 measurement	1876 estimate
Trees per hectare	3098	60
Quadratic mean diameter (cm)	11.9	48
Woody fuel loading (metric ton/ha)		
Presettlement patches	35.8	total woody fuel loading approximately 1 ton/ha
Postsettlement patches	12.2	
Grassy openings	4.2	
Herbaceous production (kg/ha)		
Presettlement patches	90	total herbaceous production over 1000 kg/ha
Postsettlement patches	240	
Grassy openings	970	

Figure 1. —A never-harvested Petran ponderosa pine forest in the Gus Pearson Natural Area, Fort Valley Experimental Forest, Arizona, USA. Following a century of fire exclusion, forest floor and vertical fuels increased to hazardous levels, exemplified by the dense "doghair" trees shown here, so a three-hectare area was decommissioned from the Natural Area in 1987 and is currently an experimental site for ecological restoration.

Measurement of all trees on the restoration site in 1992 showed a forest dominated by dense patches of small trees, over 3,000 trees per hectare with a quadratic mean diameter of 11.9 cm (table 1). Applying measurements of age and growth of living trees, as well as decomposition rates of snags and downed dead trees, the estimated reconstruction of forest structure in 1876 was strikingly different: only 60 trees/ha and a quadratic mean diameter of 48 cm, over 4 times greater than the mean 1992 diameter. The spatial distribution of trees changed from the 1876 pattern of dispersed, relatively open patches of trees in a bunchgrass matrix to the 1992 pattern in which dense pine thickets formed the matrix with grasses reduced to small openings. These changes in tree patterns had been documented previously by Covington and Sackett (1992) for a similar site 5 km from our study area. Herbaceous production in the tree-dominated majority of the site averaged only 100-200 kg/ha in 1992, but forest floor fuel loadings ranged from 12 ton/ha under postsettlement trees to 36 ton/ha under old-growth tree patches. In contrast, estimated average presettlement values in this forest type are over 1000 kg/ha of herbaceous production and around 1 ton/ha of forest floor fuel loading (Covington and Moore 1994).

Although this site has remained "undisturbed" since European-American settlement, dramatic changes in forest structure have occurred. The exact mechanisms of such changes are not clear and may vary by a complex interplay of site-specific factors (e.g., see Savage 1991, Bahre 1991), but they are consistent with fire exclusion. While the Pearson Area is an unusual ponderosa pine forest in that it has remained unharvested, similar changes in forest density, fuels, and understory production have been found in forest ecosystems adapted to frequent fire throughout the western US and Canada (Covington et al. 1994). Several negative consequences of these changes are clear (Covington and Moore 1994): economic values of the forest have been reduced as grass production, water storage, and timber growth and quality have declined; amenity values have also declined as people find dense ponderosa forests less attractive; habitats for wildlife have changed from a grass-based system to a less diverse tree-based system; and the stagnated trees have become more susceptible to insects, disease, drought, and fire.

Focusing on fire, in 1876 the restoration site was characterized by grass and needle litter fuels, with dispersed, fire-pruned large trees. An 1876 fire would be fast-moving but of low intensity. By 1992, however, the site was dominated by small trees with vertical as well as horizontal fuel continuity, meaning that fires could spread rapidly both along the ground and up into the crowns. Rotten woody fuels, quick to ignite, and deep duff layers, averaging 8 cm under the old-growth patches, had replaced the presettlement light grass fuels. Smoldering combustion of heavy fuels like these caused lethal soil temperatures and killed old-growth trees even under prescribed burning conditions at a nearby experimental site (Harrington and Sackett 1990). A fire would have substantially greater intensity in the 1992 fuels than in the 1876 fuels and could more easily torch trees or crown through stands. A 1993 wildfire near the restoration site clearly demonstrated the relationship between forest structure and fire behavior (fig. 2). As the fire passed through demonstration stands thinned to different growing stock levels, the denser stand was killed but the adjacent, more open stand had only a light surface burn with incomplete fuel consumption.

Beyond small-scale fire effects, the broad increase in forest density and fuel loading in ponderosa pine forests has brought many stands into synchrony across the landscape to support large crown fires (Covington and Moore 1992). The size of fires and the occurrence of crown fires in southwestern ponderosa pine have increased through this century (Cooper 1960, Swetnam 1990). Furthermore, regional analysis of fire occurrence and climate data by Tom Swetnam and others has shown that a pattern of severe fire years follows the recurring El Niño-Southern Oscillation events (Swetnam 1990, Swetnam and Betancourt 1990, Baisan and Swetnam 1990). The combination of potential synchronies in both fuel structures as well as weather conditions raises the prospect of increasingly destructive wildfires that could threaten both ecological sustainability and resource values.

FIRE REGIME DISRUPTION IN A MADREAN FOREST

In contrast to the century-long exclusion of fire from most western US and Canadian forests, frequent fire has continued well into this century

Figure 2.—In June, 1993, the Trick fire passed through demonstration thinning sites located 5 km from the Gus Pearson Natural Area. Passing from the rear to the foreground of the photo, the fire crowned through the denser stand causing high mortality (at left), but caused only a light surface burn in the adjacent, more open stand (at right).

and even up to the present in many northern Mexican forests for a variety of reasons (see González-Cabán and Sandberg 1989, Fulé and Covington *in press*). Even before the effects of fire exclusion were fully recognized by foresters and scientists in the US, Aldo Leopold (1937) and Joe Marshall (1957, 1962) compared pine-oak forests in southern Arizona and northern Sonora and Chihuahua, suggesting that heavier grazing and fire exclusion in the US forests had led to the dense thickets of "dwarfed" trees, increased erosion, and high fuel loading common in the southwestern US forests, but not seen in northern Mexico. In Marshall's words (1962),

> *If we grant that this contrast is too abrupt and too coincident with the international boundary to be due exclusively to climate, then we must look for man-made causes of the difference in vegetation. The outstanding cause seems to be fire... There has until very recently been no protection on the Mexico side from naturally occurring fires. These sweep through the grass, killing young junipers, eliminating debris, and leaving unscathed the tall clear trunks of the widely spaced pines.*

Little quantitative information exists about the role of fire in northern Mexican pine forests, although studies on fire recurrence and vegetation dynamics have been carried out in chaparral and piñon communities (Minnich 1983, Segura and Snook 1992). In perhaps the first Mexican forest fire history study, Jack Dieterich (1983) found that frequent fires, with a mean fire interval (MFI) around 4 years, continued into the 1970's in pine-oak forests of the Sierra de los Ajos of northern Sonora, a site which is currently being studied in greater detail by several of the other investigators in this conference (Baisan and Swetnam 1994, Villanueva-Díaz and McPherson 1994).

In order to expand our knowledge of fire-adapted ecosystems and quantify the differences in fire regime and forest structure between US and Mexican pine forests, we selected a study region in northwestern Durango at the crest of the Sierra Madre Occidental in 1993. The forests are dominated by Durango pine (*Pinus durangensis*) but a total of 8 pine species, over 4 oak species, and several other tree species including madrone (*Arbutus* spp.), alder (*Alnus* sp.), and juniper (*Juniperus* spp.) were encountered on the study sites (Fulé and Covington *in press*). This diversity reflects the high biological diversity of Mexico, which contains approximately half the world's species in the *Pinus* (Martínez 1948, Perry 1991) and *Quercus* (Nixon 1993) genera. The two never-harvested sampling sites, each approximately 70 ha in size, were closely matched in elevation, slope, aspect, slope position, and species composition. Both sites had ample evidence of fire in the form of fire-scarred trees and charred wood, but the first site, Arroyo Verde, appeared to have had little recent fire disturbance whereas the second site, Arroyo Laureles, had burned as recently as 1991.

On a 150 m X 150 m sampling grid we established plots to measure the species, condition, diameter at breast height (dbh), live crown ratio, and presence of lightning scars on each tree. We collected increment cores from all pines over 6 cm dbh. In addition, fuels were measured along a planar transect, regeneration density was tallied on nested 40 m^2 subplots, and fire scars were cut from live or dead trees within or near to each sampling plot. Further details on site characteristics, sampling methods, results, and analysis are given in Fulé and Covington (*in press*).

Fire scar analysis confirmed the apparent difference in recent fire regimes at the two sites. Frequent fires occurred at both sites prior to 1945, with an average of approximately 4 years between fires that scarred at least one sample tree at both sites. After 1945 the frequent fire regime was disrupted at Arroyo Verde (fig. 3). Arroyo Verde had only three fires, each scarring only a single sample tree, between 1945 and 1992, while Arroyo Laureles had 15 fires, 9 of which scarred 2 or more samples, in the same time period.

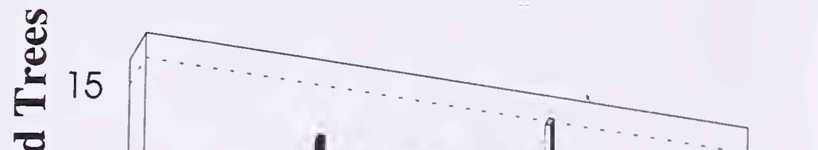

Figure 3.—Comparison of fire occurrence over the last century at Arroyo Verde (Site 1, N = 22 fire scar samples) and Arroyo Laureles (Site 2, N = 28), Durango, Mexico. Prior to 1945, fires were frequent at both sites, but fire was virtually excluded from site 1 after 1945.

Table 2.—Forest structural characteristics at two study sites in Durango, Mexico. Fires were frequent at both sites prior to 1945, but have been excluded from most of the Arroyo Verde site since 1945 (see Fulé and Covington *in press* for further information).

	Arroyo Verde	Arroyo Laureles
Trees per hectare	2730	647
Quadratic mean diameter (cm)	10.4	27.1
Woody fuel loading (metric ton/ha)	15.8	10.6

Changes in the forest structure are correlated with the disruption in fire regime at Arroyo Verde. Small pines, oaks, and other trees were dense at Arroyo Verde, averaging 2730 trees over breast height per hectare with a quadratic mean diameter of 10.4 cm (table 2). Analysis of age structure showed that approximately 60% of the current pines larger than 6 cm in dbh established after the 1945 fire, implying that the forest was far more open prior to fire exclusion. At Arroyo Laureles, where numerous large and small fires have continued up to the present, stand structure was strongly influenced by the thinning effect of frequent fire. The number of trees per hectare was an order of magnitude lower but average diameter was over twice that of Arroyo Verde (table 2). However, regeneration density (all trees below breast height) was similar at both sites, averaging 6,200 stems/ha at Arroyo Verde, 8,730 stems/ha at Arroyo Laureles (see Fulé and Covington *in press* for further information). The apparent mechanism for reducing high regeneration density to low overstory density at Arroyo Laureles is frequent fire.

Fuel structures also differed between the sites. Under fire exclusion, the woody fuel loading at Arroyo Verde was 50% greater than that of Arroyo Laureles. More importantly, the Arroyo Verde fuel load included 11.7 ton/ha of rotten woody fuels, which are highly ignitable, as opposed to only 2.6 ton/ha in this category at Arroyo Laureles. Average duff depths at Arroyo Verde were twice those of Arroyo Laureles. Finally, the frequent fires at Arroyo Laureles maintained a well-spaced overstory of trees with fire-pruned boles. Spatial distribution of the trees was generally random, approaching a uniform distribution at scales below 8 m (fig. 4). The dense forest at Arroyo Verde, on the other hand, was highly clustered into thickets of trees. The numerous small trees at Arroyo Verde provide functional fuel ladders for fires to crown.

The changes in overstory structure and fuel loading at Arroyo Verde suggest that under suitable weather conditions the next fire at the site is likely to be stand-replacing, implying that a half century of fire exclusion may have been sufficient to move this forest from a frequent, low-intensity fire regime to an infrequent, high-intensity regime. Beyond the evident economic and environmental damage such a fire would cause, the question for foresters, landowners, and scientists is: what kind of ecological community will succeed from the ashes of the uneven-aged, mixed species forests which were adapted to frequent, low-intensity fires?

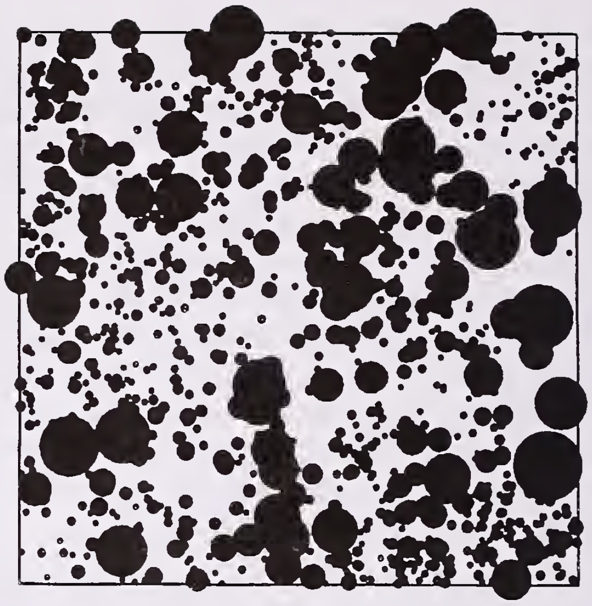

Figure 4a.—Approximate projection of live tree crowns (crown radius proportional to tree diameter at breast height) on a 2,500 m^2 stem-mapped plot at the fire-excluded Arroyo Verde site. Spatial analysis with the Ripley's k(t) statistic (Duncan 1990) showed significant clumping at all scales from 1 to 25 m.

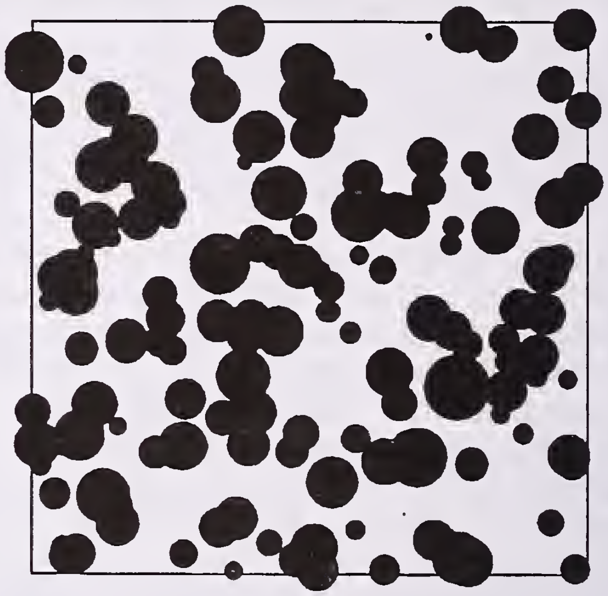

Figure 4b.—Approximate projection of live tree crowns on a 2,500 m^2 stem-mapped plot at the frequent-fire Arroyo Laureles site. Spatial analysis showed the distribution to be significantly uniform at scales below 8 m and random between 9 and 25 m.

Since quantitative information on fire occurrence and forest structure is lacking in much of northern Mexico, it is difficult to generalize about the representativeness of the Arroyo Verde and Arroyo Laureles sites. However, evidence of frequent fire in the past can be found throughout the pine forests we have visited in Durango, Chihuahua, and Sonora. Disturbing signs of change paralleling those observed earlier this century in the southwestern US are also evident, including the establishment of dense pine seedling and sapling thickets (fig. 5). Just as many US foresters responded in the 1930's, some Mexican foresters today praise the "good regeneration" on these sites without anticipating the potential problems. Tree-ring studies have shown that Madrean forests are highly sensitive to recurring climatic fluctuations (Stahle and Cleaveland 1993), raising the possibility of synchronous extreme fire weather years similar to those seen in the southwestern US (Swetnam 1990). If dense fuel conditions also synchronize across landscapes, Mexican foresters will eventually encounter increasing numbers of fires of unprecedented size and severity.

CONCLUSIONS

In comparing the fire regimes and forest structures of two unharvested pine forests, one in the Petran forest of Arizona and the other in the Madrean forest of Durango, we found that similar processes of frequent, low-intensity fire and similar structures of open forests dominated by large trees prevailed in the past. Disruption of the frequent, low-intensity fire regime and extended fire exclusion has led to similar increases in forest density, forest floor fuel loading, and spatial aggregation at the Pearson restoration site as well as the Arroyo Verde site. The Arroyo Laureles site (with continued frequent fire) stands apart as a rare example of data from a modern pine forest not yet subjected to harvesting or fire exclusion.

Figure 5.—Dense pine seedling establishment in a Madrean pine-oak forest of northwestern Durango, Mexico. Such scenes are common in this region where initial harvest and fire regime disruptions have occurred in the past few decades.

We do not mean to imply that fire is the sole determining factor of forest structure. There are many important differences in climate, soils, and species composition between the Petran and Madrean sites (Pase and Brown 1982) and even between the two Durango sites (Fulé and Covington *in press*). Only long-term data in conjunction with controlled experimental studies could distinguish among the factors of disturbance, site, life history characteristics, and many other factors. Nonetheless, the magnitude of forest structural change correlated with the striking disruption in frequent fire regimes, and the economic, ecological, and social consequences of this change, underscore the need for increased research and management intervention to prevent excessive increases in both live and dead fuels.

Several implications can be drawn from these results:

- First, disturbance regimes of frequent, low-intensity surface fires appear to be an important structuring force in Cordilleran pine forests of both the US and Mexico. Disruption of these fire regimes leads to tree irruptions and increased fuel loads which threaten ecosystem sustainability on both sides of the border.
- Second, further research is essential to characterize the forest dynamics of northern Mexico, quantifying disturbance regimes, climatic relationships, biological diversity, and vegetation structure. Unharvested sites still under frequent fire regimes are incomparable in ecological value but they are disappearing rapidly, both in the high Sierra Madre and in the dry foothill forests which cover many more millions of hectares. Research which draws together Mexican and US participants to solve common problems, as in this conference, would allow the interchange and synthesis of ideas, perceptions, and methods.
- Third, if changes in Mexican forests are indeed following the patterns of those in southwestern US forests on a broad scale, then Mexican foresters could be well served by studying the ecosystem-scale problems now encountered in the US and Canada and actively seeking to prevent their appearance in Mexico. Prescribed fire, silvicultural treatments, and management of wildlife and domestic livestock are some tools which should be explored to maintain productive, healthy, diverse forests. Simi-

larly, for US foresters trying to restore the balance in degraded ecosystems, forests of northern Mexico can present a benchmark and a testing ground for ideas about ecological restoration.

- Finally, comparative research examining the ecological and evolutionary implications of changes in fire regimes and ecosystem structure could greatly benefit by placing Madrean archipelago research into the larger context of the Petran and Madrean mainlands. In 1937 Aldo Leopold urged to us to work together when he wrote:

> *"...the Sierra Madre offers us the chance to describe, and define, in actual ecological measurements, the lineaments and physiology of an unspoiled mountain landscape. What is the mechanism of a natural forest? A natural watershed? A natural deer herd? A natural turkey range? On our side of the line we have few or no natural samples left to measure. I can see here the opportunity for a great international research enterprise which will explain our own history and enlighten the joint task of profiting by its mistakes."*

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Forest Stand Structure in Mountains of Sonora, Mexico and New Mexico, USA

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Abstract.—Age- and size-class distributions were determined for conifer dominated communities in the Animas Mountains New Mexico, U.S.A., and Sierra Los Ajos Sonora, Mexico. Stand structure was studied in three forest communities in each mountain range: (1) Douglas-fir/gambel oak forests found on northern aspects above 2200 m, (2) southwestern white pine/chihuahua pine/ponderosa pine forests found at intermediate elevations, and (3) pinyon pine/juniper/oak forests found at low elevations bordering grasslands. Frequency of age-class closely approximates a negative exponential distribution for the forest communities of Animas Mountains, New Mexico. Stand structure apparently has been influenced by an unusual fire regime for the semiarid forest of the southwestern U.S., characterized by a mixture of low-intensity surface fire and sweeping fires. Age-class distributions for forest communities in Sierra Los Ajos, Sonora, Mexico are being determined. However, preliminary results for those communities indicate a greater fire influence, characterized by presence of younger forest stands, and greater annual ring-growth.

INTRODUCTION

The appropriate management and creative utilization of biotic systems ultimately hinges on a thorough understanding of their ecology. However, current understanding of the structure and function of dryland forest systems, and the factors regulating the distribution and abundance of plants comprising them is extremely limited.

Knowledge of stand structure is a fundamental first step in understanding stand function and ecosystem processes. Coniferous forests of the southwestern United States and northern Mexico are among the least studied ecosystems in North America (Peet 1988). Even rudimentary information concerning structural organization and development of vegetation has not been detailed, although various authors (e.g., Pase and Brown 1982, Niering and Lowe 1984, Peet 1988) have broadly described these communities.

Analysis of age- and size-class distributions can be used to make inferences about stand level processes (e.g., disturbance frequency and severity, successional patterns). Studies which encompass different historical land uses are particularly insightful. However, detailed analyses of age-or size-class distributions in the American southwest (United States and Mexico) have been restricted to high-elevation spruce-fir forests (Stromberg and Patten 1991). Studies in forests below 2800 m, and comparative studies, are conspicuously absent. Therefore, stand-level processes are largely unknown in southwestern mountains. Various authors (e.g., Niering and Lowe 1984, Peet 1988 and references therein) have hypothesized about successional pathways. However, their interpretations are based on observations of species dominance, not on studies of age-class distributions. Stand structure and function are completely unstudied in the Animas Mountains (New Mexico, USA) and Sierra Los Ajos (Sonora, Mexico).

Our objective is to assess stand structure in conifer forests of the southwestern United States and northern Mexico, and to define the influence of land-use history on the structural patterns. Specifically, age- and size-class distributions will be determined for conifer-dominated communities in the Animas Mountains (New Mexico, USA) and Sierra Los Ajos (Sonora, Mexico). Low-elevation forests in the former range are expected to differ

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structurally from those in the latter range as a result of post-1900 fire suppression in the United States. Whether differences in fire history (if any) carry over to stand structure at higher elevations is a question of considerable interest.

Our working hypotheses are: (1) age structure of forest communities in Animas Mountains and Sierra Los Ajos is dependent on fire frequency, and (2) forest communities with similar physiographic characteristics will differ in age structure due to differences in fire frequency.

STUDY SITE

The Animas Mountains are the highest range in southwestern New Mexico, west of the Rio Grande and south of the Mogollon Plateau (31° 35′ N latitude, 108° 47′ W longitude). They are located in southern Hidalgo County, with the major peaks some 28 kilometers north of the Mexican border (fig. 1).

Animas Peak rises to 2600 meters, and approaching that height are sister peaks to the south. The study area is roughly 40 kilometers north to south by 24 kilometers east to west. The enclosed area encompasses approximately 960 square kilometers. The mountain ranges, ridges and hills which are widely distributed throughout the county are included in the Rockland-Lehmans association (Soil Conservation Service 1973). A characteristic feature of this unit is the steep to extremely steep slopes and shallow rocky soils with numerous exposures of bedrock types. The area has a bimodal precipitation pattern with about 60% of the average annual precipitation (450-750 mm, depending on elevation) received in July-September and most of the rest received in the winter months (Wagner 1973). Evaporation rates are relatively high due to a combination of high temperature, topography, and soil.

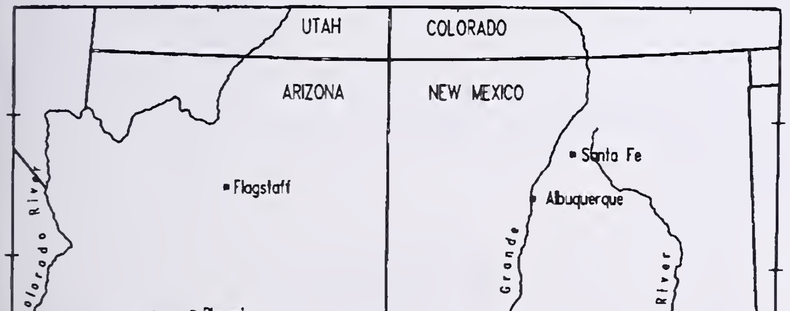

Figure 1.—Location of study area

Wagner (1973) categorized the vegetation into three basic types: lower encinal, upper encinal, and forests (including Douglas-fir and mixed pine forests). Major species occurring in the study area are Douglas-fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa* var. *arizonica*), chihuahua pine (*Pinus leiophyla* var. *chihuahuana*), apache pine (*Pinus engelmannii*), pinyon pine (*Pinus discolor*), southwestern white pine (*Pinus strobiformis*), emory oak (*Quercus emoryi*), gambel oak (*Quercus gambelii*), Arizona white oak (*Quercus arizonica*) and alligator juniper (*Juniperus deppeana*). Detailed descriptions of the flora within the Animas Mountains can be found in Wagner (1973) and Hubbard (1977).

Sierra Los Ajos is located in the state of Sonora, Mexico (30° 55′ N latitude, 109° 55′ W longitude). Its main peak rises above 2600 m and the upper elevations support coniferous forest (COTECOCA 1973, Baisan and Swetnam 1993). The enclosed area encompasses approximately 171 square kilometers. Nearby mountains to the south of Sierra Los Ajos are Sierra "Buenos Aires" and Sierra "La Purica" which along to the former mountain constitute a national forest reserve with a total area of 212 square kilometers. Ecological characteristics presumably are similar as those described for the Animas Mountains, although they have not been studied.

Sierra los Ajos is characterized as having a rough topography with steep to extremely steep slopes; rocky to shallow soils are characteristics of this mountain with depths ranging from 0 to 50 cm, and dominant textures sandy or sandy loam. The area has a climate similar to the nearby Animas Mountains. Average annual precipitation is 550 mm to 750 mm, depending on elevation, with most of the precipitation falling during the summer months (July through September), with the remainder occurring during winter (December through March). The area supports forest communities dominated by pines, Douglas-fir, oak, and pinyon pine (SARH 1992, Garza 1993). Higher elevations support pine communities dominated by *Pinus engelmannii, Pinus ponderosa* var. *arizonica, Pinus leiophyla* var. *chihuahuana,* and *Pinus ayacahuite* var. *brachyptera.* North aspects are dominated by *Abies concolor* and *Pseudotsuga menziesii,* associated with *Populus tremuloides, Quercus gambelii, Quercus hypoleucoides,* and madroño (*Arbutus arizonica*). Species present at lower elevations are *Pinus leiophyla* var *chihuahuana, Pinus discolor, Quercus arizonica,* and *Quercus emoryi.*

HISTORICAL LAND USES

Changes in the structure and composition of the forest result from the constant demand of each individual tree for more space and from the eventual death of even the most dominant individuals (Spurr and Barnes 1980, Young and Giese 1990). However, forest structural changes can also be brought about and accelerated by disturbances (e.g., fire and flooding). Analyses of age-size distributions have been used to understand successional or "fire dependent" communities (Day 1972, Aplet et al. 1988). However, only one study has been conducted in southwestern conifer forest (Stromberg and Patten 1991), and it was restricted to high-elevation spruce-fir forests.

Forest fire is a potentially important factor for structuring vegetation and was a frequent phenomenon in the southwestern United States before Anglo Americans arrived (Wright and Bailey 1982, Niering and Lowe 1984, Bahre 1991). Anglo colonization and the introduction of large numbers of cattle in the late 1870s and early 1880s led to severe overgrazing and the removal of fine fuel, thus reducing the frequency of widespread wildfire (Bahre 1985, 1991). Grazing intensities in the Animas Mountains during these early days are not reliably known (Wagner 1977). Valleys and foothills of the Animas Mountains continue to be used for grazing, while the mountain proper is currently used only for scientific study (Brown 1990).

Fires that have occurred in the southwestern United States have been largely suppressed during this century (USDA Forest Service 1986). Grazing and post-1900 fire suppression in the United States may have triggered several environmental and vegetation changes, including arroyo cutting, invasion of desert grassland by shrubs, and replacement of pine stands by Douglas-fir and other species more shade tolerant than pine at high elevations (Leopold 1924, Sawyer and Kinraide 1980, Archer and Smeins 1991, Barton 1993).

Land-use in the adjacent Mexico is relatively unknown. Fire suppression probably has been less efficient and less successful in Mexico than in the United States. Bahre (1991) indicated that before 1881, ranchers from overgrazed areas in Texas, New Mexico and the Mexican states of Durango, Chihuahua and Sonora began moving their herds into southern Arizona where the rangeland condition was better. Rangeland conditions in the Mexican border states apparently have not improved considerably: spatial contrasts in vegetation across the Arizona-Sonora boundary indicate higher intensity of grazing in Mexico than in the United States (Bahre and Bradbury 1978). Although other land-uses account for some contrasts in the vegetation, impacts are mainly due to different perceptions about, and management of, grazing in the United States and Mexico.

Sierra Los Ajos has been subjected to a variety of land uses (SARH 1992, Garza 1993). Before 1936 logging activities and fuelwood extraction were allowed to support mining by the Wheeler Land Company. Although the mountain was decreed National Forest Reserve in 1936, logging activities were reported again in 1941. However, no information related to logged volumes is available. Again in 1978 a volume of 10,000 cubic meters was allowed to be logged in a 2-year period. Lately saplings of *Psedotsuga menziesii* and *Abies concolor* have been exploited illegally for Christmas trees (SARH 1992).

Grazing activities in Sierra Los Ajos are not well documented. A number of grazing permits have been reported for the period 1968-1984, but the intensity of grazing and number of animals per hectare for each one of the prescribed lots are unknown. Cattle grazing is still practiced throughout the entire mountain range (personal observation).

A comparative study of fire frequency in Animas Mountains and Sierra Los Ajos indicated that the fire regime in the Animas Mountains is characterized by a mixture of low-intensity, short-interval (3-15 years) surface fires and of higher intensity fires, at longer intervals (20-50 years). By comparison, Sierra Los Ajos shows episodic fires (short interval) even for this century, which is rarely observed on the U.S. side of the border (Dieterich 1983, Baisan and Swetnam 1993).

METHODS

Stand structure was studied in three forest communities in each mountain range: (1) Douglas-fir/gambel oak forests found on northern aspects above 2200 m, (2) southwestern white pine/chihuahua pine/ponderosa pine forests found at intermediate elevations, and pinyon pine/juniper/oak forests found at low elevations bordering grasslands. Following aerial reconnaissance, four representative stands of each community in each mountain range were selected for intensive study (total=24 stands). Stand selection was closely coordinated with a fire history study being conducted concurrently by the Laboratory of Tree-Ring Research.

One, 20 X 50 m (0.1 ha) permanent plot was established in each stand. Each plot was divided into 10, 10 X 10 m subplots, in which (1) diameter at breast height (dbh) of each woody plant stem was measured, (2) shrub cover, herb cover and tree seedling density were estimated and flora determined, (3) age (years) was determined by growth-ring analysis of two randomly-selected trees (total= 20 trees/plot). Two increment cores per tree were taken from each of sampled tree and age determined by standard dendrochronological analyses (Fritts 1976). Skeleton plots were constructed for each of the collected cores and crossdated with composite skeleton plots developed from Douglas-fir and ponderosa pine cores collected in both mountain ranges.

All stands were analyzed for vegetational composition and age distribution in 5-year age intervals; size distributions were also produced, using dbh classes. Analysis of residuals was conducted and regression analysis was used to determine the relationship between stand age and dbh for each sampled stand, as well as for a combination of sites in specific communities in each mountain range. Then, regression equations for each site were derived for age estimations (dependent variable) considering dbh as an independent variable. For comparison purposes, density was extrapolated to one hectare.

To analyze the influence of fire, stand age structure for Douglas-fir and southwestern white pine communities was compared with the fire dates recorded at each site in the Animas Mountains. Similar comparisons were done for ponderosa pine in Sierra Los Ajos. However, a composite fire chronology was used for Sierra Los Ajos due to the lack of specific fire dates for ponderosa pine sites.

Comparisons of dbh and age distributions between similar communities with similar physiographic characteristics were performed to assess the differences of land-use between mountain ranges. For example, the most similar stands in each community from each mountain range (with respect to elevation, aspect, and slope) were compared with respect to dbh and age distributions.

RESULTS AND DISCUSSION

The regression of dbh vs. age for all sampled Douglas-fir trees in the Animas Mountains resulted in an r^2=0.34; the southwestern white pine regression had an r^2=0.60. For Sierra Los Ajos all combined ponderosa pine trees had an r^2=0.22. Likewise, square correlations from single plots were usually high (Table 1). Therefore, regression equations from these stands were used for estimating age of these species and sites.

The majority of recruitment of Douglas-fir trees in all stands of the Animas Mountains was after the last fire (1879 for 3 stands, 1900 for 1 stand). Trees recruited into stands before 1879 did not survive that fire (fig.2). However, a few trees survived fires as indicated for fires occurring in 1825, 1857, and 1879 in stand Animas 8565TN. Although some individuals survive fires, Douglas-fir appears to be late-successional species in the Animas Mountains, achieving dominance only when fires are excluded.

Size distributions of Douglas-fir stands with similar physiographic characteristics (e.g., eleva-

Table 1.—Comparative r^2 values between dbh and age for forest communities in Animas Mountains and Sierra Los Ajos.

Stand	Dominant Species	r^2	Combined stands (r^2)
Animas Saddle	*Pseudotsuga menziesii*	0.48	
Animas Saddle West	"	0.52	0.34
Animas South	"	0.80	
Animas 8565TN	"	0.89	
Animas Peak1	*Pinus strobiformis*	0.63	0.60
Animas Peak2	"	0.71	
Animas Peak3	"	0.68	
Pinyon 7420T	N*Pinus discolor*	0.87	
Pinyon 4WD	"	0.80	
Los Ajos Nuevos	*Pinus ponderosa*	0.68	0.22
C. Las Flores	*Pseudotsuga menziesii*	0.50	
La Sal	*Pinus discolor*	0.83	

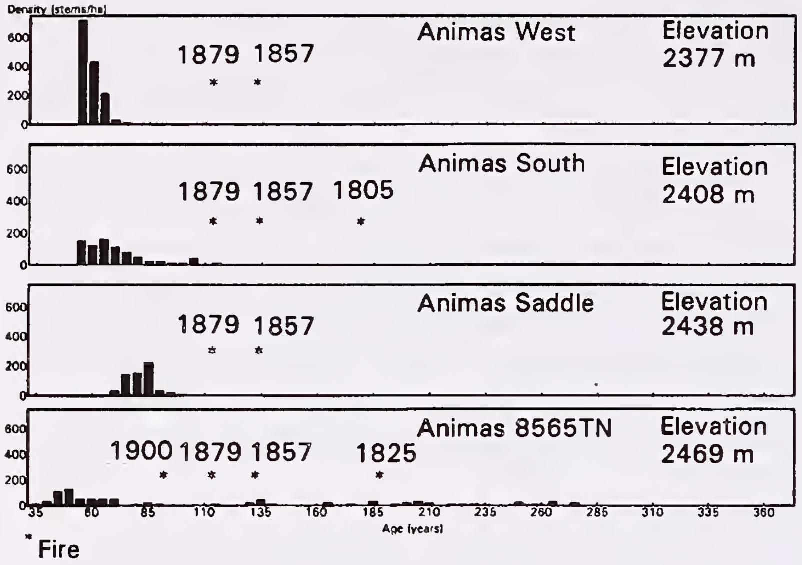

Figure 2.—Age class distribution and fire regime for Douglas-fir communities in the Animas Mountains, NM.

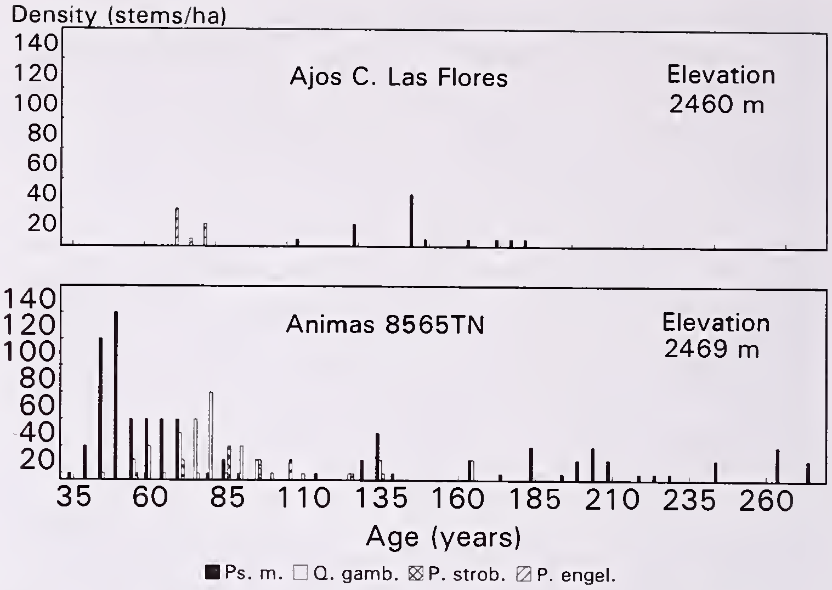

Figure 4.—Age class distribution comparison between two Douglas-fir communities in the Animas Mountains, NM., and Sierra Los Ajos, Sonora.

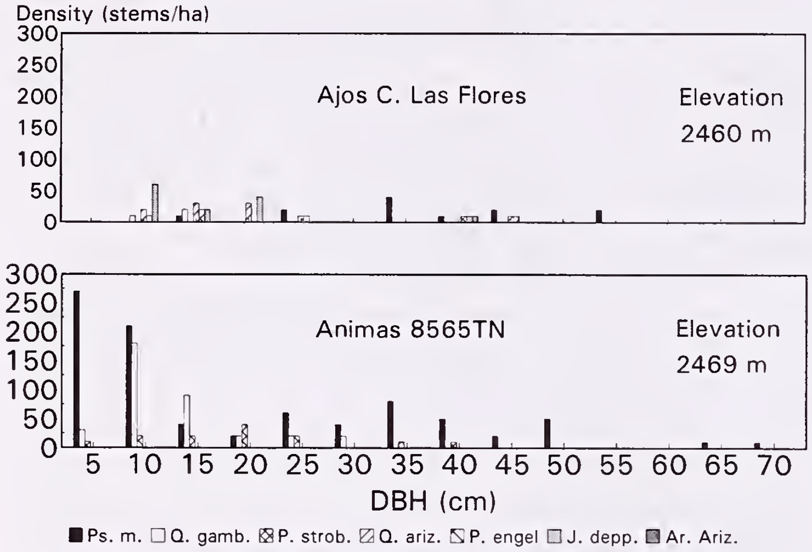

Figure 3.—Size class distribution comparisons between two Douglas-fir communities in the Animas Mountains, NM., and Sierra Los Ajos, Sonora.

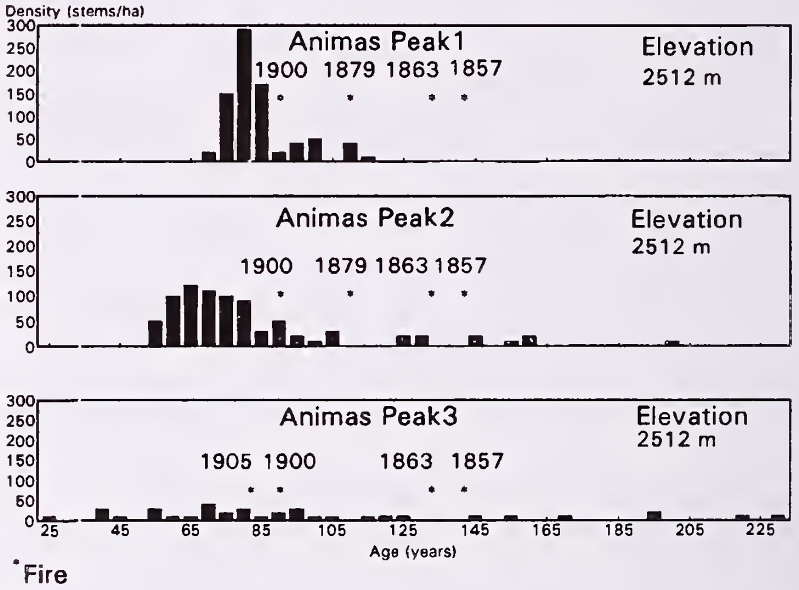

Figure 5.— Age class distribution and fire regime for southwestern white pine communities in the Animas Mountains, NM.

tion, aspect, slope) were different between mountain ranges. Animas 8565TN (elevation 2469 m, aspect north, slope 40°) is dominated by Douglas-fir with size classes ranging from 5 to 50 cm, and with densities for the smaller classes greater than 200 stems/ha. Codominant species are southwestern white pine, gambel oak, and Arizona oak. Post-1900 recruitment is dominated by Douglas-fir, and other species recruited for this period in relatively high densities are gambel oak and southwestern white pine. Ajos C. Las Flores (elevation 2460 m, aspect northwest, slope 39°) is also dominated by Douglas-fir with size classes ranging from 15 to 55 cm, but with few trees/size class. Other associated species are apache pine, alligator juniper, and madroño (fig. 3), also in low densities. Post-1900 recruitment included a few individuals of Douglas-fir and apache pine (fig. 4).

Tree recruitment for mixed pine communities in the Animas Mountains showed excellent agreement with the fire regime. Maximum tree establishment of existing trees occurred after 1900 (fig. 5). Animas Peak3 had the oldest southwestern white pine trees with discontinuous and low recruitment between 1760 and 1870, but almost continuous tree establishment after 1870. Animas Peak1 and Animas Peak2 had age distribution patterns very similar to one another with few existing trees that established before 1880 and most existing trees establishing between 1880 and 1940. Maximum tree establishment occurred after 1900.

Stand structural patterns in the Animas Mountains are consistent with a common interpretation of stand dynamics in Rocky Mountain Forests: increased grazing and decreased incidence of fire after 1880 may have triggered a shift in tree species composition, with reduced importance of ponderosa pine and increased importance of more shade-tolerant but less fire-tolerant species (e.g., *Pinus strobiformis* and *Pseudotsuga menziesii*). However, an alternative explanation is possible: species composition may have been similar pre- and post-1880, with similar fire-induced mortality in all species. Considering the large variation between species in post-fire survival (Wright and Bailey 1982), the latter explanation seems unlikely.

In contrast to the Animas Mountains, Sierra Los Ajos mixed pine stands are dominated by few individuals of ponderosa pine, with nearly all trees less than 90 years old. Good agreement was found between establishment of trees and the composite fire chronology for the site (fig. 6). Variations in recruitment are observed between plots, especially after the fire of 1916. The virtual absence of old ponderosa pine trees could be attributed to logging activities but probably not to the effect of fires: ponderosa pine trees are very fire-tolerant (Wright and Bailey, 1982), and many individuals are survived several fires in this study.

Size class distributions varied between mountain ranges for ponderosa pine stands. Five tree species are present in Animas South Canyon (elevation 2200 m, aspect northeast, slope 12°), with ponderosa pine dominant in size classes 30 and 55 cm. Smaller size class are dominated by oaks and alligator juniper (5 to 15 cm), and southwestern white pine (25 to 30 cm). Ajos C. Nevada Gate stand (elevation 2200 m, aspect southeast, slope 12°) has ponderosa pine trees dominating all size categories (5 to 55 cm), with oaks, apache pine and madroño present but in relatively low densities (fig. 7).

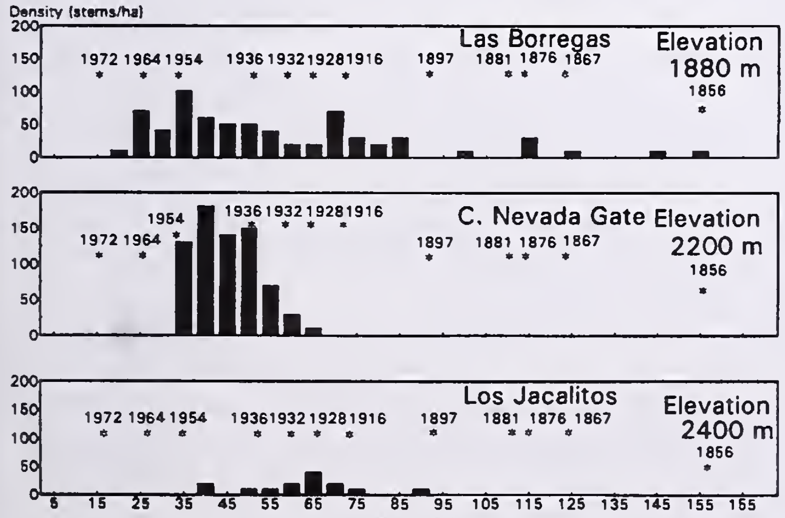

Figure 6.—Age class distribution and fire regime for ponderosa pine communities in Sierra Los Ajos, Sonora.

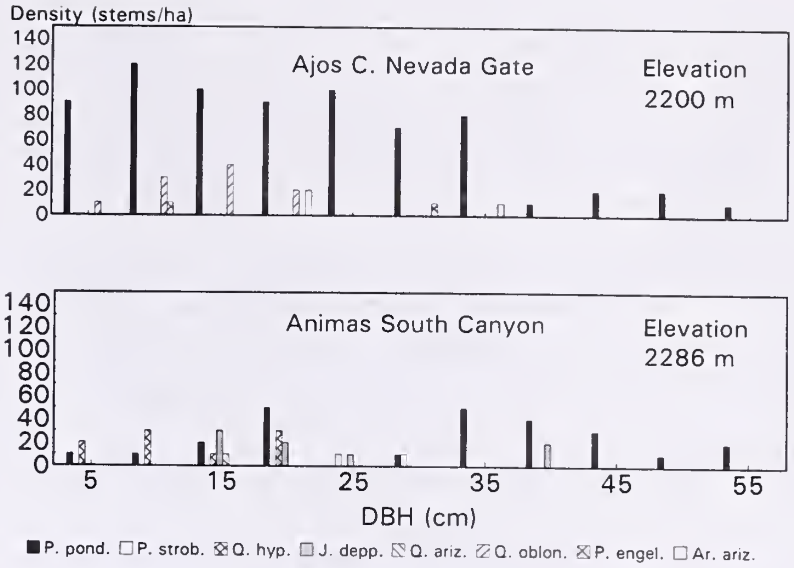

Figure 7.—Size class distribution comparison between two ponderosa pine communities in the Animas Mountains, NM., and Sierra Los Ajos, Sonora.

Age structure of ponderosa pine stands reflects the same general trends observed for size structure. For Animas South Canyon, establishment was relatively continuous from 1810 through 1900, and then establishment declines markedly (fig. 8). Southwestern white pine trees established after 1880, probably as consequence of fire suppression. The opposite case is indicated for Ajos C. Nevada Gate with a young population of ponderosa pine (40 to 70 years old), and some recruitment of apache pine (40 to 45 years old). The paucity of old trees in ponderosa pine stands of Sierra Los Ajos may be due to logging activities allowed in the area before 1936 and after 1941.

Low-elevation stands of pinyon pine in the Animas Mountains were similar to those in Sierra Los Ajos. Animas Pinyon 7420TN (elevation 2195 m, aspect southeast, slope 15°) has a high frequency of small stems, with a few individuals larger than 15 cm (fig. 9). Similarly, the Ajos La Sal pinyon stand (elevation 2200 m, aspect southwest, slope 18°) in Sierra Los Ajos was characterized by many trees in the 10- and 15-cm classes. Associated species in both stands included Arizona oak, alligator juniper, and ponderosa pine.

Establishment of pinyon pine trees has occurred since 1730 in the Animas Mountains (fig. 10). However, most existing trees established after 1850, with a peak of establishment from 1910-1940.

The pinyon pine stand in Sierra Los Ajos (elevation 2200 m, aspect southwest, slope 18°) is dominated by young trees (20 to 60 years old). Stand age structure is similar to Animas Pinyon

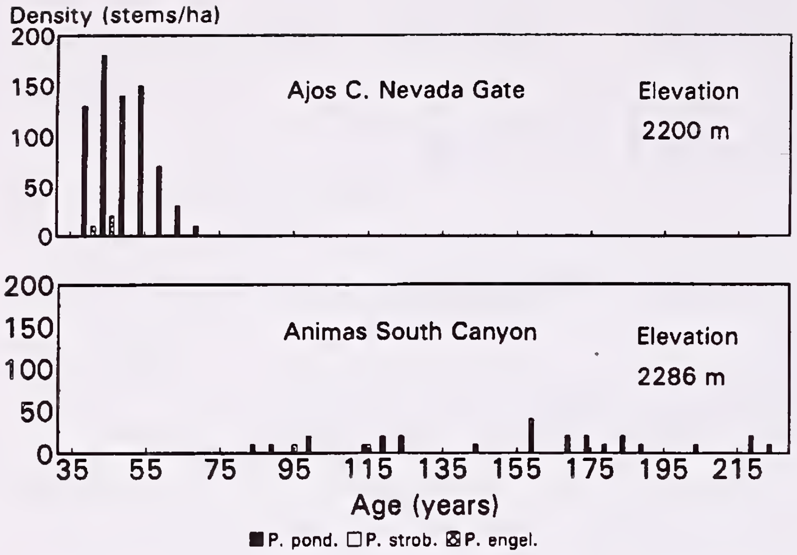

Figure 8.—Age class distribution comparison between two ponderosa pine communities in the Animas Mountains, NM., and Sierra Los Ajos, Sonora.

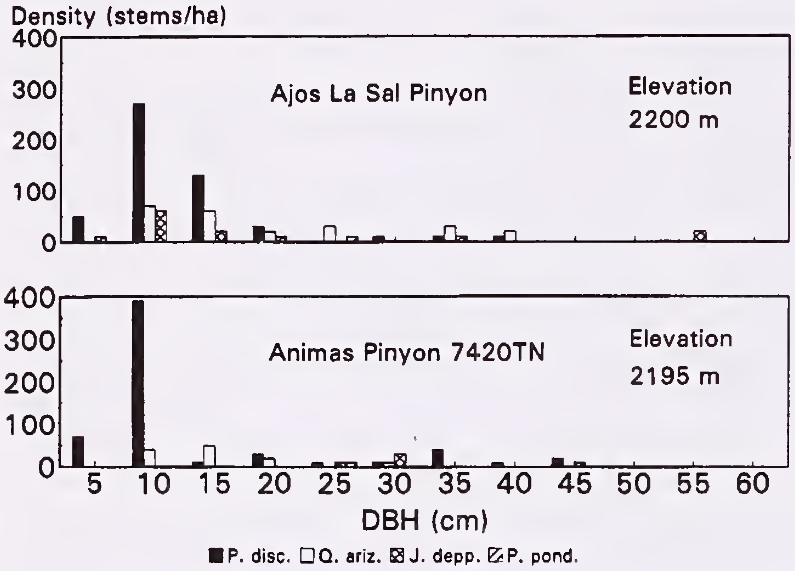

Figure 9.—Size class distribution comparisons between two pinyon pine communities in the Animas Mountains, NM., and Sierra Los Ajos, Sonora.

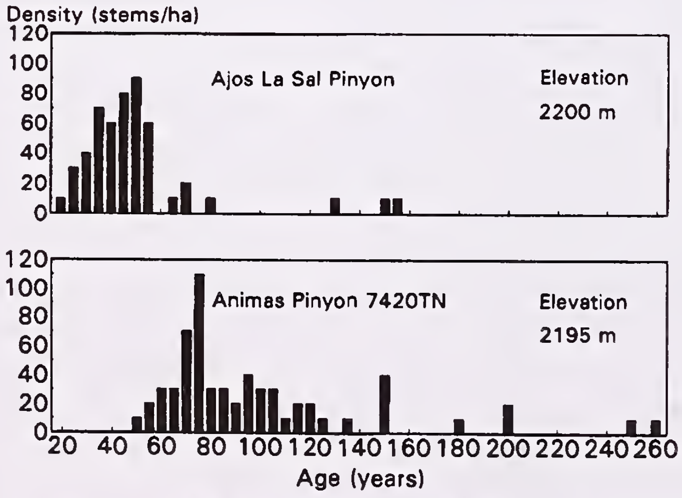

Figure 10.—Age class distribution comparison between two pinyon pine communities in the Animas Mountains, NM., and Sierra Los Ajos, Sonora.

7420TN, with few old trees and a recent wave of recruitment. However, the peak of recruitment occurred later in Ajos La Sal Pinyon than Animas Pinyon 7420TN, there were fewer old trees, and total density was less (440 trees/ha, vs. 610 tres/ha). Logging activities before 1936, may have removed many trees, especially old pinyons.

Pinyon pine communities in some parts of Mexico are strongly influenced by natural and human disturbance events, particularly fires. Size distributions less than 20 cm dbh for young trees (less than 50 years old) were common for a pinyon pine stand located in the rain-shadow of the eastern Sierra Madre Mountains, Veracruz, Mexico (Segura and Snook 1992). Similar structure distribution was described for Los Ajos Sal Pinyon. However, logging activities apparently have influenced in a greater extent the structure of this community.

CONCLUSIONS

High-elevation forests in the Animas Mountains (US) were markedly different with respect to stand structure than stands in Sierra Los Ajos (Mexico).

There is little doubt that these differences are attributable, at least in part, to differences in land-use history. For example, post-1900 fire suppression policy in the U.S., along with increasing grazing activities, may have triggered a shift in species composition in mixed pine communities in the Animas Mountains. These stands, previously dominated by ponderosa pine are increasingly dominated by southwestern white pine, a more shade-tolerant and less fire-resistant species. On the other hand, a less aggressive and usually less effective fire suppression policy in Mexico has contributed to continued dominance of ponderosa pine in Sierra Los Ajos. This situation has been enhanced by logging activities in Mexico that have favored shade-intolerant ponderosa pine. Different land-use patterns have also influenced age-class distribution, with pine stands dominated by young trees in Mexico and a variety of age-classes in the U.S.

Much recent literature has attributed variations in species composition over time to non-equilibrium processes (e.g., Sprugel 1991, Campbell and McAndrews 1993) implying that community response to disturbance (or to the absence of disturbance) is not predictable. Given the small variability in stand structure within a mountain range (compared to between mountain ranges) observed in this study, it seems clear that stand structure is controlled at a coarse level of resolution by climate and land-use patterns. Therefore, stand structure may be predicted, with reasonable accuracy, from knowledge of species, life-history characteristics, climate, and land-use patterns.

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Postfire Regeneration in Arizona's Giant Saguaro Shrub Community

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Abstract.—In May 1993, an arsonist set numerous fires in the saguaro shrub vegetation type on the Mesa Ranger District, Tonto National Forest. In January 1994, we began a postfire examination in these burned areas to determine the potential of the shrub species for resprouting after fire. Fire girdled saguaros and charred shrub skeletons covered the burned areas. Shrub skeletons were examined for basal sprouts or branch regrowth. Resprouting from branches of shrubs was evident within islands of partially burned areas and along the edges of the burns. Basal sprouting was observed on plants that had no apparent viable upper branches. This implies that some shrub species in the saguaro shrub association studied have the potential to regenerate after a spring wildfire.

INTRODUCTION

A review of current fire records, 1973 to 1992, from the Tonto National Forest, Arizona, reveals a continuing increase in fire frequency and acreage burned in upland Sonoran desert communities. The number of fires in desert habitats approaches those in timber, but exceeds all other habitats in actual acres burned (Narog et. al. in press). Earlier studies of fire occurrence reported similar increases in desert-shrub and desert-grassland fires (Rogers 1986, Rogers and Vint 1987, Schmid and Rogers 1988). Consequently, internationally renowned scenic vistas, composed of giant saguaros (*Carnegiea gigantea)* and associated vegetation, are becoming severely degraded by this recent change in fire regime. Modern fire records for this desert habitat do not provide the type of documentation necessary to understand fire dynamics from a historical perspective. However, fire histories from adjacent montane habitats have been reconstructed from dendrological analyses (Baisan and Swetnam 1990) and may be useful.

Sonoran desert communities, with their species rich patches (Silvertown and Wilson 1994), present us with a complex and dynamic mosaic of vegetation. Areas once characterized by small infrequent fires, now support flammable exotic grasses that connect many of these patches and purportedly increase ignitions and acreage burned.

The role of fire and grazing in Arizona desert grassland-shrub communities has been debated and evaluated for over 70 years. Leopold (1924) called for a serious consideration of his perceived problem of shrub encroachment into grasslands. He attributed the shrub encroachment to overgrazing and decreased fire occurrence into the uplands. The majority of research on fire in the desert has focused on conversion of the desert shrubland to grassland (Phillips 1962, Martin and Turner 1977). Others have documented and weighed responses of desert-grassland-shrub species to fire against anthropogenic factors (e.g., Cable 1972, Rogers and Steele 1980, Ahlstrand 1982, McLaughlin and Bowers 1982, Martin 1983, Cave and Patten 1984, Humphrey 1984, Rogers 1985, Goldberg and Turner 1986, Cox, Ibarra and Martin 1988, Davis 1989, and Thomas 1991). All these studies combined suggest more questions than they answer for managing fire in these desert ecosystems. Wright (1988) summed up the problem when he wrote, "The historical role of fire in the semidesert grass-shrub community is somewhat perplexing." Multiple-use management, and changing needs and interests have further confounded fuels and fire management. Therefore today, fire remains problematic for many desert land managers.

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Following recurrent fire problems, the Tonto National Forest, Arizona, requested assistance in developing alternative fire management policies in desert-shrub saguaro habitats. They were concerned that the increasing fire frequency would decimate the dwindling population of highly prized saguaro resource. We, therefore, initiated a study on the effects of fire on this saguaro community. This paper presents preliminary observations and survey results of 1-year post-fire plant growth responses as contrasted with plants on an adjacent unburned plot.

METHODS

Study Area

This study is being conducted on the Mesa Ranger District of the Tonto National Forest, Arizona. Our research is confined to approximately a 16-square mile area located about 40 miles northeast of Phoenix along the B-line Highway (Highway 87), southwest of Four Peaks Mountains, and northeast of Adams Mesa (fig. 1). It is in the mid-elevation range, ca. 800 m, of saguaro habitat with generally uniform slope and aspect. This land is heavily used for recreation and as open rangeland for cattle. Data reported here are from two of nine plots identified for this research project. These two plots were placed at the May 4, 1993, Vista View burn site. Both plots were aligned east to west along the same slope contour to minimize geological, elevational and vegetation gradients. The unburned (fig. 2) plot was east of the wildfire in vegetation without prior fire history. The burned (fig. 3) plot was due west of the unburned plot and had been placed 100 m within the burned area perimeter. Both plots established for this study were on adjacent similar terrain and were evaluated during the spring of 1994.

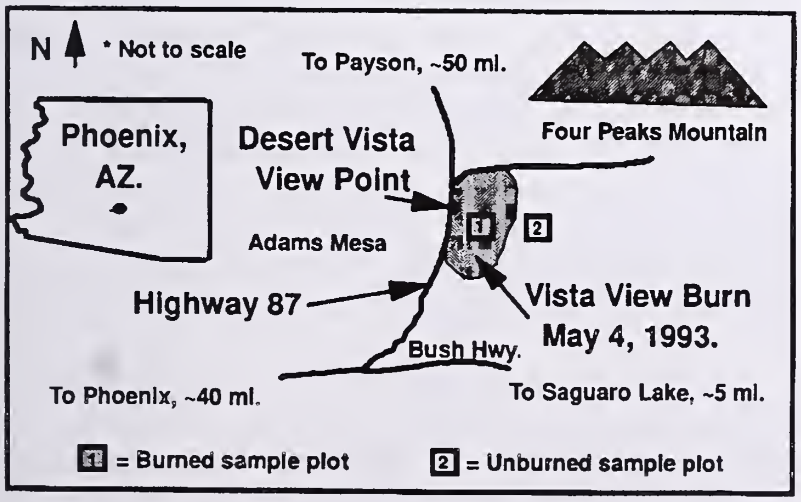

Figure 1.—Study site location on the May 4, 1993 Vista View burn, Mesa District, Tonto National Forest, Arizona. Note: map is not to scale.

Figure 2.—Unburned saguaro community adjacent to the May, 1993 Vista View burn, Tonto National Forest, Arizona.

Figure 3.—Burned saguaro community 1 year after the May, 1993 Vista View burn, Tonto National Forest, Arizona.

Experimental Design

Standard ecological methods and calculations as outlined by Cox (1990) were modified and adjusted to make their application appropriate in size and scope for this vegetation type. An integrated combination of line intercepts and quadrats was used to survey cover, density and frequency of occurrence for trees and shrubs in adjacent and similar unburned and burned permanent 1ha plots. Information on the herbaceous layer is not addressed in this paper, and future reference to plants will include only trees and shrubs. Each plot was subdivided into five 20m X 100m belt transects. Within each belt transect, a set of 10 contiguous quadrats was sampled adjacent to a randomly placed 100m line (fig. 4). Data for the line were recorded in 10m subunits coincident with the adjacent quadrat. Plants were counted in quadrats and measured on line intercepts. Obvious new growth from basal sprouts or branch regrowth on trees and shrubs were counted as resprouts. Other plant dimensions and community parameters were measured but are not reported here.

Analysis

Taxonomic determinations were made using available keys (Kearney and Peebles 1960, Elmore 1976, Earle 1980, Fisher 1989, Parker 1990, Bowers 1993, Hickman 1993). And voucher specimens were collected. For this preliminary examination of plant differences between unburned and burned plots, we arranged the species in a series of seven growth-form classes: trees, shrubs-large, shrubs-medium, shrubs-small, yucca, cactus and perennials. These were based on plant height, growth form, apparent woodiness and succulence.

Numerical analyses were based on individual totals divided by 50 sample units for each plot studied. Each sample unit included a 10m line segment adjacent to a 10m X 10m quadrat. Means are presented as the average cover per 10m segment or mean density per 10m X 10m quadrat.

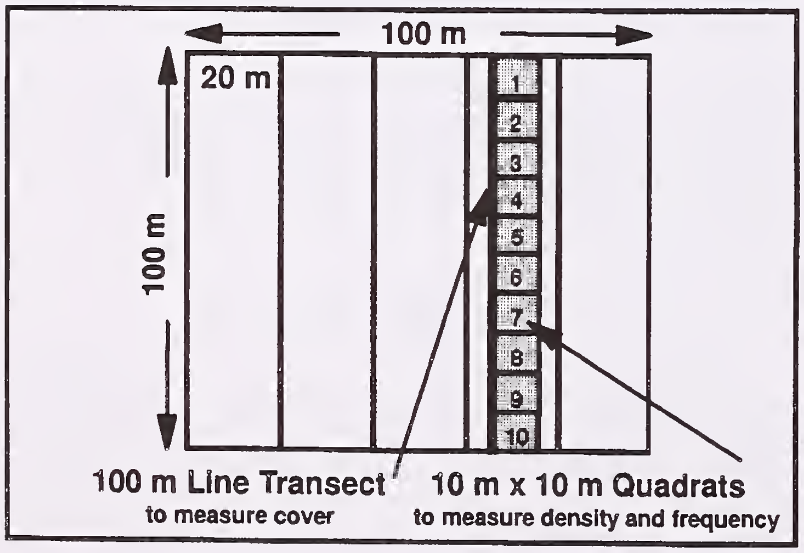

Figure 4.—Within each of the five 20m x 100m belt transects, a randomly placed 100 m line transect and ten 10m x 10m quadrats were placed for vegetation sampling in each hectare surveyed 1 year after the May, 1993 Vista View burn, Tonto National Forest, Arizona.

Relative percent cover was calculated from line data. Percent and relative percent frequency and relative percent density were calculated from quadrat data. Importance values as presented are the sum of relative percent cover, density and frequency, divided by 3.

RESULTS

Thirty-five plant species were counted and grouped into the growth-form classes: 2 trees, 5 shrubs-large, 13 shrubs-medium, 3 shrubs-small, 1 yucca, 7 cacti, and 4 perennials (Table 1). Of the 30 species found on the burned plot, 28 were observed resprouting. Species also noted to resprout by Rogers and Steele (1980) are identified in Table 1.

Both cover and density (Table 2) were less in the burned than in the unburned plot. In the unburned plot, the overlapping plants and clustered pattern of diverse species was reflected by the amount of cover on the line. The portion of the line that had living plants had a mean of about 109 percent cover. The rank order of plant frequency was similar in both the burned and unburned plots (Table 2), with the exception of a lower frequency of cactus in the burned plot. Even though absolute cover, density and frequency values may be lower in the burned plot, their calculated importance values show vegetation type composition and patterns similar to those of unburned sample units (fig. 5).

Total cover for live plants (fig. 6) in the burned plot was 15 percent as compared to 41 percent in the unburned plot. After only 1 year, resprouting plants accounted for the majority of the 15 percent cover in the burned plot (fig. 7).

Among the growth-form classes, cactus showed the greatest difference in density between the unburned and the burned plots (Table 3). Notably, 88 percent of all plants counted in the burned plot were resprouting at this time. Compared with the 3,126 individuals counted in the unburned plot, the 1,741 individuals in the burned sample represent a possible 55 percent survival.

In the unburned plot, many saguaros were observed growing in close proximity to shrubs and trees (fig. 8). Saguaros were often severely injured when their associated plant complex was burned (fig. 9). The ultimate impact of the fire on the standing saguaros cannot be estimated from the data collected at this 1-year post-fire sampling. A

Table 1. Saguaro community species presence and resprouting densities on unburned[1] and burned plots 1year after the May, 1993 Vista View burn, Tonto National Forest, Arizona.

Growth form *Scientific name*	Common name	Unburned density (.5 ha)	Burned density (.5 ha)	Post-fire resprouts[2] (.5 ha)	
Trees					
Canotia holacantha	Crucifixion thorn	39[1]	43	36	S
Cercidium microphyllum	Foothill palo verde	46	16	12	S
Shrubs-large					
Acacia constricta	Whitethorn	76	72	72	S
Acacia greggii	Catclaw	44	42	42	S
Jatropha cuneata	Wedgeleaf limberberry	1	5	5	
Lycium californicum	Desert thorn	5	4	4	
Lycium parishii	Wolfberry	52	33	33	G
Shrubs-medium					
Ambrosia deltoidea	Triangle leaf bur sage	183	113	10	S
Callandra eriophylla	Fairy duster	168	196	195	S
Encelia farinosa	Brittle bush	30	27	25	S
Encelia frutescens	Green brittle bush	0	17	17	
Ephedra asperca	Mormon tea	61	63	55	
Ephedra trifurca	Mormon tea	81	117	110	
Ericameria cooperi	Cooper golden bush	594	1	1	
Ericameria larcifolia	Turpentine bush	116[1]	25	27	
Eriogonum fasciculatum	Wild buckwheat	157	0	0	
Helianthus annuus	Sunflower	15	0	0	
Krameria grayi	White ratany	137	153	147	S
Psilostrophe cooperi	Paper flower	97	12	12	
Thamnosma montana	Turpentine broom	100	41	39	
Shrubs-small					
Palafoxia linearis	Spanish needle	82	9	9	
Senna covesii	Cassia	86	0	0	S
Sphaeralcea ambigua	Globe mallow	85	153	144	
Yucca					
Yucca torreyi	Yucca	107	105	95	
Cacti					
Carnegiea gigantea	Saguaro	5	14	0	
Echinocereus engelmannii	Strawberry hedgehog	35[1]	3	2	
Mammillaria tetrancistra	Corky-seed fishhook	18	4	2	
Opuntia bigelovii	Teddy bear cholla	1	0	0	
Opuntia engelmannii	Prickly pear	12	2	1	
Opuntia leptocaulis	Desert christmas cactus	37	9	4	S
Opuntia versicolor	Staghorn cholla	228	28	19	
Perennials					
Baileya multiradiata	Desert marigold	374	332	322	
Cersium neomexicana	Thistle	21	99	0	
Haplopappus spinulosus	Yellow aster	15	1	1	
Stipa sp.	Bunch grass	18	0	0	

[1] Unburned area resprouts include: 1 *Canotia*, 2 *Ericameria laricifolia*, and 1 *Echinocereus engelmannii.*

[2] Plants also identified as resprouting by Rogers & Steele (1980):
S = identified to species level and G =only identified to genus level.

high proportion of each fire-damaged saguaro still maintained photosynthetically active tissue. Numerous saguaros were observed flowering and producing fruit even though their bases had been severely girdled or charred.

DISCUSSION

The natural range of saguaro is limited by cold intolerance (Steenbergh and Lowe 1971, 1983). Successful recruitment and establishment of saguaro seedlings requires protection from unpredictable, extreme fluctuations in temperature and rainfall, as well as from biotic factors such as herbivory. This subtropical cactus is often found shielded from these hazards by association with a nurse plant (Nobel 1980, Vandermeer 1980, McAuliffe 1984, Gibson and Nobel 1986). However, when fire becomes a frequent component of this ecosystem, the nurse plants may become a liability. They may supply adequate fuel in close proximity so that the cactus is destroyed. Our observations suggest this may be more likely to occur where this habitat has been degraded by continuous grazing and invaded after wet winters by fine-fueled exotic grasses.

Table 2. Mean[1] plant cover per 10m segments and total number of hits for five 100m line intercepts in a saguaro community on unburned and burned plots one year after the May, 1993 Vista View burn, Tonto National Forest, AZ.

GROWTH FORM	UNBURNED Mean(cm)	UNBURNED Hits	BURNED May, 1993 Mean(cm)	BURNED May, 1993 Hits
Tree	102.7	34	36.8	26
Shrub-large	94.6	53	55.9	33
Shrub-medium	156.2	156	31.4	53
Shrub-small	11.1	27	2.4	4
Yucca	44.8	19	15.1	19
Cacti	10.9	34	3.0	9
Perennial	3.6	19	12.1	22
SUBTOTALS				
All plants	423.9	342	156.8	166
Dead plants	9.1	7	44.3	22
Ground	613.2	225	812.1	248
TOTAL	1,046.2	674	1,013.2	436

[1] N=5, m=10, sample units=50.

Table 3. Density[1] comparisons of plants and their resprouts[2] in unburned and burned plots of a saguaro community 1 year after the May, 1993 Vista View burn, Tonto National Forest, Arizona.

GROWTH FORM	UNBURNED Number of Plants observed	UNBURNED Number of Plants resprouting	BURNED Number of Plants observed	BURNED Number of Plants resprouting
Tree	85	1	59	48
Shrub-large	178		156	156
Shrub-medium	1,739	2	765	731
Shrub-small	253		163	154
Yucca	107		105	95
Cacti	336	1	61	30
Perennial	428		432	323
TOTAL	3,126	4	1,741	1,537

[1] Number per 0.5 ha.

[2] New growth emerging from basal sprouts or branch regrowth.

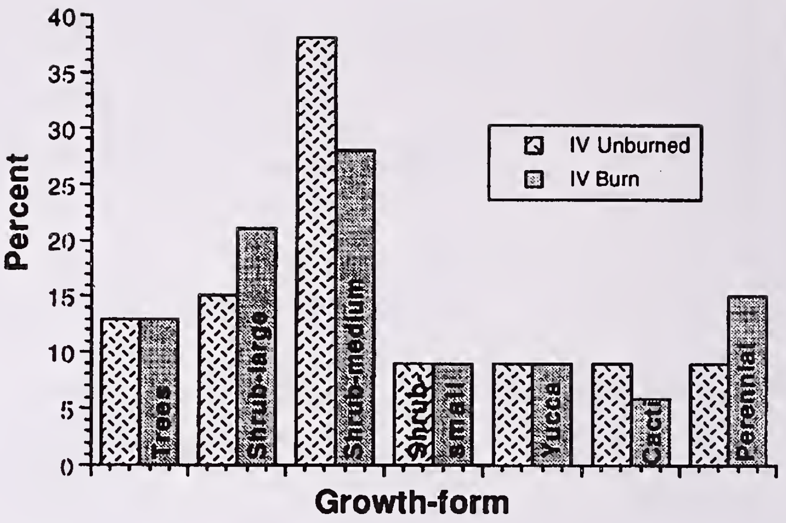

Figure 5.—Relative importance values (IV) among growth forms on unburned and burned plots in a saguaro community 1 year after the May, 1993 Vista View burn, Tonto National Forest, Arizona.

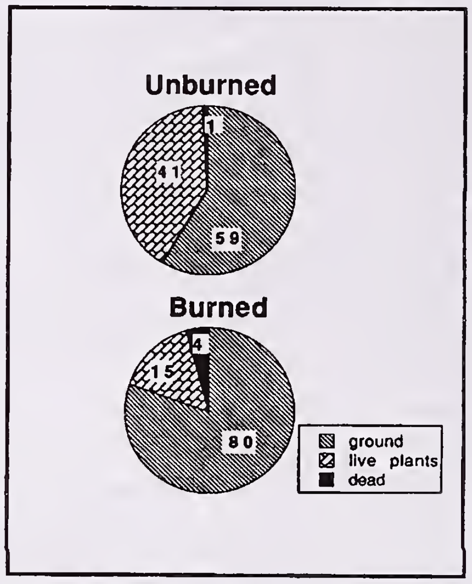

Figure 6.—Relative percent cover observed on an unburned and burned site in a saguaro community on the Tonto National Forest, Arizona. Note: Percentages are rounded to nearest one percent.

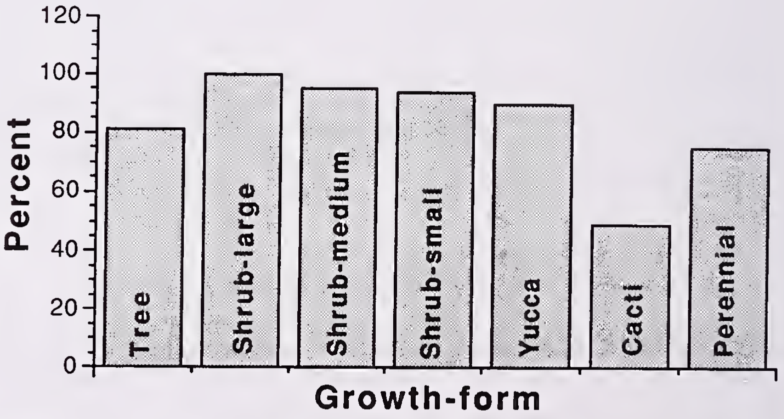

Figure 7.—Percent of plants resprouting in .5 ha of a saguaro community 1 year after the May, 1993 Vista View burn, Tonto National Forest, Arizona.

Figure 8.—Unburned saguaro and palo verde adjacent to May, 1993 Vista View burn, Tonto National Forest, Arizona.

Figure 9.—Fire-girdled saguaro 1 year after the May, 1993 Vista View burn, Tonto National Forest, Arizona.

Saguaro individuals may continue to stand and even reproduce seeds for several years after being mortally injured. Saguaro seeds reportedly must germinate and establish seedlings within their first season because the seeds are not viable beyond 1-year (Steenbergh and Lowe 1977). This paper focuses on the resprout response of plants associated with saguaro and whether they can survive fire. If saguaro is to remain an important component in this plant communitiy, then the significance of resprouting becomes apparent when we consider the immediate need for the quick post-fire re-establishment of the associated 'shelter' shrub species.

Palo verde is most often identified as the typical nurse plant for saguaros, however, other species may serve as potential shelter. Saguaro individuals may benefit from various degrees of shelter during their development and life history. Differences in biodiversity of associated vegetation may impact saguaro success. We found 35 associated species of potential shelter plants in our plots. Saguaros were often observed surrounded by trees and large shrubs, e.g., Canotia, Cercidium, Acacia spp. and Lycium spp. The potential role of other species is of interest, but undocumented. Further investigations are required to make that determination.

The saguaro community we studied is not unlike desert-shrub communities described by Silverton and Wilson (1994). Islands of species diversity are scattered throughout the area, separated by bands of bare ground. Our comparison of unburned with adjacent burned saguaro habitat showed five fewer species encountered in the unburned compared to the burned plot. In our unburned plot, live tree/shrub "islands" accounted for 41 percent of the cover on the line transect. Within that 41 percent we observed, 109 percent tree/shrub overlap. Live plant cover for the burned plot was only 27 percent of the unburned, while the average plant density in the burned plot was 59 percent of the unburned. When we consider this information with the fact that 88 percent of the plants encountered in our burned study plot were resprouting 1 year after the wildfire, it becomes apparent that a high percentage of plants in this saguaro community have the capacity to rapidly recover after fire. Shrubs that resprout may thus provide immediately needed post-fire shelter for saguaro seedling establishment, yet may ultimately contribute to a potential fire hazard. However, long-term monitoring of these associated plants is required to determine whether they will recover, or like the saguaro, eventually die.

Clear documentation of the detrimental impact of cattle grazing on saguaro seedlings is presented by Abouhaidar (1992) for fenced plots on the Saguaro National Monument, Tucson. Our observations on the Tonto National Forest of the complex community structure and interplay of both biotic and abiotic natural and introduced factors, parallel those identified by Turner (1992) for the Saguaro National Monument, Rincon Mountain District, Tucson.

Post-fire mortality has been clearly documented for the giant saguaro cactus (Steenbergh and Lowe 1977, 1983, McLaughlin and Bowers 1982, Rogers 1985). Rogers (1986) noted that the mortality of saguaros has been underestimated because of the long lag between injury and death of individual saguaros. In his reevaluation of the area studied by McLaughlin and Bowers (1982), Rogers (1985) suggests "... that saguaro could be virtually eliminated by a sequence of fires that occur at intervals of less than 30 years, because saguaro requires 30 years to reach reproductive maturity ...".

Declines in these giant cactus forests have been precipitated by the combined assaults of urban encroachment, grazing, fire and natural climatic factors. Few saguaros will remain in many parts of its range if this trend is not reversed. Therefore, integrated efforts of scientists, managers and politicians, dedicated to programs of detailed studies, holistic management and political commitment, are needed to preserve the biodiversity of this unique ecosystem.

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The National Center of Sustainable Agriculture in Mexico

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Abstract.—The National Center of Sustainable Agriculture in Mexico is conducting research on basic processes which, in turn, can be used for generating appropriate technology for sustainable agricultural production at the farmer level. A holistic research strategy is being followed in this endeavor.

INTRODUCTION

The people of the world are becoming increasingly concerned about the natural resources deterioration caused by applications of either high-level technologies in agricultural production or subsistence agricultural production systems, which in both cases lead to the destruction of soil and biota, and general environmental degradation. If allowed to continue, this situation can dangerously decrease food production for the growing human populations, whose needs are also growing at increasing rates. It, therefore, is urgent to consider drastic changes in food technology and agricultural production in Mexico, other regions of the Sky Islands territory, and throughout the world. The change must start with research on basic processes which, in turn, can be used for generating for generating appropriate technology for sustainable agricultural production at the farmer-level.

NATIONAL CENTER OF SUSTAINABLE AGRICULTURE

This effort is just starting in Mexico at the National Center of Sustainable Agriculture, which is charged with the coordination of specified research efforts with Regional Centers of the National Institute of Forestry, Agriculture and Animal Production Research (INIFAP), and with other national and international organizations. The National Center of Sustainable Agriculture has a small, highly trained research group which carries out their own research projects and coordinates the research activities of national networks throughout Mexico. The primary functions of the Center are to:

- Generate appropriate technology for sustainable agricultural production.
- Establish and maintain institutional standards on sustainable agricultural production technology.
- Provide technical training at all levels.
- Make diagnoses and undertake special projects related to sustainable agricultural production.

The following research projects are currently being conducted by the in-house personal of the Center:

- Conservation tillage.
- Other alternative agricultural production systems, e.g., organic agriculture, indigenous production systems, etc.
- Small farm mechanization possibilities.
- Integrated resources management, including soil, water, and watershed management, alley cropping, etc.
- Analysis of the energy budgets used in agricultural production systems.
- Integrated pest control.

The relationships of these research projects to one another within the structure of the National Center for Sustainable Agriculture are shown in figure 1.

RESEARCH STRATEGY

The Center follows a strategy of selecting high priority problems that are identified in relation to specific agricultural production systems. The resulting research effort is carried out not only in reference to the problems themselves, but for the whole system being considered. All of the agricul-

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tural production system components are analyzed, including:

- Environmental factors.
- Degree of pollution.
- Inputs and outputs of the agricultural production systems studied.
- Socioeconomic parameters.

The specific agricultural production system studied is then "introduced" to the most viable of six the in-house research projects being conducted by the personal of the Center for solving the problem. Once inside the Center's structure, the system also "passes through" the five remaining research projects to achieve holistic solutions to the problems identified, a process that is illustrated in figure 2. In following this strategy, one becomes confident that the most important aspects related to sustainable agricultural production have been addressed according to the current level of knowledge when that system goes from the Center to the farmers.

A research strategy of this type is too complex to be implemented satisfactorily by a single institution. Therefore, it is necessary that INIFAP collaborates efficiently with key teaching, development, and research efforts of national and international organizations. The National Center of Sustainable Agriculture does not duplicate the generation of sustainable agricultural production generation in INIFAP or the country. The Center is using this holistic research approach to fill a present vacuum.

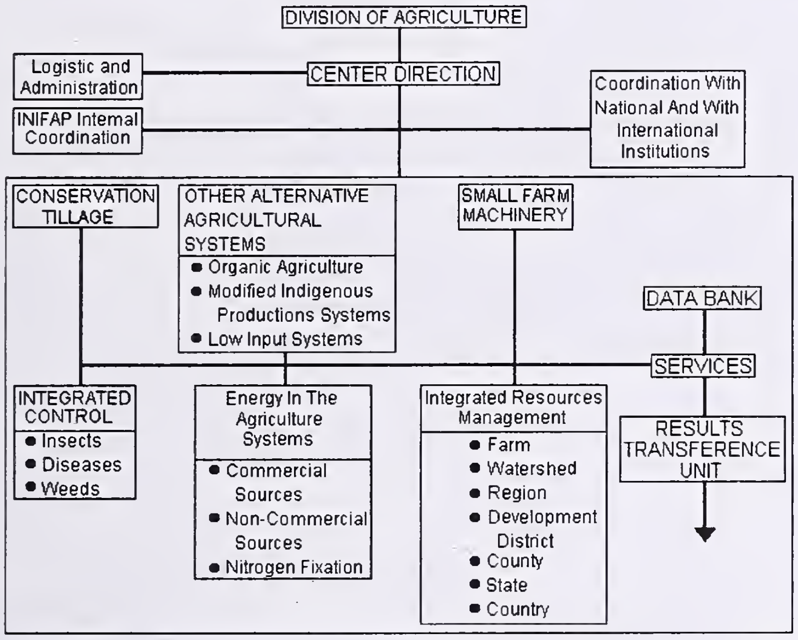

Figure 1.—Structure of the National Center of Sustainable Agriculture.

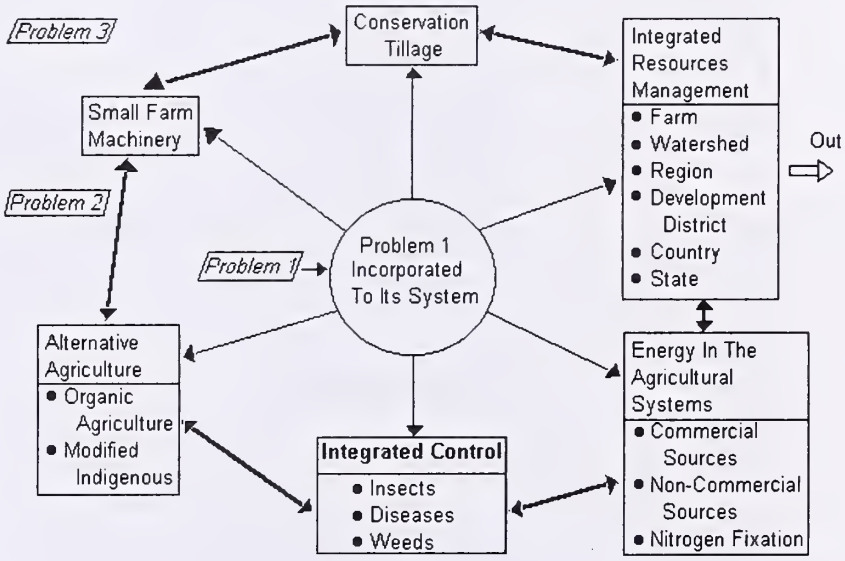

Figure 2.—Holistic research strategy of the National Center of Sustainable Agriculture.

Ecological Impacts of Cattle Grazing on the Vegetation, Soils, and Wildlife of the Mountains of Sonora

Donald Johnson[1]

Abstract.—The mountainous region of eastern Sonora, known as "La Sierra", was chosen for settlement by the first colonizers over the more extensive, flatter and arid costal plains because of its higher precipitation, streams, and fertile valleys. Despite the efforts of State and Federal government agencies, most of the high country of eastern Sonora has not kept apace with the development in the rest of the state. The dependence on ranching and subsistence agriculture is beginning to give way to other economic activities and to the realization that one the most important resources of the region is water, stored in dams, large and small, and used mostly by the large cities below for the increasing industrial and population growth and in the irrigation of the desert. The management and rational use of all the natural resources of the Sonoran Mountains, including the protection and conservation of some unique areas, is in its infancy and offers a challenge to legislators, planners, managers, and residents of this relatively little studied region of Sonora.

INTRODUCTION

For his presentation I have divided eastern Sonora into three regions, Northern, Central and Southern, composed of 14 municipalities. These regions form a contiguous mass of the mountains and valleys of the "Sierra Madre Occiodental", but do not include the isolated sky islands of northern and central Sonora and seems to be located somewhat west of what is being mapped as the "Madrean Archipelago". These three regions do include the greater part of the mountainous terrain of Sonora and should prove adequate to present at least the principal aspects of the "Sierra" of Sonora. (Map of Sonora)

The northern region is composed of the seven municipalities of: Bacadéhuachi , Bacerác, Huachineras, Nácori Chico, Nacozari de García and Villa Hidalgo (Oputo).

The central region is composed of the three municipalities of Arivechi, Bacanora and Sahuaripa, and the southern region of the four municipalities of Alamos, Quiriego, Rosario de Tezopaco and Yécora.

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The raising of beef cattle first entered eastern Sonora around 1670 and has been an important economic, social, cultural and ecological factor for the last 323 years.

Table 1 summarizes the total land area of the three regions, while table 2 presents the number of reproducing cows of the area, the total number of animal units (AU): defined as a cow and her calf or their equivalent, including bulls, replacement heifers, weaned calves that had not been sold at the time of the inventory, horses, mules, burros, sheep and goats. It also presents the area used for grazing cattle, improved pasture, mostly buffelgrass Cenchus ciliaris, and the land area of mostly subsistence agriculture, of which forage crops for cattle form a considerable portion.

Table 1.—Municipalities and land area of the three mountainous region of Sonora, México.

MUNICIPALITIES	LAND AREA
NORTHERN REGION	
Bacadéhuachi Bacerác Bavispe Huachinera Nácori chico Nacozari de García Villa Hidalgo (Oputo)	1, 273, 000 ha 3, 144, 310 A
CENTRAL REGION	
Arivechi Bacanora Sahuaripa	729, 400 ha 1, 801, 618 A
SOUTHERN REGION	
Alamos Quiriego Rosario de Tesopaco Yécora	1, 766, 413 ha 4, 363, 040 A
TOTAL	**3, 768, 813 ha** **9, 308, 968 A**

Table 2.—Numbers of reproducing cows, total animal units and areas of range land, improved pasture, subsistance agriculture of the three mountainous regiones of Sonora.

COWS	A.U.	RANGE LAND	IMPROVED PASTURE	SUBSISTENCE AGRICULTURE
		NORTHERN REGION		
57, 852	102, 459	1, 239, 669 ha 3, 061, 982 A	1, 256 ha 3, 102 A	5, 331 ha 13, 167 A
		CENTRAL REGION		
49, 748	74,107	717, 721 ha 1, 772, 770 A	6, 079 ha 15, 015 A	4, 400 ha 10, 868 A
		SOUTHERN REGION		
93, 885	142, 416	1, 521, 984 ha 3, 759, 300 A	49, 948 ha 123, 371 A	35, 495 ha 87, 672 A
		TOTALS		
201, 485	318, 982	3, 479, 374 ha 8, 594, 052 A	57, 283 ha 141, 489 A	45, 226 ha 111, 708 A

Table 3.—Grazing coefficients for the three mountainous regions of Sonora.

RANGE + PASTURE	A.U.	GRAZING COEFICIENT
	NORTHERN REGION	
1, 240, 925 ha	102, 459	12.11 ha/AU
3, 065, 084 A	102, 459	29.91 A/AU
	CENTRAL REGION	
723, 800 ha	74, 107	9.77 ha/AU
1, 787, 785 A	74, 107	24.12 A/AU
	SOUTHERN REGION	
1, 571, 932 ha	142, 416	11.03 ha/AU
3, 882, 671 A	142, 416	27.26 A/AU
	TOTAL	
2, 536, 657 ha	318, 982 AU	10.91 ha/AU
8, 735, 540 A	318, 982 AU	27.10 A/AU

As can be seen in table 3, the observed grazing coefficient, considering both range land and improved pasture but not forage crops, is 10.91 hectares per animal unit (ha/AU). This has resulted in a generalized over grazing, but is very near the observed state average of 10ha/AU on all range land.

Table 4 presents the population pattern of eastern Sonora. Of 761 centers of population (including ranches) of the area. 732 have no more than 1-100 inhabitants, while the six largest centers of the area only have a population of 1, 000 - 10,000. Actually, only one even nears the 10,000 inhabitants level.

Table 5 presents the four general types of vegetation of the area: forest, tropical forest, grass-land and shrubland. As can be seen, while forests represent 23.49 % of the area, only five municipalities: Bacadéhuachi, Nácori Chico, Arivechi, Alamos and Yécora are reported as producing lumber, a total of 65, 478 m3, with Yécora producing almost half, 31, 330 m3.

CATTLE PRODUCTION

Sonoran ranchers, as well as cattlemen in general, have traditionally confronted economic problems such as inflation and high costs of production by increasing their cow herds in order to improve earning with little or no regard to future environmental problems that they may have to face. This practice has led to wholesale overgrazing and deteriorated range condition. Almost all of the area mentioned has been determined to have a range condition class of regular to poor, which means that actual forage production is one half or less than the potential. Quite possibly

Table 4.—Centers of population of the three mountainous regions of Sonora.

REGION	SMALLEST CENTERS OF POPULATION NUMBER - POPULATION	LARGEST CENTERS OF POPULATION NUMBER - POPULATION
NORTHERN	105 CENTERS OF POPULATION 81 (1-100)	4 (1, 000 - 2, 000)
CENTRAL	80 CENTERS OF POPULATION 61 (1 - 100)	1 (2, 500 - 5, 000)
SOUTHERN	676 CENTERS OF POPULATION 590 (1 - 100)	1 (5, 000 - 10, 000)
TOTALS	761 CENTERS OF POPULATION 732 (1 - 100)	6 (5, 000 - 10, 000)

Table 5.—Land area and percentages of vegetation types of the three regions of easthern Sonora.

VEGETATION TYPE	TOTAL AREA (ha)	TOTAL AREA (A)	PERCENTAGE (%)
	NORTHERN REGION		
FOREST	338, 000	834, 860	26.55
GRASSLAND	562, 000	1, 388, 140	44.15
SHRUBLAND	373, 000	921, 310	29.30
	CENTRAL REGION		
FOREST	345, 124	852, 456	47.52
TROPICAL FOREST	6, 952	17, 171	0.95
GRASSLAND	9, 996	24, 690	1.37
SHRUBLAND	367, 328	907, 300	50.36
	SOUTHERN REGION		
FOREST	198, 010	489, 085	11.21
TROPICAL FOREST	968, 553	2, 392, 326	54.83
GRASSLAND	178, 865	441, 796	10.13
SHRUBLAND	420, 985	1, 039, 833	23.83
	TOTALS		
FOREST	881, 134	2, 185, 401	23.49
TROPICAL FOREST	975, 505	2, 409, 497	26.50
GRASSLAND	750, 861	1, 854, 626	20.02
SHRUBLAND	1, 125, 313	2, 868, 443	30.00

overgrazing has been a factor in the increase of shrubland at the expense of reduced grassland and forest. The impact of overgrazing is noticeable, not only in vegetational changes, but also in changes of soils, wildlife, and hydrology.

Soils are eroding, wildlife habitat is being destroyed and created, and domestic cattle and wildlife compete for browse on all but the most inaccessible sites. Dams are short-lived because of silting, while underground water is not reaching aquifers in the coastal plains west of the mountains where it is used for irrigated agriculture, an expanding industry, and a booming population at a much faster rate than it is being recharged.

The mountainous area of Sonora has a total of 57,283 hectares (141,489A) of seeded dry land pasture,of which almost all is buffelgrass, found at lower elevations in the shrublands where freezes are few and rainfall is adequate. An exception is the southern region where tropical forest has been cleared for pasture establishment.

In the recent past improved pastures were almost completely cleared of woody vegetation, except for a few shade trees and known browse species. Now, a new forestry law prohibits this kind of clearing and ranchers who wish to establish pastures must pay for trained and certified technicians to conduct an impact study which is evaluated by a committee on range improvement before permission is granted. Any previous pastures are also evaluated and no permission is given until overgrazed, poorly managed pastures are rehabilitated. The law also states that no more tropical forest is to be cleared for pasture establishment.

Some of the guidelines to determine the adaptability of a site for pasture development are: no sites are to be cleared completely, a minimum of 15% of the existing woody vegetation must be left untouched; no sites with less than 250 mm (10") mean yearly precipitation, nor with more than 15% slope, nor with clay soils can be planted to buffelgrass. No sites above 800 m (2,600′) will be planted to bufflelgrass, and 20-30 m (63.3 - 126.6′) must be left uncleared on both side of arroyos as well as wildlife corridors.

Government technicians, both federal as well as state, are trying hard to demonstrate to ranchers that it is unnecessary to establish large areas of pasture, when seeding 15% of the grazing area can increase the carrying capacity of the range 35 - 45% in areas less productive and up to 85% in areas of maximum productivity. They are also trying to teach ranchers the economic advantages of multiple use including big and small game production and the rational use of other natural resources such as medicinal, industrial, and ornamental plants. The "Centro de Investigación y Desarrollo de los Recursos Naturales de Sonora", (CIDESON) a state research center, has just received two grants to study the production of bacanora and the cultivation of Agave pacifica.

In conclusion, Sonoran ranchers have a legitimate right to graze their cattle on the mountains and in the mountain vallys of eastern Sonora, but some way must be found to communicate to them the importance of maintaining a sustainible level of animal production, the concepts of multiple use (call it ecosystem management if you will) and the conservation of what is left of this unique area.

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Biodiversity Versus Mining — A Collision of Priorities in Cave Creek Canyon

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Abstract.–Under present federal laws, mining is considered a priority use of federal lands, unless areas are specifically withdrawn from mineral entry by administrative action of federal agencies or by formal Congressional withdrawal. This preemptive dominance of mining over traditional multiple uses, such as wildlife, recreation, timbering, and grazing, has led in recent years to widespread calls for reform of federal laws to allow federal agencies more discretion in managing the lands under their control.

In late 1990, a proposal to conduct exploratory mining activities on Forest Service lands at the mouth of Cave Creek Canyon in the Chiricahuas raised a storm of protest from local citizens, biologists, and wildlife enthusiasts from across the country. This proposal, covering a square mile of lands that might have become subject to open-pit pulverization and cyanide leaching for gold extraction, raised issues of conflict with other long-standing uses and values of the lands involved. In particular, Cave Creek Canyon is world renowned for its exceptional biodiversity and for the Southwestern Research Station of the American Museum, which has served as a focus for numerous terrestrial biological studies. Large-scale mining activities in the canyon could be expected to have diverse negative impacts on such values, as well as on many other values.

Fortunately, massive citizen persuasion was successful in convincing Newmont Mining Corporation to voluntarily abandon its mining proposal for the canyon, and Congressman Jim Kolbe was then successful in gaining passage of the Cave Creek Protection Act in 1993, which withdrew all federal lands in the Cave Creek drainage from mining. However, the larger issue of exactly how the lands within the Cave Creek drainage will be managed by the Forest Service in the future still remains unresolved.

INTRODUCTION

Cave Creek Canyon of the Chiricahua Mountains has long been renowned as the site of an impressive amount of research in terrestrial biology. Much of this research has been conducted out of the Southwestern Research Station of the American Museum of Natural History, which is situated in the upper basin of the canyon and has been in operation since 1955. A substantial number of our nation's most prominent organismal biologists have conducted studies in the canyon, and well over 1,000 scientific papers have been published on various aspects of the natural history and ecology of the area.

Some of the studies conducted in the canyon, such as a 25-year-long investigation of Mexican jays (*Aphelocoma ultramarina*) by Jerram and Esther Brown, have been long-term research programs that have yielded especially significant dividends in scientific advancement. Cave Creek Canyon has in fact become one of the most intensively studied terrestrial locations anywhere in the world, and has been the scene of a number of important breakthroughs in man's understanding

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of nature. It would be difficult to name another location in the United States that has had more importance as a field research and training center for the terrestrial biological sciences. This record argues strongly for a continued emphasis on scientific endeavors in the canyon. The maintenance of this valuable scientific role depends critically on preservation of the ecological integrity of the canyon.

In addition to having important values for science, Cave Creek Canyon has been a favored destination for avocational nature enthusiasts, such as bird watchers, reptile aficionados, and insect collectors. Further, the hiking trails and scenic formations of the canyon have attracted a loyal clientele of visitors who value dispersed low-impact recreational activities and an opportunity for solitude in an undeveloped setting. One of the most notable features of the canyon is Crystal Cave, located a mile upstream from the research station. This giant labyrinth of exquisite limestone formations was once proposed as a national monument in itself, and has been explored by a stream of caving enthusiasts, not to mention bats, for many decades.

Many of the scientific and avocational values of Cave Creek Canyon depend directly on the outstanding roster of living creatures that can be found here. We have already heard an impressive amount of documentation at this conference of the extremely high biodiversity to be found in the Sky Islands of SE Arizona (see also Barton and Sloane 1992). Cave Creek Canyon is blessed with an especially impressive representation of this biodiversity, owing in large measure to its extensive and well-watered riparian zone.

Most of the upper elevations of Cave Creek Canyon (above 1,500 m) lie within the jurisdiction of the U.S. Forest Service, as part of the Coronado National Forest. The Forest Service has traditionally administered these lands in accordance with its legislative mandate for multiple-use, allowing a wide variety of activities, ranging from hunting and fishing to hiking, camping, caving, and cattle grazing. These activities have proved relatively compatible with one another, and most users of the canyon, including ranchers, recreationists, and scientists, have been content with the mix of uses (Shaw et al. 1979), although there is little doubt that some practices in the Chiricahuas have led to slow vegetational and faunal changes over the years (see Swetnam et al. 1992).

However, in mid-1990 an issue arose which led to a major confrontation between established and potential users of the canyon — the prospect of major mining development near the entrance of the canyon. In the ensuing debates, users of Cave Creek Canyon, both on a national and international scale, became aware that the canyon they believed to be safe from major changes under existing Forest Service management was actually highly vulnerable to modification.

GOLD EXPLORATION PLANS OF NEWMONT MINING CORPORATION

In June of 1990 Newmont Mining Corporation filed claims on approximately a square mile of U.S. Forest Service lands not far to the southeast of Portal and requested a permit from the Forest Service to initiate exploratory drilling for gold. These actions were in full accord with provisions of the 1872 Mining Law, which allows mining activities on federal lands that have not been specifically "withdrawn" from mineral entry.

Earlier, Newmont prospectors had taken samples of surface rocks on the site and had found enough gold to justify these steps. As the largest gold-mining concern operating in the states, Newmont usually conducts mining operations with modern large-scale open-pit technology, including cyanide leaching of piles of pulverized rock material. The cyanide leaching process is highly efficient and allows profitable mining of rock containing only minute amounts of gold, but it leaves an aftermath of spectacularly large open craters and mountains of leached residue.

Residents of the area and personnel at the Southwestern Research Station became aware of Newmont's intentions in September of 1990, when the Forest Service convened a public meeting at the Portal Ranger Station to describe agency procedures in processing the permit request and to describe Newmont's drilling plans. Those who attended the meeting were surprised to learn that mining is not one of the "multiple uses" that the Forest Service can either grant or refuse, but under terms of federal law is instead a priority use that preempts all other uses. The stated position of the Forest Service was that there was no way it could deny the permit for exploratory drilling, and if the drilling proved the existence of a substantial ore body, there would be no way to prevent full-scale mining development. Attendees at the meeting also learned that the Forest Service did not plan any comprehensive review of the effects of the whole concept of large-scale mineral development in the Portal area through preparation of an environmental impact statement on the permit request. At best, the Forest Service could and would insist on some environmental controls on how the drilling would proceed.

The reaction of residents and expatriate users of the canyon was overwhelmingly one of disbelief that the Forest Service could do nothing to prevent potential large-scale mining development of the mouth of the canyon, and dismay that such mining development might have a great variety of negative effects on the region and its inhabitants, ranging from dust pollution and the potential for cyanide contamination of ground water supplies to direct and indirect effects on the superlative biodiversity of the canyon and major unwanted social effects on the local community.

DEVELOPMENT OF A RESPONSE TO THE MINING THREAT

The threats to Cave Creek Canyon represented by large-scale mining were apparent to nearly all observers and led rapidly to the formation of a grassroots organization called the Portal Mining Action Coalition (PMAC). This organization was comprised of a broad cross-section of interest groups, both within the local community and from across the nation. The immediate goals of PMAC were to gain reliable information on mining law and to establish contacts with other organizations that could supply expertise on mining/conservation issues. These efforts were followed quickly by development of an education and action program that included the preparation of an administrative appeal of the Forest Service's decision to allow exploratory drilling by Newmont.

Ultimately, PMAC, together with other parties, especially personnel of the Southwestern Research Station, was successful in (1) persuading Newmont Mining Corporation to abandon mining plans for the area, and (2) persuading Congress to withdraw all federal lands in the Cave Creek drainage system from mineral entry. However, the process was frustrating and complex, and is worth reviewing for the insights that can be gained into the behavior of government agencies. Despite the original stated position of the Forest Service and the imperatives of the 1872 Mining Law, there was indeed a great deal that could be done to prevent mining development of the canyon. Success in these efforts, however, demanded a tremendous investment of time, money, and effort from a concerned public.

DISCUSSIONS WITH NEWMONT

Surprisingly, the least problematic aspect of the process was persuading Newmont Mining Corporation that its own interests would best be served by recognizing the unique values of Cave Creek Canyon and voluntarily refraining from developing its claims. This was accomplished early in the dispute both by meeting with representatives of the corporation and by encouraging private citizens, especially scientists familiar with the canyon, to write to Newmont, the Forest Service, and elected governmental representatives to express their concerns. The deluge of letters that resulted indicated that a great many people across the country and internationally cared very deeply about protecting Cave Creek Canyon.

In addition, a highly successful effort was made to publicize the threats of mining development in the canyon through the Arizona and national media, culminating in articles in the New York Times (December 4, 1990) and Science magazine (December 14, 1990).

Newmont's response to this approach was both cautious and fair. The corporation sent its own team of experts to Cave Creek Canyon to make an independent assessment of the values involved. Then on December 21, 1990 Newmont announced that based on this assessment and the many letters of concern it had received, it agreed that the area was indeed worthy of protection from mining development. Newmont indicated that it would support legal withdrawal of the lands from mineral entry, would retain its claims until that was accomplished to prevent other parties from staking the area, and would then voluntarily forfeit its claims without demanding compensation from the federal government.

PURSUIT OF WITHDRAWAL

The pullback of Newmont relieved the Forest Service of any need to respond to PMAC's appeal of its permit to Newmont, and the door was wide open for legal withdrawal of federal lands within Cave Creek Canyon, either by an administrative withdrawal through the Forest Service or by act of Congress. The PMAC and its allies favored simultaneous pursuit of both alternatives in hopes that at least one might succeed. However, Congressional withdrawal was clearly preferable because it offered permanent protection, whereas administrative withdrawal would always be vulnerable to administrative reopening.

Initially, the Forest Service was receptive to having PMAC prepare an administrative withdrawal request, and the coalition invested considerable time and resources in preparing a detailed proposal. However, by the time this task was completed in the spring of 1991, the Forest Service had jumped to an entirely new track: now it was suggesting withdrawal of a considerably larger region, but still including Cave Creek Canyon, as part of a National Recreation Area (NRA) proposal for the Chiricahua, Graham, and Catalina Mountains. The NRA proposal followed President Bush's announcement of his "Great Outdoors Initiative," with some $600 million earmarked for recreation expenditures within the Forest Service.

Recognizing that a National Recreation Area designation might represent a misreading of the primary values of many of the lands involved, and recognizing that such a proposal would be met by broad public resistance, PMAC urged the Forest Service to consider its Cave Creek Canyon withdrawal proposal separately and was assured that it would be. Nevertheless, shortly thereafter the Forest Service tabled PMAC's withdrawal proposal and indicated that it would oppose any withdrawal proposal for Cave Creek Canyon separate from its NRA proposal.

By late summer of 1991, the Forest Service had proceeded ahead with "segregation" (temporary withdrawal) of the lands involved, but this protection would automatically lapse in two years if the National Recreation Area proposal was not passed by Congress. Despite the fact that the proposed NRA would have provided an apparent solution to the mining threat to Cave Creek Canyon, the PMAC, along with other regional organizations, declined to endorse it. By the spring of 1992, the NRA proposal was abandoned for lack of public and Congressional support. Along with it died any realistic hope for permanent withdrawal of Cave Creek Canyon through Forest Service initiatives.

Meanwhile, efforts to pursue the Congressional withdrawal route proved much more encouraging. Congressman Jim Kolbe introduced a bill for Congressional withdrawal of the entire Cave Creek drainage in the spring of 1991. This bill soon attracted support from the rest of the Arizona delegation and from the Arizona State Legislature, but not from the Forest Service. The opposition of the Forest Service to Congressional withdrawal lay in a stance that withdrawals should be a prerogative of the Forest Service rather than Congress. This posture was baffling to many members of the coalition and was likewise mystifying to Congress, since many withdrawals go through the Congressional route and since the Forest Service had just recognized the intrinsic values of withdrawing these very lands by its own administrative segregation action, which would have led ultimately to Congressional withdrawal anyway if the NRA proposal had proved viable.

Despite the opposition of the Forest Service, Congressman Kolbe's bill passed the House without difficulty and was sent on to the Senate in the fall of 1991. Here the bill ran into some complications in that the Senate committee insisted on some minor changes in wording that meant the bill would have to go back to the House for reapproval following action in the Senate. By the time of the Senate hearings on the bill in the spring of 1992, the Forest Service finally dropped its opposition to the bill, although it still refused to support the bill.

Unfortunately, the Cave Creek Protection Act got trapped in a logjam of other legislation that was part of the torturous politics and procedures of the Senate, and it passed only on the last day of the Senate's session in 1992. Sadly, the House had adjourned a day earlier, so there was no way for the different House and Senate versions to be harmonized, and thus the bill died in 1992.

True to his commitment to protect the canyon, Congressman Kolbe reintroduced his bill in the next session of Congress. This time the bill sped quickly through both houses of Congress, at last with support from the Forest Service, and was signed into law by President Clinton on August 2, 1993.

DISCUSSION

The successful efforts to protect Cave Creek Canyon from mining degradation took nearly three years and an investment of about $20,000 of privately raised monies, not to count the many thousands of hours of donated time and effort from concerned citizens across the country. This was a relatively clear issue, and its proper resolution had strong bipartisan political support and almost unanimous public support, including that of Newmont Mining Corporation, and ultimately the Forest Service.

Nevertheless, many participants felt that his battle should never have been necessary in the first place. In particular, many people expressed bewilderment and anger that this country still tolerates antiquated mineral laws dating from 1872 that automatically elevate mineral exploitation of federal lands above all other uses, regardless of the values being sacrificed. Unfortunately, repeated attempts to reform this law have so far failed in Congress, perhaps as much due to a lack of general public involvement in the issues as to a major and skillful effort of the mining industry to defend its position of privilege.

Even given the limitations of the 1872 Mining Law, some observers questioned whether the Forest Service could not have done more to safeguard the canyon than it did. In fact, some argued that the original application of Newmont to conduct exploratory drilling could have been refused by the Forest Service because Newmont at that time had not technically made a "discovery," which is to say that it had not yet proved the existence of an economically minable deposit. Up until the point of discovery, a mining concern in fact has no legally vested interests in federal lands, and federal agencies can freely initiate withdrawal of lands under their control.

However, the Forest Service has traditionally been loath to take any actions that might give the appearance of ad hoc negative responses to mining proposals. As a result, miners often acquire the equivalent of vested interests just by staking federal lands — long before they can prove a defensible discovery. The Forest Service did not deviate from its normal policy of not challenging mining proposals in the instance of Cave Creek Canyon.

More distressingly, many observers to this day are at a loss to understand the quixotic failure of the Forest Service to support Congressman Kolbe's bill for Congressional withdrawal of the canyon until its passage became inevitable. Clearly on the one hand, the Forest Service had recognized that the lands involved had special values by segregating them for its own NRA proposal. But its refusal to support withdrawal of these lands on any other basis until nearly the end of the controversy — two years after Kolbe's bill was first introduced — suggested a lack of consistency and a reluctance to recognize an overwhelming public concern.

Despite passage of the Cave Creek Canyon Protection Act, the future management of the canyon remains in question. It seems likely that the historic mix of multiple uses that has characterized the canyon over the decades can remain viable only if use levels remain relatively low. At higher intensities, uses could be expected to have a strong tendency to come into conflict with one another and to degrade basic natural resources, necessitating a clear determination of priorities.

Despite the acknowledged fragility of the lands in question, especially the riparian ecosystems, the Forest Service has demonstrated a strong interest in promoting recreation development on these lands in recent years, while various citizen groups have argued that substantial recreational development can be expected to have major negative effects on other traditional uses and values. The reaction in public meetings to the proposed National Recreation Area was extraordinarily negative, not because the public expressed any general desires to curtail recreation on the lands in question, but because of a general recognition that other values of the lands might be more important and a widespread appreciation that the NRA proposal was driven primarily by short-term internal budgetary concerns of the Forest Service.

As yet the Forest Service has not made any clear priority recognition of what many users feel are perhaps the most important values of Cave Creek Canyon — its biodiversity values and research values to the biological sciences. These values have not been a threat to other uses of the canyon in the past, but they will surely suffer if intensive recreational uses of the canyon are not kept to a minimum and managed with care.

Many observers, including ourselves, believe that it would be entirely appropriate for the Forest Service and Congress to recognize the unique biological, scientific, and aesthetic values of Cave Creek Canyon and other important Sky Island regions by a special designation that would ensure the primacy of these values, but which at the same time would recognize other secondary values and uses under careful management. In this time of "Reinventing the Forest Service," a time of general public dissatisfaction with management of public lands, the development of plans for future management of Cave Creek Canyon and other sensitive areas on the Coronado National Forest offers a crucial opportunity for the Forest Service to redefine its commitment to "Caring for the Land and Serving People."

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Comparison of Methods for Assessing Genetic Diversity in Plants: Applications in Conservation Biology

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Abstract.—Information on levels and patterns of genetic variation is important for efforts aimed at the conservation of biodiversity. Genetic variation in plants can be assessed in a variety of ways, ranging from measurement of morphological traits to molecular genetic markers, with each method having advantages and disadvantages. The different methods may not yield concordant results because patterns of variation for molecular genetic markers are generally more strongly influenced by genetic drift and gene flow among populations, and morphological traits often show a greater effect of selection based on environmental factors. Depending on the trait examined, one might come to different conclusions regarding important conservation decisions. Studies using both approaches will provide the best information on which to base these decisions.

WHY GENETICS?

The biodiversity that we see around us in the world is the product of millions of years of evolution. The evolutionary processes that have led us to the present state continue to operate and will create the biodiversity of the future (or the lack of it). In order to effectively manage biodiversity, we must be able to assess its levels and patterns (Frankel 1983). Biodiversity occurs at several levels. Most people think of biodiversity as the number of species (species richness) in an area. This certainly is an important component of variation, but there are other important components as well. A large amount of genetic diversity resides within species, both among and within populations. Ultimately, the processes that shape the genetic variation within species are the same ones that lead to diversity among species.

The levels of genetic variation within species and populations are of interest to conservation biologists because this variation serves as the raw material for evolution and is related to the ability of a population to adapt to environmental changes (Fisher 1930). The patterns of genetic variation within species are of interest because they can help us set conservation priorities. If there are very few differences among populations, then the loss of any one population is less important because we are not losing a genetically unique entity. In contrast, if the populations are highly differentiated, then each one represents a unique genetic resource and we may need to develop a more extensive array of special management zones to conserve these resources. Measuring and interpreting the levels and patterns of genetic variation requires an understanding of the evolutionary forces that shape this variation.

A LITTLE GENETIC TERMINOLOGY

Let us begin with a few brief definitions. A population is a group of freely interbreeding individuals. This is deceptively easy to define on paper and often quite difficult to define in the field because we do not usually have good information on the mating patterns of individuals in nature. A gene is simply a segment of DNA that encodes the information necessary for producing proteins (and in some cases RNA), the building blocks of all organisms. An allele is the particular sequence present at a gene. For example there are

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alleles at a genes in many plants that code for disease resistance or the alternative form, susceptibility.

Most plants are diploid, meaning that they have two copies of each gene, one allele from the maternal parent and the other from the paternal parent. If the alleles it received from the two parents are the same, it is referred to as homozygous for that gene. If they are different, it is heterozygous. Within a heterozygous individual, these alleles may interact in different ways. In some cases, the heterozygote has an appearance intermediate to the two alternate homozygotes. An example would be in some species, where a seedling homozygous for a dysfunctional allele in the chlorophyll biosynthesis pathway will be albino (and die soon after germination), the alternate homozygote will be green, and the heterozygote will be yellow. In other cases, one allele is dominant to the other (the recessive allele). Albinism shows this kind of gene action in other species. The seedling homozygous for the dysfunctional allele will once again be albino, but both the alternate homozygote and the heterozygote will be green. This is because having only one copy of the functional allele is still sufficient to produce a normal seedling.

EVOLUTIONARY FORCES

The first evolutionary force is mutation, a heritable change in DNA. Mutations occur with relatively low frequency, so over short periods of time this force is less important than others. Over the long term, however, mutation is an extremely important force since it creates new alleles and is the ultimate source of all genetic variation.

Selection is the force most familiar to most people. It is simply the differential reproduction of different genotypes. Those genotypes (carrying particular alleles) that are more fit are those that leave more offspring, effectively passing more of their genes to subsequent generations. This permits their genes to increase in frequency in the population at the expense of the genes of others. Selection can act to differentiate or homogenize populations, depending on the nature of the environment to which it is responding. If the environments are different, differentiation will occur. If the environments are similar, homogenization will occur.

Gene flow (migration) is the movement of alleles from one population to another. This can take place in plants by the movement of pollen and seeds between populations. The net effect of this movement is to make the two populations more similar. Gene flow can occur between species by interspecific hybridization followed by backcrossing to one or both of the parent species (introgression).

Genetic drift is a sampling process that is of particular importance in small populations. It can best be illustrated by considering an urn filled with colored balls, half red and half white. If I were to draw 100 balls from the urn at random and obtained 50, 53, or even 60 red balls, you would probably not be very surprised. If on the other hand, I had drawn 0 or 100 red balls, you would be extremely surprised and would strongly suspect that I had not been drawing at random. Now, if I only drew five balls from the urn and obtained zero or five red balls, you might be slightly surprised, but would not consider it an extremely exceptional outcome. In small samples, the random fluctuations associated with sampling have a much larger effect. The process of reproduction in living organisms is much like the example of drawing balls from an urn. Each generation, alleles are drawn from the pool of all alleles to constitute the next generation. If the sample drawn is very small, random sampling may lead to the subsequent generation being very different from its predecessor. In the extreme case, it can lead to the loss of an allele from the population. Because drift is a random process, its outcome is not the same in each population, so it will lead to differentiation among populations.

Another example of genetic drift is the founder effect. If a new population is founded by a small number of founders and, due to random sampling, the few founders are not representative of the population from which they came, then the new population that they found will be different from the original population. These differences will then persist unless altered by evolution.

The mating system is another important force. It does not alter allele frequencies in populations, but recombination during the sexual cycle can generate a large amount of variation by creating new combinations of alleles. For example, considering only ten genes with two alternative alleles at each gene, the number of possible genotypes is 59049. The immense power of recombination is greatly diminished by inbreeding, mating among related individuals. In many normally outcrossing species, inbreeding can lead to a loss of vigor (inbreeding depression) (Hartl and Clark 1989). Normally, most individuals carry a number of deleterious recessive allele, but since the individuals are heterozygous at these genes, the deleterious alleles have no effect. Inbreeding, however, increases the frequency of homozygotes, producing more individuals carrying two copies of a deleterious recessive allele. This can be a particular concern in small populations where the number of unrelated potential mates is small. There are, however, many plant species that reproduce almost exclusively by self-fertilization, the most extreme form of inbreeding, without any apparent loss of vigor. This is likely due to a long history of selection having eliminated most deleterious recessive alleles from the species.

MORPHOLOGICAL VARIATION

When we look at a plant, we see its phenotype (appearance), which is the result of the interaction between its genotype and the environment in which it is growing. The same genotype may produce different phenotypes when grown in different environments (e.g., nutrient -rich vs. nutrient-poor sites). Hence, when we look at two individuals of a species growing in very different environments, it is difficult to say how different they are genetically because this is confounded by the effects of the environment. Likewise, the variation we see among populations is partly due to genetic differences and partly due to differences in the environments in which they are growing, and we do not know the relative contributions of the two factors. This is the big challenge we face in trying to measure the levels and patterns of genetic variation.

The easiest way to attempt to measure levels and patterns of genetic variation is by looking directly at morphological variation in the field. We simply measure one or more traits in the field and analyze the variation. This is relatively inexpensive, rapid, and technically simple, but suffers from the previously discussed confounding effects of environmental variation. There are, however, traits on which the environment has very little effect. An example is flower color in many species. In these species, the flower color of a given genotype will be the same regardless of the environment in which it is grown. In this case, we can measure the levels and patterns of variation for this trait by directly observing it. Unfortunately, the number of morphological traits that are simply inherited with little environmental effect is relatively low.

Many traits of adaptive significance, such as growth rate and reproductive output are, however, affected strongly by the environment. Measuring genetic variation for these traits is much more difficult, since we cannot simply measure the individuals in nature and be confident that we are measuring genetic variation. One option we do have is to plant the different genotypes (either by seed or clonal propagules) at a single environmentally uniform site. Here, all of the genotypes experience a common environment, hence, any differences that we see among the plants can be attributed entirely to genetic effects. Such common garden studies have revealed much about patterns of genetic variation in plants.

An example of a common garden study is the recent work of Rehfeldt (1993) on patterns of genetic variation ponderosa pine (*Pinus ponderosa*) and the related Arizona (*P. arizonica*) and Apache (*P. engelmannii*) pines in Arizona, New Mexico, southern Colorado, and southern Utah. Seeds were collected from ten trees in each of 97 populations spread over this region (95 of ponderosa pine and one each of the other two species). Seedlings were then grown to four years of age in common gardens at three different sites. A variety of traits were measured, including height, diameter, and mortality at different ages, dates of shoot growth initiation and cessation, leaf length and width, and shoot color. Population differentiation was assessed for 28 variables by analysis of variance. Differentiation was significant (p 0.05) for all but one variable, and for ten of the variables, differences among populations accounted for at least 40% of the total variation (72% for one trait). Regression analyses showed significant associations between a number of these traits and environmental variables, such as latitude, longitude, and elevation of the source population. These relationships suggest that selection has had a strong role in molding the patterns of genetic variation in ponderosa pine in this region. Evidence was also found for introgression between ponderosa and Arizona pines in one population.

MOLECULAR GENETIC MARKERS

The past 25 years have seen many developments in the field of molecular biology, and many of these have proven useful to population geneticists, evolutionary biologists, and conservation biologists (Avise 1994; Clegg 1989; Schaal et al. 1991). They have provided us with a means to assess genetic variation at the levels of proteins and DNA. DNA fingerprinting is probably the most widely known of these methods, but there are others.

Isozyme analysis is probably the most widely used of these molecular marker methods (Wendel and Weeden 1989). One simply collects tissue from the plants of interest, grinds the tissue, places the extract into a gel medium (starch, polyacrylamide, or cellulose acetate), and applies an electric current to the gel. The proteins migrate through the gel at different rates, depending on their size and charge. One can then stain the gel for particular proteins and look for differences among individuals in the rates of migration. These differences trace back to differences among individuals in the amino acid sequences of the proteins, which trace back to differences among individuals in the DNA sequences. These differences in protein migration rates are very rarely subject to variation in the environment at the sites where the plants are collected, thus allowing us to directly measure genetic variation without having to resort to a common garden.

More recently, methods have been developed that permit us to directly observe differences among individuals in their DNA sequences, allowing us to observe genetic variation directly at its source (Avise 1994; Clegg 1989; Schaal et al. 1991). Among these methods are analyses of restriction fragment length polymorphisms (RFLPs) and randomly amplified polymorphic DNAs (RAPDs). These methods all involve the extraction of DNA from the plant, treatment of the DNA with enzymes, and separation of DNA fragments by size on a gel medium. Because we are measuring variation directly at the level of the DNA, we need not be concerned with the confounding effects of environmental variation.

Many evolutionary models have been developed that consider data from individual genes (Avise 1994; Hartl and Clark 1989; Weir 1990). Molecular genetic markers and simply inherited morphological traits (e.g., flower color) provide this type of information, whereas data from quantitative traits such as growth rate and reproductive output present a much greater challenge, since we often do not know the number of genes affecting these traits. Hence, we cannot specify the genotype exactly. Simply inherited markers that do not display dominant gene action (e.g., some morphological markers, isozymes, RFLPs) also permit us to estimate levels of inbreeding in natural plant populations. Some morphological markers and RAPDs are dominant, and do not permit us to estimate levels of inbreeding.

The more characters that we measure, the better picture we will obtain of patterns of genetic variation. For molecular markers, this means assaying as many markers as is possible. As previously mentioned, the number of simply inherited morphological traits that are not affected by the environment is relatively low. In contrast, it is quite often possible to assay 10-35 isozyme markers, this number being limited largely by the number of enzymes for which stains are available. For DNA markers such as RFLPs and RAPDs, the numbers of markers are limited essentially only by the amount of time an investigator wishes to spend in the laboratory and the available money. This is the real power of DNA-based markers. This power comes at the cost of the higher price and greater time required to obtain DNA data, although the rapid development of the field of molecular biology will likely eliminate much of this cost and time disadvantage.

Molecular markers generally are not strongly affected by selection. Individual molecular markers can sometimes have strong adaptive significance, such as a mutation that eliminates or greatly reduces the activity of a necessary enzyme, but most of the time there is not a significant difference in adaptive value of the alternate alleles that we observe at a genetic marker. Hence, molecular markers usually do not show strong associations with environmental variables at the source populations. Because they are not strongly affected by selection, they are particularly well suited to assessing levels of gene flow and genetic drift. If population differentiation has occurred primarily due to the effects of drift and/or a lack of gene flow, then we are likely to detect this differentiation using molecular genetic markers. If, however, differentiation has been primarily due to the effects of selection based on environmental differences among locations, then we will likely see relatively little differentiation for molecular markers.

COMPARISONS AMONG METHODS

The different methods vary in the time and money necessary to obtain the data and in the quality of the data. Morphological data from the field can be collected with a minimum of costly equipment and by people with a minimum of technical training, but the number of traits we can assess genetically is limited. Common garden studies also require little equipment and the measurements are not technically complex, but they require space and time to grow the plants until they can be adequately assessed, factors that may be quite significant in long-lived perennials. One also needs seeds or vegetative propagules to conduct common garden studies, something that may be difficult to obtain for some species, since there are many perennial species that only produce seeds infrequently and cannot be easily vegetatively propagated. These studies can, however, provide valuable information on patterns of adaptive genetic variation.

The collection of molecular data requires more expensive equipment and trained technicians and the chemicals involved in some of the processes can be rather expensive. Molecular methods can, however, provide data relatively rapidly, in a day in the case of isozymes. They also do not require the ability to propagate the plants, only the ability to collect tissue. They can provide valuable information on levels of gene flow, genetic drift, and inbreeding. In many cases, however, they do not adequately reveal patterns of adaptive variation.

Because the balance of evolutionary forces acting differs among traits, we should not necessarily expect data from different traits to give us the same picture (Endler 1986). A number of studies have compared levels and patterns of isozyme and morphological variation, with significant associations being found in some cases, but not in others (Hamrick 1989; Price et al. 1984). The differences are more pronounced in outcrossing plants because inbreeding tends to better preserve genetic linkages (associations) among traits, such that the genotype at a particular molecular marker may be associated with the genotype at genes controlling a morphological trait (Brown and Burdon 1987; Hamrick et al. 1991; Price et al. 1984). Let us consider a few examples of comparisons between morphological and isozyme data from outcrossing tree species.

Merkle and Adams (1987) studied isozyme variation in Douglas-fir (*Pseudotsuga menziesii*) from 22 tree breeding zones in southwestern Oregon. The sample spanned distances of approximately 200 km in both north-south and east-west directions. This is an area of rugged mountains, with great differences in temperatures, precipitation, and length of growing season along gradients of elevation, latitude, and distance from the Pacific Ocean. Previous common garden studies have shown very significant genetic differences among populations in this region for seed size and germination rate, seedling growth rate and phenology, and shoot/root ratio (Campbell 1986, 1991; Sorensen 1983). This variation shows significant associations with environmental variables. In striking contrast, less than 1% of the total isozyme variation in the region was due to differences among locations and this small amount of variation among locations did not occur in patterns that were related to environmental factors nor to the distances among locations (Merkle and Adams 1987).

In a rangewide study of 22 white spruce (*Picea glauca*) populations, only 3.8% of the total isozyme variation was due to differences among populations, the vast majority being variation among trees within populations. In contrast, common garden measurements of these same trees revealed that 48% of the genetic variation for height at age nine was due to differences among populations (Furnier et al. 1991). Similarly, in a rangewide study of lodgepole pine (*Pinus contorta*), 6% of the total isozyme variation and 38% of the total variation in a series of morphological traits were due to differences among populations (Wheeler and Guries 1982). Lund et al. (1992) found no significant differences in isozyme allele frequencies among nine populations of trembling aspen (*Populus tremuloides*) covering the range of the species in Minnesota. Over the same range, there are quite significant differences among populations in growth rates (Anderson et al. 1990).

The apparent discrepancies in the patterns of variation for these traits is relatively easily explained. Traits such as seed size, growth rate, dates of budburst in the spring and budset in the autumn, and shoot/root ratio can strongly affect survival and reproductive success. Hence, they are of great adaptive significance and likely to be strongly influenced by selection. In contrast, the isozymes are selectively nearly neutral. Thus the evolutionary forces are likely acting in a differential manner on the different traits. Low levels of interpopulation differentiation for isozymes likely reflect significant levels of gene flow among populations, something that is to be expected in wind-pollinated trees. Despite this significant gene flow, selection is acting to differentiate the populations with respect to traits of great adaptive significance.

The discrepancies in the patterns observed for the two types of traits does not imply that one is better than the other. Both give us useful information. In the previously cited examples, the isozyme data tell us that there are quite significant levels of gene flow among the populations, something that we may not have concluded from the morphological data. The morphological data give us very valuable information on local adaptation, something we would not have detected from the isozyme analyses.

Because they have only recently been applied to studies of population genetics, there are relatively few studies directly comparing estimates of levels of genetic diversity obtained for DNA-based markers and isozymes. Estimates of variation obtained from isozymes were somewhat lower than those from RFLPs for maize (*Zea mays*; Messmer et al. 1991), *Brassica campestris*; McGrath and Quieros 1992), and bigtooth aspen (*Populus grandidentata*; Liu and Furnier 1993), comparable for bean (*Phaseolus vulgaris*; Chase et al. 1991) and trembling aspen (*Populus tremuloides*; Liu and Furnier 1993), and higher for cotton (*Gossypium hirsutum*; Brubaker and Wendel 1993). RAPD markers are a more recent development and there are even fewer comparisons. Liu and Furnier (1993) found relatively similar estimates of genetic variation for isozymes, RFLPs, and RAPDs in trembling aspen, but much higher estimates from RAPDs for bigtooth aspen. This suggests caution in trying to compare data sets obtained from different species using different types of molecular markers.

MANAGEMENT IMPLICATIONS

Many species are of high economic importance, either because they are of economic value themselves, are necessary for the survival of other economically valuable species, or because their conservation would block development of economic importance. In these cases, we may have the resources to conduct genetic analyses, but we will never have the resources to adequately assess the levels and patterns of genetic variation in all plant species throughout their ranges. Thus it is important to synthesize the existing data to see whether we can draw inferences about expected patterns of genetic diversity in unstudied plant species.

Hamrick and his colleagues (Hamrick and Godt 1989; Hamrick et al. 1991) have examined relationships between isozyme variation and a variety of plant life characteristics, including taxonomic status, regional distribution, geographical range, life form, mode of reproduction, breeding system, seed dispersal mechanism, and successional status. Levels and patterns of isozyme variation showed a significant correlation with a number of these characteristics. These relationships give us some ability to make predictions, although we must remain cautious because there was also much unexplained variation.

There is a real danger in formulating management strategies based on incomplete information, although we are often forced to do so. In the previously cited examples from trees, if we had used only the isozyme data, we might have concluded that there was very little interpopulation differentiation, allowing us to conserve the vast majority of genetic variation in the species by sampling only a few populations. The morphological data point out that this would be a great mistake. The use of a combination of methods for assessing levels and patterns of genetic variation remains the best strategy for conservation biologists.

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Obstacles to Achieving Federal Land Management Goals: The Disjunction Between Planning and Funding

A Case Study of the Coronado National Forest, Arizona

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Abstract.—All across the country national forest management plans are not being effectively implemented. The reasons for this are several: (1) Many management plans are not nearly as "rational" as they appear on the surface. For example, different elements of the plan may conflict with each other, crucial information might be missing or inaccurate, assumptions about technology, economics, social acceptability, environmental response, mitigation potentials, etc. may be untenable. (2) Both the plans and subsequent management actions must be responsive to changing policy guidance and annual output targets from higher levels of the federal bureaucracy. (3) Management intentions become actions only insofar as the agency is *enabled* to act through its budgetary and personnel resources, *yet a large, mostly unexamined disjunction exists between national forest planning and Forest Service funding*. This paper will focus especially on the last element, using the Coronado National Forest as a case study. The author argues that managers and forest planners fail to take fiscal realities adequately into account when writing forest plans, thus rendering many management objectives little more than wishful thinking. Furthermore, federal budgetary politics are shown to be erratic, unbalanced, and greatly disconnected from the planning process, thus rendering the good intentions of many forest plans moot.

My academic research has mainly focused on the history of national forest management; specifically the social, political, and economic context within which resource management decisions are made and how those decisions are carried out or not carried out as the case may be. I got interested in this subject over a decade ago while contributing to Sierra Club comments on the Coronado National Forest's (CNF) 1982 and 1985 draft forest plans. I noticed then that the CNF plans often made improbable commitments to resource development or resource rehabilitation that depended for success on a benevolent nature, cooperative resource users, greatly intensified management, and significantly higher budget allocations than historical trends. The plans promised sustained or increased outputs of goods and services, even where resources were already overused. These optimistic promises seemed designed to satisfy pressure groups and federal policies regardless of whether they were in fact implementable. This appeared to be a curiously ineffective form of land management planning. With more than half a decade of Coronado National Forest plan implementation behind us now, and with a five-year monitoring report recently issued by the CNF, it seems appropriate to analyze how well the optimistic promises in the plan have been achieved.

The availability of funding is one key factor—though not the only one—in determining the success of forest plan implementation. Curiously, however, few people analyze its influence. Congress moved to line item rather than lump sum

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budget allocations for the Forest Service shortly after World War Two in order to extend its influence over land management priorities. As budget line items have proliferated over the years, the discretion of land managers has correspondingly declined. (There is currently a movement advocating a return to lump sum allocations in order to increase agency discretion.) Thus, the annual congressional appropriations process wields considerable control over how money is spent on the national forests. For example, the availability of funds in specific budget categories determines much of what the agency can accomplish in road and trail construction and maintenance, campgrounds and facilities maintenance, structural developments on rangelands and riparian areas, allotment management plans, threatened and endangered species status reports, habitat improvements, new personnel for special projects, travel costs and salary time for in-the-field work, etc.

Only a few scholars have been interested in the relationship between planning and funding_perhaps because tracing expenditures is complicated and tedious. There is nothing romantic about sifting through endless reams of budget allocation tables. Historians, in particular, have trouble tracing the relationship between planning and funding over time because budget records are not scheduled for permanent retention at federal archives. (This is something to ponder.) Getting budget data requires more digging than many people have time or patience for. Data on budget requests and expenditures can also be inconsistently recorded. Furthermore, local managers have a limited ability to shift funds from one category to another and can sometimes do so without leaving a paper trail. Thus, budget analysis is difficult and imprecise, but nonetheless relevant.

I am aware of three researchers besides myself who analyze the influence of budget politics on national forest management. V. Alaric Sample of American Forests (Sample 1990), Randal O'Toole of Cascade Holistic Economic Consultants (O'Toole 1992), and Tim Farnham of the University of Michigan, Ann Arbor (Farnham 1994). All four of us approach the subject mainly from a national perspective. Farnham and O'Toole take on the period from the mid-1980s to the present, Sample focused on the early post-NFMA period from 1977-1986, and I, as a historian, filled in the years from 1955-1974 (Hirt 1994). Some very interesting patterns emerge when you compare trends across decades, and these patterns provide a good context within which to interpret the Coronado National Forest in a contemporary setting.

Since at least Word War Two, the Forest Service has never received the total amount nor the appropriate balance of funding needed to implement management plans. Political authorities higher than the agency_including the Department of Agriculture, the Office of Management and Budget, and Congress_have overlaid their own priorities on the Forest Service budget. This has had a deleterious affect on the agency's ability to implement management plans. Making matters even more difficult, the mix of funding for national forest management has historically been skewed toward commodity programs and economic development with resource protection programs largely neglected. While timber sales and road construction received most of the funds needed to achieve timber production targets during the 1950s-1980s, resource protection and rehabilitation programs received only a fraction of identified funding needs so that those accomplishments remained heavily backlogged. The fate of the Forest Service's first nationwide comprehensive land management plan published in 1959 established the pattern and precedent for this imbalance. The agency had attached to its 1959 plan an optimum budget target to be achieved within five years for each resource program. Eisenhower's proposed budget for FY 1961 included 75% of the agency's optimum target funding level for timber sales. In contrast, recreation got only 48% of its target funding level, wildlife habitat management got 18% of its target, and reforestation and stand improvement got a mere 8% of its target. The degree of imbalance in the Forest Service budget declined slowly during the 1960s and 1970s, but never achieved anything close to a true balance even in the judgment of the Forest Service itself. (Hirt 1994: chs. 9-11). As Chief Edward Cliff stated in the 1970s after his retirement:

> *We always, without exception, were trying to get funded on a balanced basis, but were not successful in getting the recognition needed for the non-revenue-producing or low-revenue activities. Even in timber management it was out of balance. We could get money for timber sales, but money for reforestation and stand improvement was way behind, was under the recommended program level. (Cliff 1981: 190)*

During the Reagan administration, finding imbalances actually increased, eliminating many of the gains made in the late 1970s after the passage of the Resources Planning Act and the National Forest Management Act.

Al Sample, a forest economist with American Forests, specifically tested the degree to which management planning and budgeting were coordinated in the RPA plans and traced the effect of the budget on RPA goal accomplishment between 1977 and 1986. Not surprisingly, he found that accomplishments of RPA goals ranged from as low as 21% to as high as 119%, with resource protection at the bottom and commodity production at the top. "If the budget and planning processes are indeed linked, the fact is not apparent from the outcomes," he concluded. Tim Farnham, looking at 1983-1992 found a slow shift toward more funding for noncommodity programs, especially after 1989, but still, "...there was a lack of integration between the management planning and the budget process." Interestingly, based on the budget data Farnham concluded that Congress has recently approved noncommodity program funding at a *higher level* than Forest Service budget requests, hypothesizing that the cart is leading the horse.

There are some limitations that must be kept in mind when looking at national congressional appropriations. First, budgets filter through layers of bureaucracy: the Washington Office, to the regional offices, to the forest supervisors' offices, to the district rangers' offices. Secondly, forest managers have some limited flexibility in their expenditures. Third, national budget data does not tell us everything we want to know about the relationship between plans, expenditures, and program accomplishments. Thus, the Coronado National Forest's 5-year monitoring report on the implementation of its 1986 Forest Plan gives us a grassroots reality check on this problem. The monitoring report was released in 1993 and assesses the years 1987-1991, the first half of the ten-year planning cycle. What did it have to say?

First, the Coronado has made substantial progress in achieving Forest Plan objectives, but it is substantially behind schedule on many activities. In essence, the plan as a whole is not being successfully implemented. The monitoring report identified a lack of coordination between planning and funding as a major obstacle (Coronado NF 1993: 5). In 1987, the first year of Forest Plan implementation, the Coronado received 47% of the annual budget level necessary for full implementation of the plan_in other words, its normal budget was half that needed to implement the plan. Funding levels rose steadily in real dollars after 1989, however, until by FYs 1991-1993 the Coronado got over 70% of what it needed in each of those two years to implement the plan. But this is still a very significant shortfall (fig. 1).

The monitoring report noted that of even greater concern than overall shortfalls were individual program shortfalls and year by year erratic funding. For example, the Coronado had received no recreation site maintenance or development funds for over a decade prior to 1987 leaving the forest a huge backlog of maintenance needs and unmet construction plans. The five-year evaluation acknowledged that the backlog would not be eliminated at the end of ten years as planned, and that new site development would be substantially behind schedule. Why? "National priority setting at the Congressional appropriations level is the single most inhibiting factor preventing the Forest from responding to the backlog needs." (CNF 1993: 50. See also figs. 2-4 at end of paper.)

The situation regarding many other resource management programs was similar:

Trails: The Forest Plan proposed to accomplish 2,000 miles of trial maintenance in the 10-year implementation period. Only 286 miles (about 14%) were accomplished at the half-way mark. The plan also proposed to construct or reconstruct 190 miles of new trail. A little over a quarter had been accomplished at the half-way mark. The budget allocations for trail construction and maintenance figure prominently in this failure to achieve management objectives. In the first half of the implementation period, the CNF received only a little more than a fifth of its total ten year budget needs for trails (CNF 1993: 51-53. See also fig. 5 at end of paper).

Range management: The forest plan proposed to improve range conditions on 31,000 acres through "vegetation manipulation" and developments such as fences and stock tanks. At the mid-point in plan implementation only 3,247 acres (10%) had been improved. The forest plan also proposed to complete field analyses on at least 5% of grazing allotments every year. Here is what the monitoring report said about this:

> *"For a number of years, the Coronado has decided to forgo any detailed range analysis. This is based on the fact that budgets are tight [so on the ground improvement must be sought by more cost-effective means].... Field analysis of 5% of the Forest's allotments has not been accomplished in any of the five years of thereporting period. Available data on condition and trend of the Coronado's ranges is so out of date as to be meaningless.*

Many allotments have not had an analysis to R-3 standards for 20 years or more." (Coronado NF 1993: 141. figs. 6-7).

Wildlife: The CNF planned to accomplish a total of 35,100 acres of wildlife habitat improvement in the ten year implementation period. After five years, only 4,011 acres of improvements had been accomplished_less than 1/8th of the total. The monitoring report blamed the shortfall on a number of factors, including the loss of K-V funds, the higher costs of prescribed fires, and the following: "Another problem has been the lack of adequate funding of the forest's wildlife program." Although funds had increased, the report acknowledged, in 1991 "it was still 42% short of the [needed] average for the next five years which includes backlog and other work necessary for full implementation to meet all of the program objectives" (CNF 1993: 63. See fig. 8).

Many other programs experienced funding substantially below needed levels, including wilderness management, soil and water management, cultural resources management, and general purpose roads and facilities (figs. 9-13).

Another way of looking at this same problem is to compare annual CNF budget requests with actual expenditures (the latter based on appropriations from Congress and allocations from higher levels of the Forest Service). Based on data provided to me from the annual "Coronado National Forest Plan Implementation and Monitoring Spreadsheets" I compiled a second series of graphs for the years 1988-1992 showing this comparison (figs. 14-27). The graphs show that in only rare instances did the Coronado receive the funds they requested for a particular program in a particular year.

This appears to be a problem that can be blamed on Congress since Congress controls the government purse strings. However, to do so would miss an important point. It takes two to tango. The Coronado National Forest contributed to this problem of failed implementation by developing a plan in 1986 that required funding levels *substantially higher than what could be realistically expected.* There were reasons for this: The Forest Service gets no kudos for restricting resource use to achieve environmental protection objectives, but it gains politically and organizationally when it promises to provide goods and services in response to public demands. In the face of competing demands, the agency trod the path of least resistance by promising to supply high levels of all desired goods and services while simultaneously protecting the environment. All this would supposedly be accomplished through more intensive management fed by more congressional appropriations. This is a very common defensive tactic for resource management agencies under pressure_to promise to satisfy all users by expanding the resource pie, and to promise to balance production and preservation by applying more capital, labor, and technology to forest management. I refer to this as a "conspiracy of optimism" (Hirt 1994).

There is another way in which the CNF contributed to the failure to fully implement its own management plan. The forest planners formulate annual budget requests according to flexible considerations of what the next year's "priorities" should be and how much funding they think they can reasonably request. If extra federal money is suddenly available in one program area the forest planners will often increase their budget requests for that activity. If Congress is skimping in another program area, the planners will often reduce their budget requests accordingly. These practices essentially make the forest plans moot, as private negotiations by the planning staff reestablish each year's management priorities. As the CNF monitoring report discreetly acknowledged: "The Forest recognized early that implementation of Forest Plan direction on every acre for every program during the first decade was not likely. This concern was due to monetary and personnel constraints.... As a result, work priorities are identified each year as part of the out-year program and budget development process. Priorities are reviewed again when funds are actually allocated" (CNF 1993: 5). In one sense this is quite an astonishing admission. The *forest plan* is supposed to establish management goals and priorities, but because the plan is so unrealistic the CNF has liberated itself from the plan's constraints and returned to an internal decision making process insulated from public review and negotiation. Essentially, the old pre-NFMA ad hoc decision making process has been reestablished. Once again, this inhibits successful implementation of the publicly negotiated forest plan.

To get better results from the agencies that manage public lands, we need reforms designed to increase the *implementability* of management plans. Such reforms should include requirements to:

(1) Disclose historic budget trends in environmental impact statements.

(2) Constrain proposed actions to realistic budget levels—such as 10 or 20 percent of the past ten year average.

(3) Include contingency plans for shortfalls in funding; i.e., make specific commitments regarding which activities will have priority if projected funding levels are not realized.

(4) Make accomplishments of resource rehabilitation objectives a *prerequisite* to continuing resource development when the two activities are related—i.e., logging & reforestation; range improvement & deferred AUM reductions, etc.

(5) Redouble support for integrated funding to go along with integrated management plans.

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All data for figures 1-13 are derived from the Coronado National Forest's Forest Plan Five Year Review Report, FY 1987 through FY 1991. Dollars shown are "constant 1992 dollars." Data for figures 14-26 are derived from "Coronado National Forest Plan Implementation and Monitoring Spreadsheets," provided by the CNF planning staff. Dollars shown are "constant 1992 dollars."

FIGURE 1
Total Funding for National Forest System Programs
Coronado National Forest

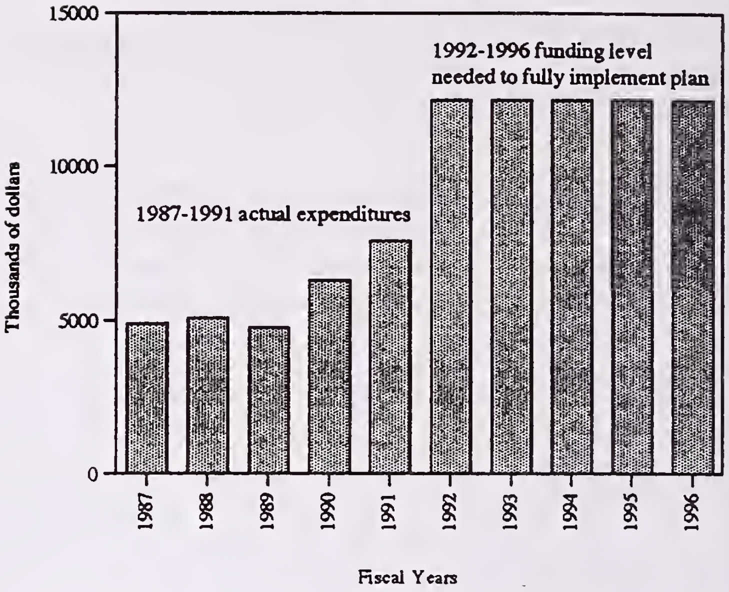


FIGURE 2
Recreation Facilities
Construction/Reconstruction

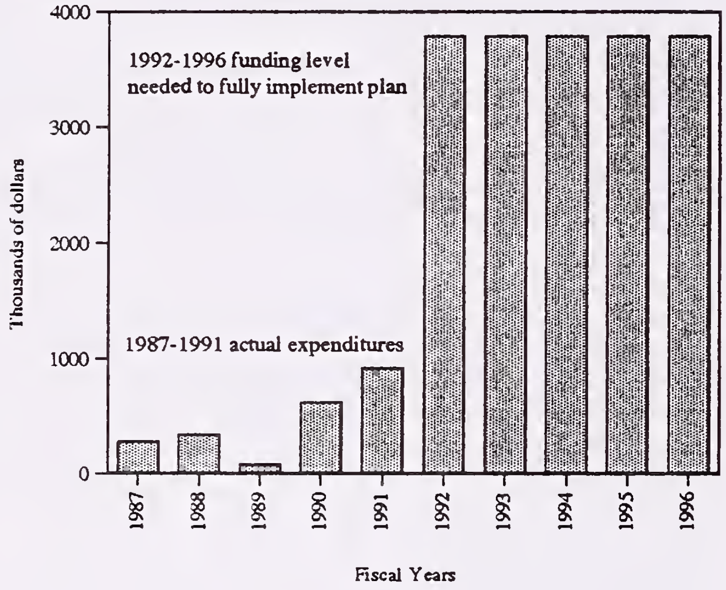


FIGURE 3
Recreation Management

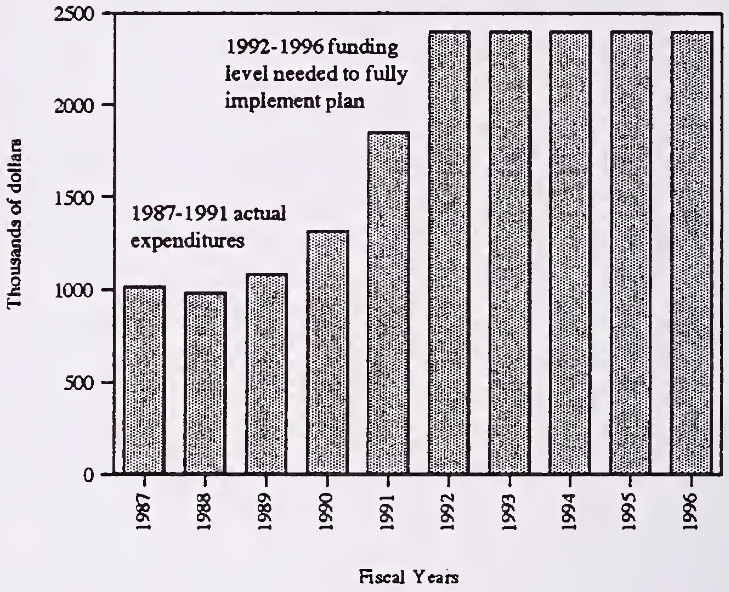


FIGURE 4
Recreation Roads Construction/Support

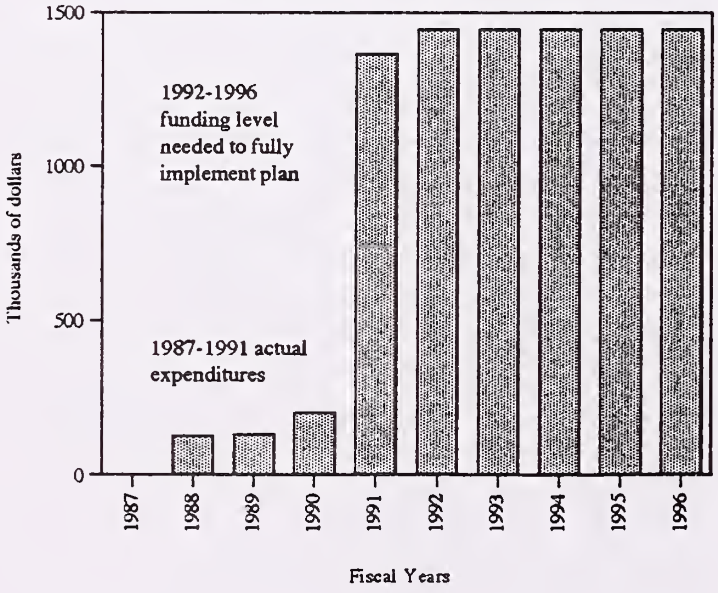


FIGURE 5
Trail Construction and Maintenance

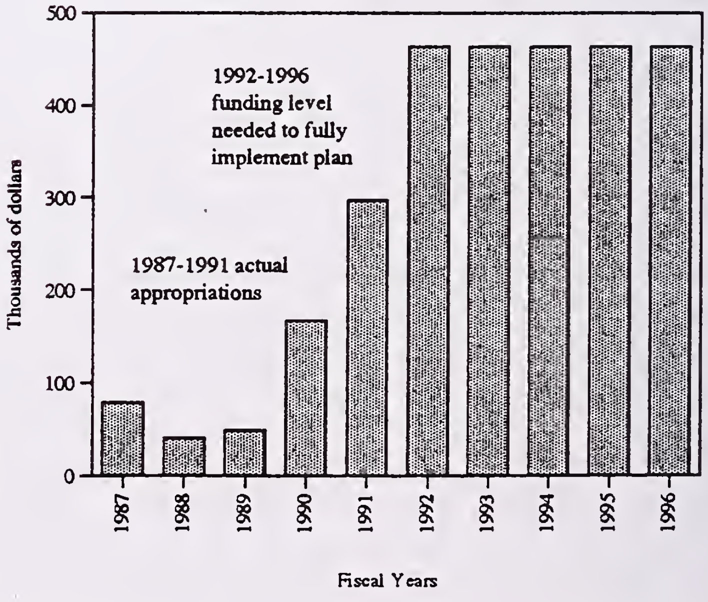


FIGURE 6
Range Vegetation Management

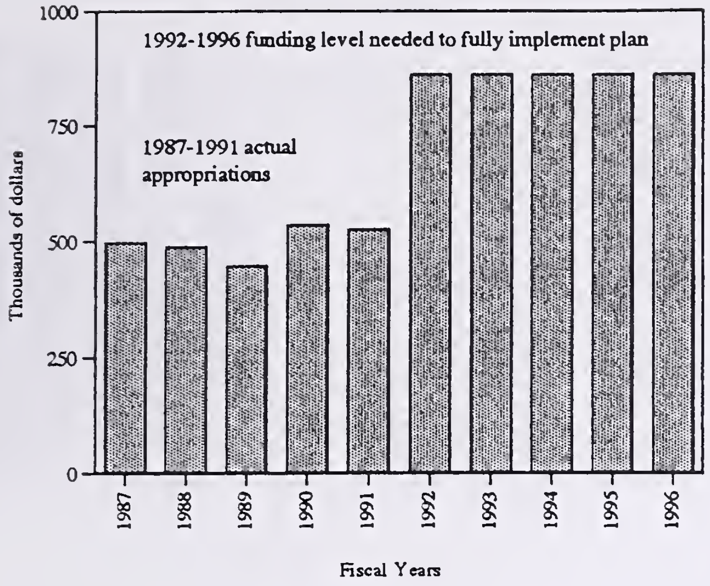


FIGURE 7
Range Developments
(Including Range Betterment Fund)

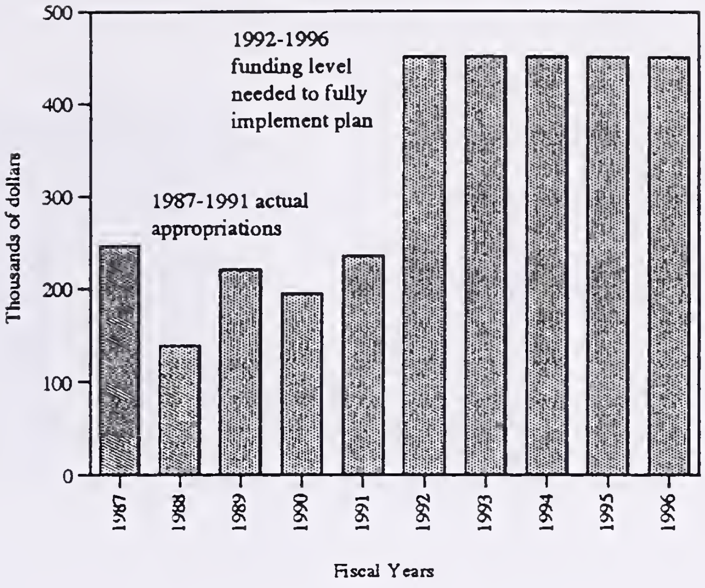


FIGURE 8
Wildlife and Fish Management

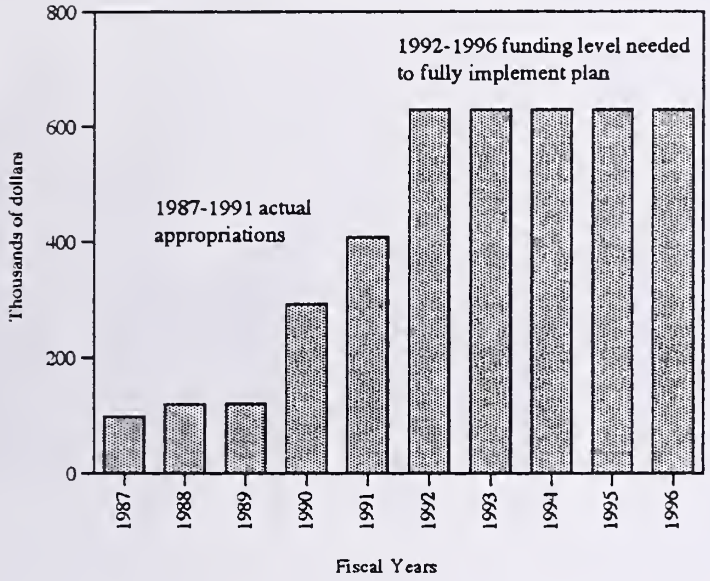


FIGURE 9
Wilderness Management

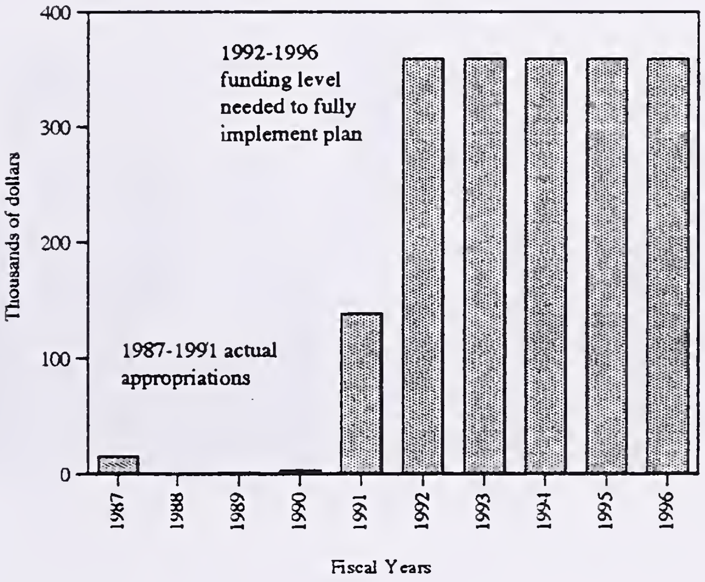


FIGURE 10
Soil, Water, and Air Management

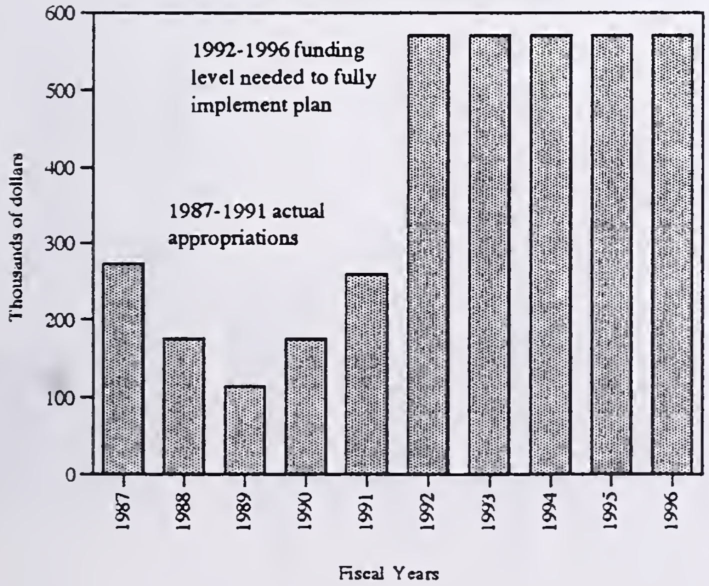


FIGURE 11
Cultural Resources Management

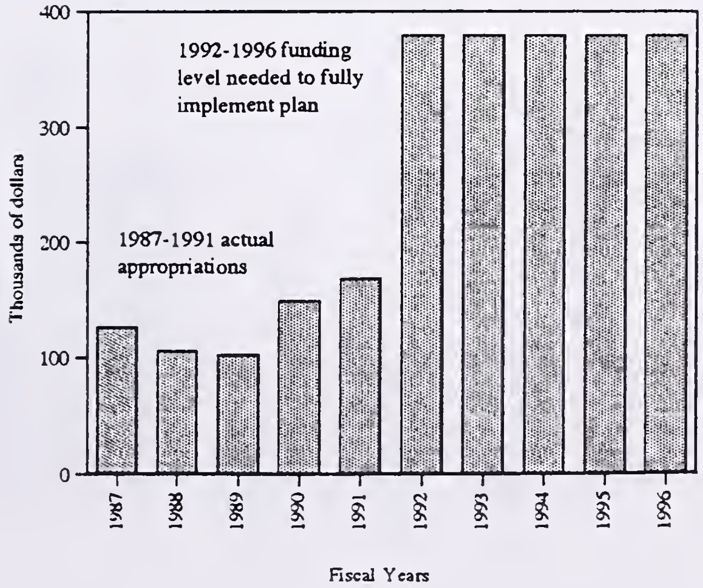


FIGURE 12
Administrative Facilities Construction/Maintenance

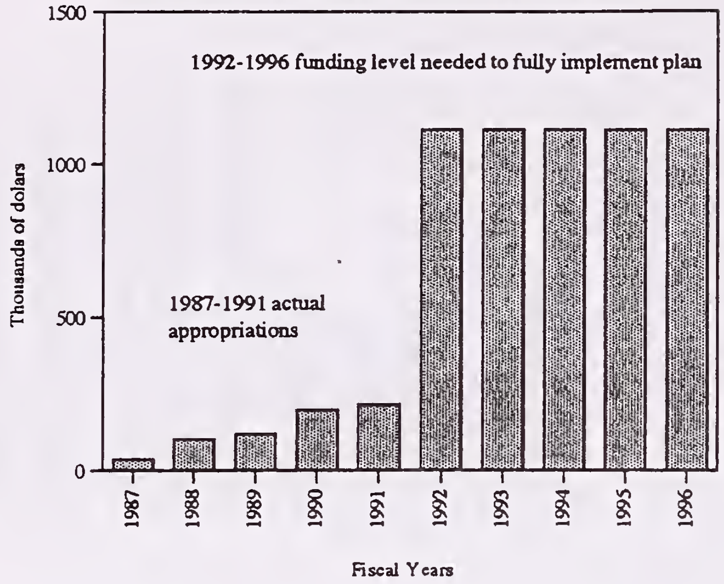


FIGURE 13
General Purpose Roads Construction/Support

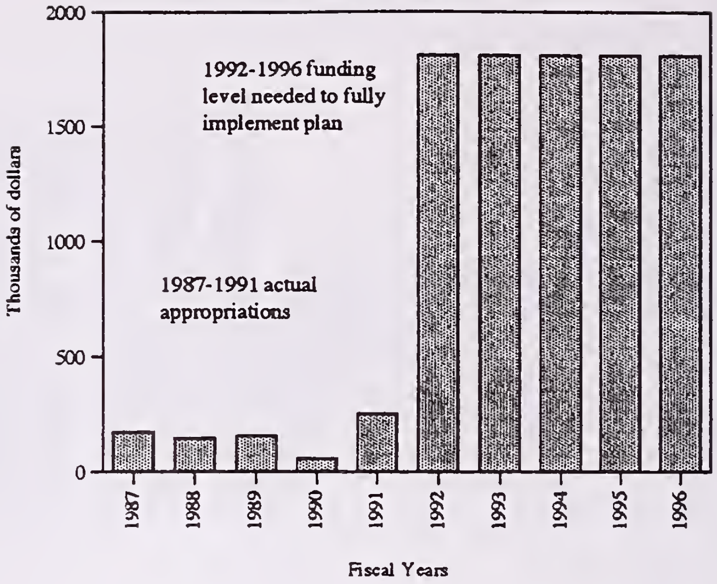


FIGURE 14
Recreation Facilities Construction Budget

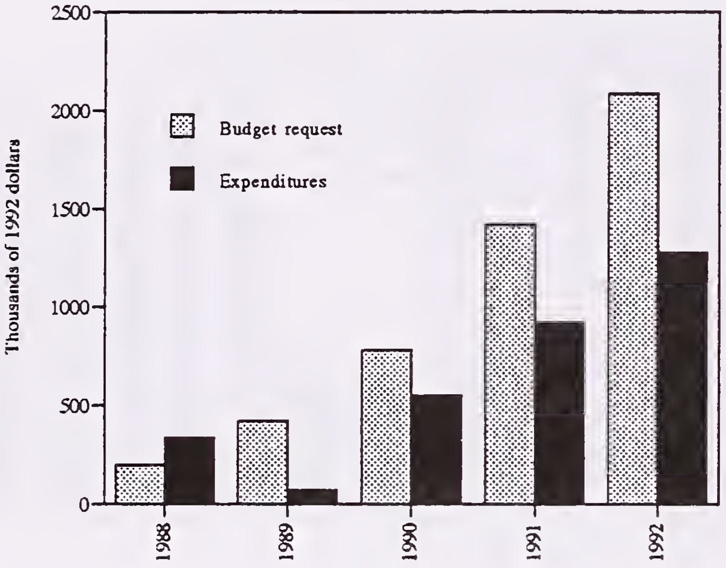


FIGURE 15
Recreation and Wilderness Management Budget

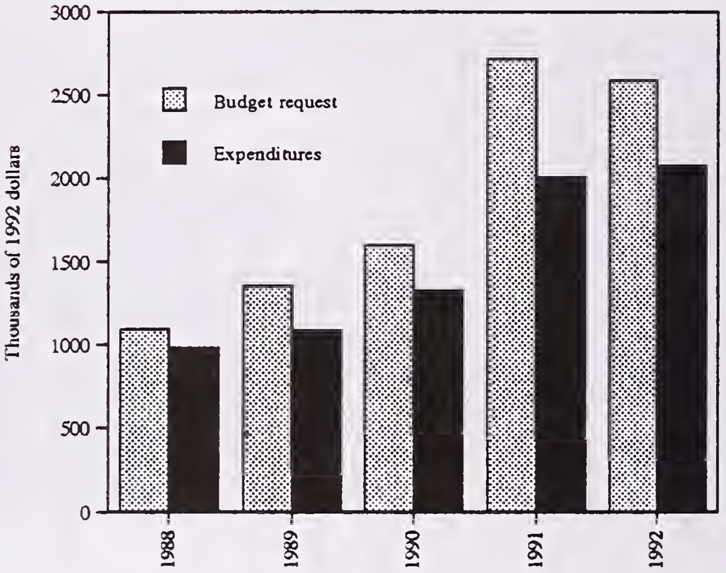


FIGURE 16
Recreation Roads Operation and Development

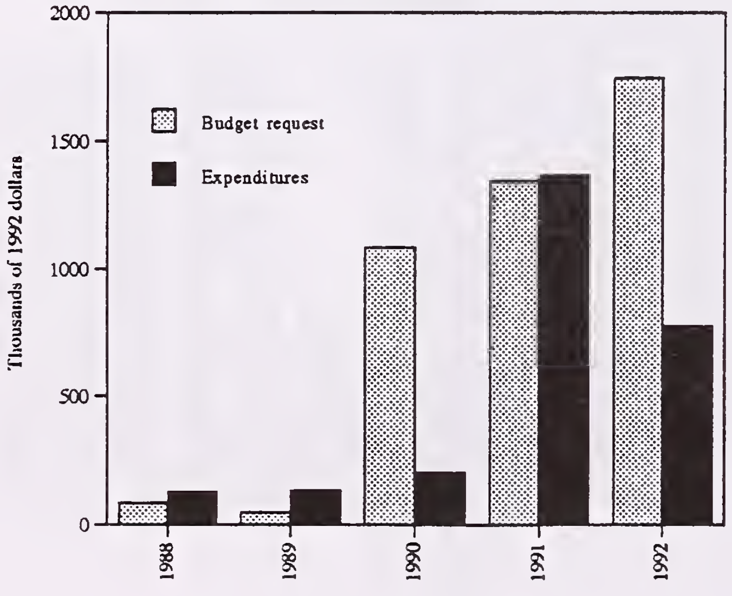
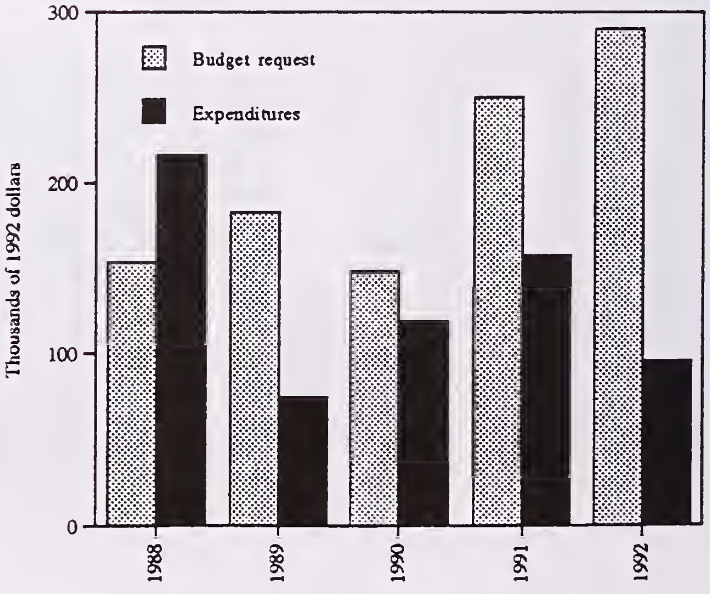


FIGURE 17
Trails Operation and Maintenance Budget



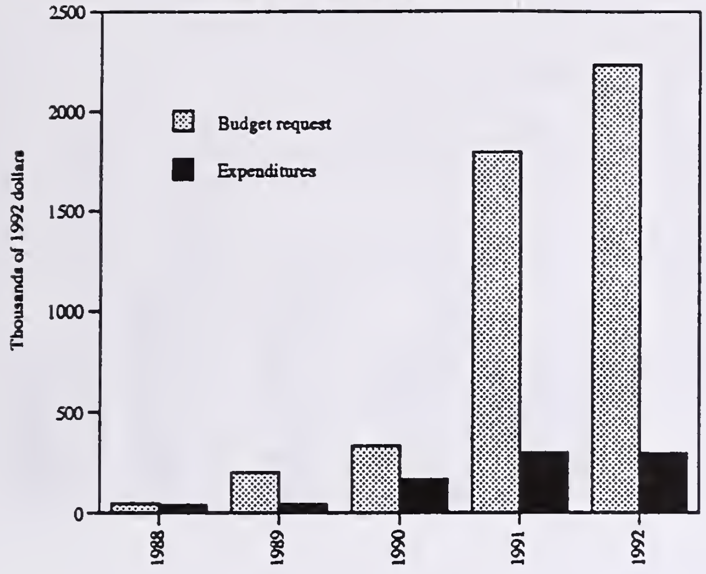


FIGURE 18
Trails Construction Budget

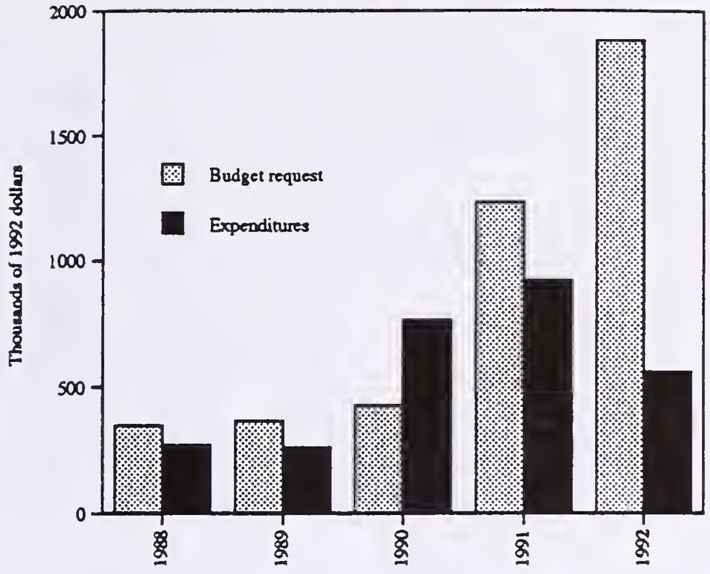


FIGURE 19
Wildlife and Fish Management Budget

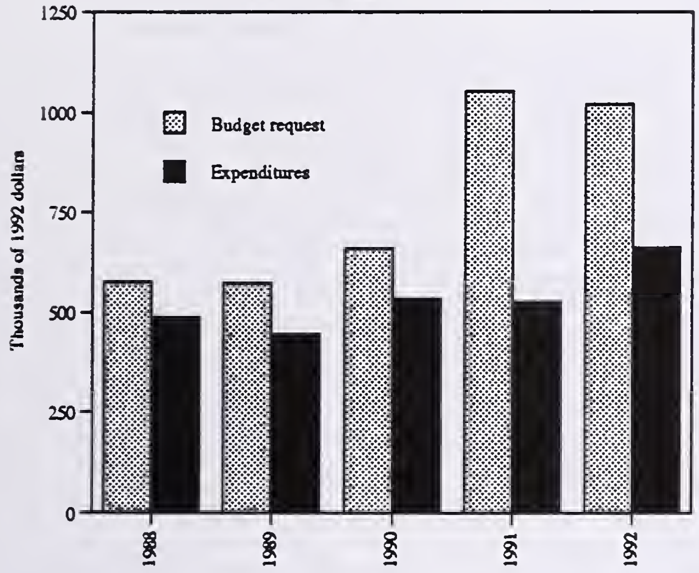


FIGURE 20
Range Management Budget

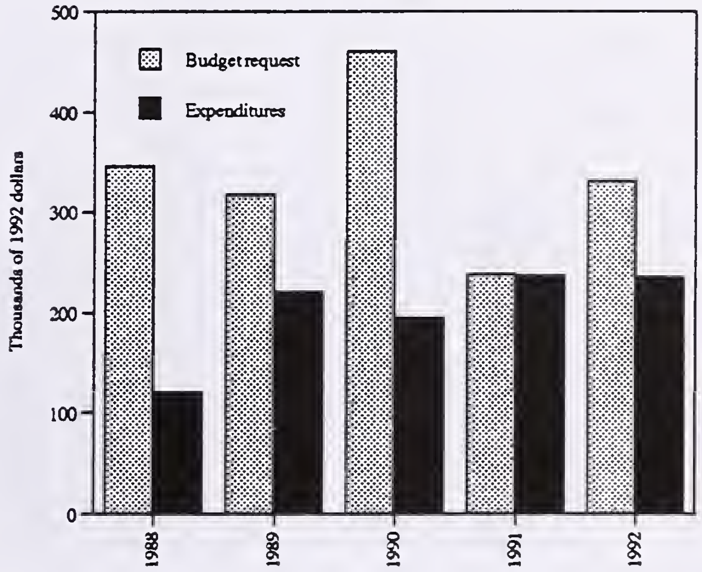


FIGURE 21
Range Betterment Fund

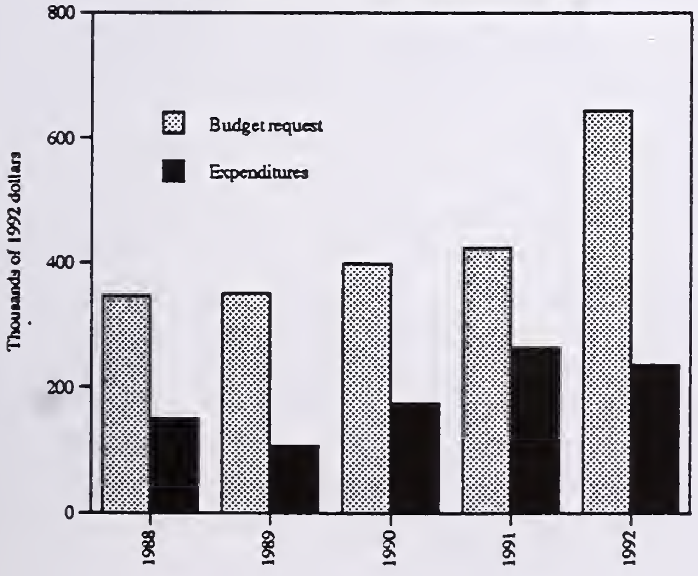


FIGURE 22
Soil, Water, and Air Management Budget

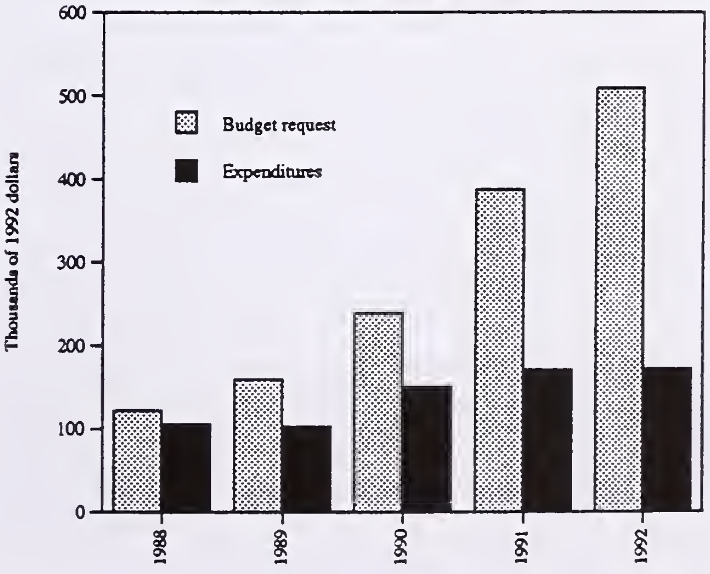


FIGURE 23
Cultural Resources Management Budget

FIGURE 24
General Purpose Roads Operation and Development

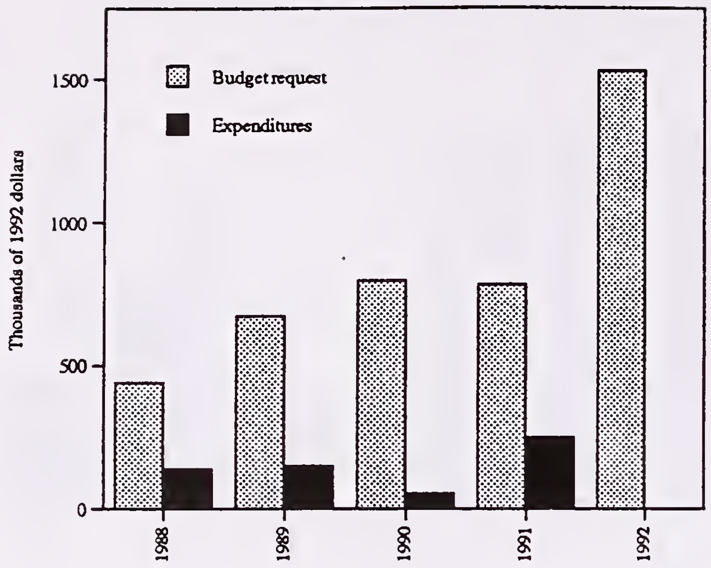


FIGURE 25
Road Maintenance Budget

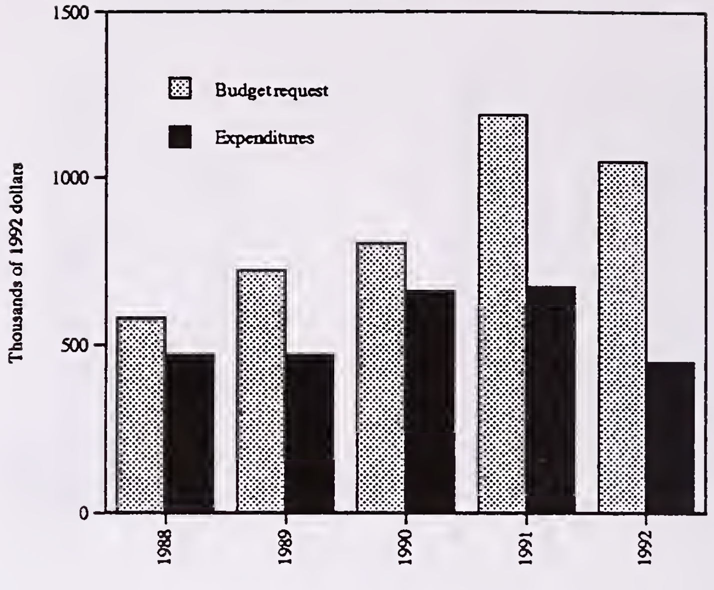


FIGURE 26
Fire Management Budget

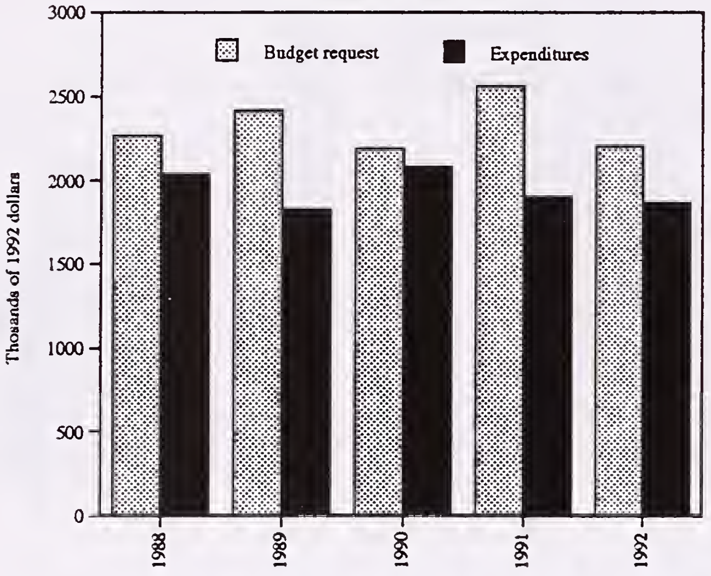
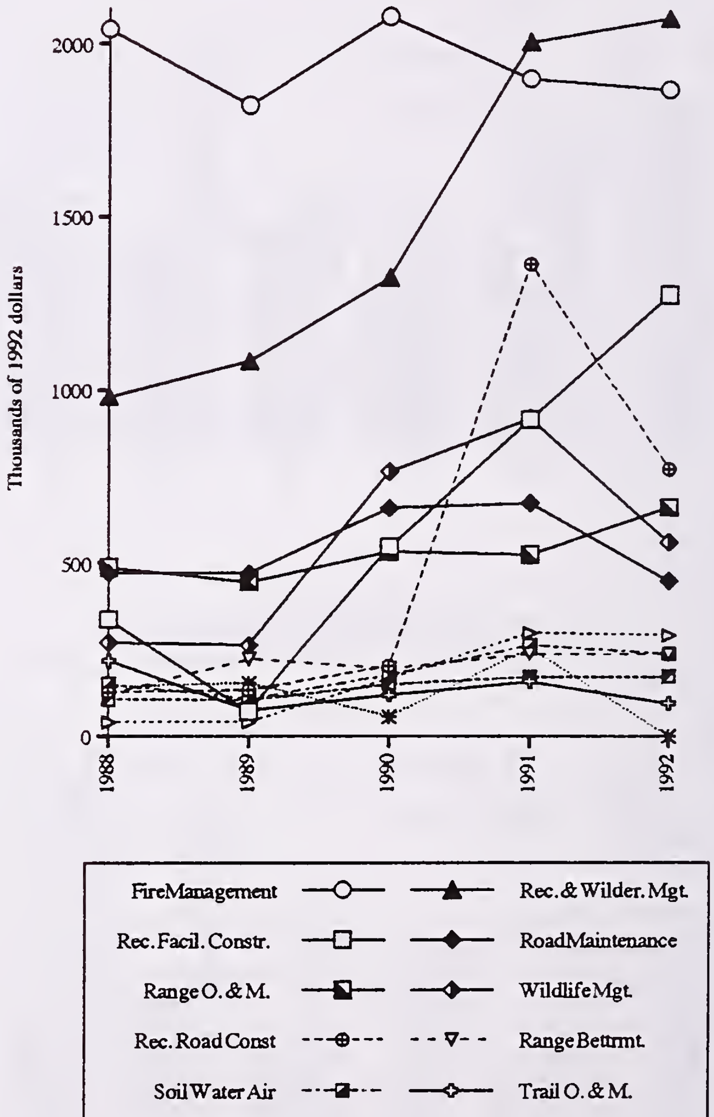


FIGURE 27
Funding for Selected Programs



Management Practices to Benefit Gould's Turkeys in the Peloncillo Mountains, New Mexico

Sanford D. Schemnitz and Mark L. Zornes[1]

Abstract.— Feeding areas should be maintained with a minimum of 50% mast-producing trees. Stocking levels of livestock should be adjusted to allow a maximum of 35% utilization of herbaceous vegetation. Summer brood habitat should include openings that contain herbaceous plants of not less than 30 cm in height after grazing. Ideal herbaceous biomass should be 400-600 kg/ha. Distance to forest or shrub cover types should be d m. Openings created by management should not exceed 150-200 m in width and be irregular in shape. All livestock grazing within key brood habitats should be deferred until September 1. Openings should not make up less than 15% of turkey habitat and be well scattered. Temporary or permanent closure of roads through brood habitat is encouraged. Pruning of closely-spaced limbs on thick crowned trees and clearing of understory vegetation will help increase use of roost sites. Chihuahua pine stands should be protected as present and future roost sites. No new roads should be built through roost sties. Water sites can be improved for poults by providing entrance and exit ramps. Additional watering sites need to be provided in canyon sites where rock header dams can be constructed. Feral hog populations need control. Enforcement of existing rules and regulations should be increased, particularly in regard to illegal fuelwood harvest.

Wild turkeys are specified as a management indicator species on many National Forests in the West since they are sensitive to various land-use practices such as livestock grazing and timber management.

Studies of Gould's turkeys in the Peloncillo Mountains were initiated in 1982 and continued until 1993. The initial population estimate by Potter (1984) was 12 birds. The population has been monitored and has increased to an estimated of 75 by 1993.

Prior studies have focused on food habits (Potter, 1984), roost site characteristics (Willging 1987), nesting biology (Figert 1989) and male mobility and habitat use characteristics (Zornes 1993).

Gould's turkeys in southwestern New Mexico and southeastern Arizona are at the northern extremities of their subspecies range which extends southward into northern and central Mexico (Schemnitz and Zeedyk 1992). In contrast to other subspecies Goul'sd turkeys have received little scientific study. Leopold (1948, 1959), first assessed the bird's status in Mexico.

Gould's turkey are a unique subspecies of wild turkey. They are the largest of the 5 subspecies (fig. 1). They thrive in pine-oak woodlands and use riparian corridors extensively. The riparian habitats contain the majority of the feeding, roosting and brood-rearing sites. We suggest that riparian sites should receive major management emphasis.

Detailed management guidelines have been developed for Merriam's turkeys (Hoffman et. al. 1993). We have attempted to provide similar guidelines based on a more limited research base in this paper.

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MANAGEMENT PRACTICES

Improvement of Roost Trees and Sites

Chihuahua pines (*Pinus leiophylla*), 5 or more in a group, are the primary roost sites. Other trees used occasionally for turkey roosts included Emory oak (*Quercus emoryi*), Arizona sycamore (*Platanus wrightii*) and cottonwood (*Populus fremonti*). Turkeys on our study area preferred open crowned, overmature trees having large horizontal branches. Often younger trees, approximately 50 years old, have a potential to become suitable roost trees as they age and increase in height and diameter. Open crowns are necessary for entrance to the tree. Many of these trees could be improved in quality for roosting by pruning of closely-spaced limbs thus allowing turkey access at other sites. Turkeys often are denied access to suitable large Chihuahua pines by excessive dense understory shrub vegetation. Clearing or thinning of this understory vegetation would promote increased access and roosting use by turkeys. Stands of young Chihuahua pine should be located, thinned and protected to encourage rapid growth to roost tree size (av. 17m tall, av. dbh 58cm). This is especially important where suitable roost sites are lacking in otherwise good habitat. Cottonwood poles could be planted in some areas to provide additional roost sites.

Feeding Site Enhancement

Mast producing trees and shrubs including alligator juniper (*Juniperus deppeana*), oaks (*Quercus* spp.) and manzanita (*Arctostaphylos pungens*) are very important food sources for Gould's turkeys. Other heavily utilized mast producers but less reliable in mast production include pinyon (*Pinus discolor*) and canyon grape (*Vitis arizonica*). We recommend that mast producing stands be maintained with a minimum of 100 trees 20 cm dbh/ha. Feeding areas should be maintained in at least 50% mast producing tree cover.

Water Site Development

Water is a key component of Gould's turkey habitat (fig. 2). Water was often in short supply in May and June when rainfall rates were low. We used time lapse photography (super 8 movie cameras with an intervolometer) to census turkeys that visited a few permanent water sites. Ideally, available water sources should be present at 1.6 kilometer distances or closer. Priority should be given to developing water sources to enhance areas that are otherwise good brood rearing and nesting habitat.

Man-made water holding structures such as metal tanks or cement troughs can be improved by providing access and escape ramps. These improvements are of particular value for young turkey poults that cannot fly up to perches to drink.

Fencing a part of each watering unit from livestock use would allow vegetation to develop for escape cover and promote the growth of aquatic vegetation for turkey food. The building of rock header dams is a low cost and low maintenance procedure for providing water for turkeys and other wildlife as well as a means of establishing and enhancing riparian vegetation. The dams

Figure 1.—A magnificent strutting adult male Gould's turkey during the breeding season, Peloncillo Mountains, Coronado National Forest, New Mexico.

Figure 2.—Adult male Gould's turkey feeding on aquatic plants, Big Lake, Peloncello Mountains, Coronado National Forest, New Mexico.

should be built on an unfractured bedrock base and sides in pairs so that water spills over the upstream dam with the water action removing accumulated sediments in the lower dam. Dams should be 6-7m across or less and 3 rocks wide or 1m at the base and 0.5-0.7m in width at the top. Mortar should be a minimum of 2-3cm between rocks. Dams have been built in 4-6 hours in the Peloncillos with a team of 10-15 Wild Turkey Federation volunteers supervised by a U.S. Forest Service wildlife biologist.

Livestock Grazing Management

Turkey brood habitat was found to be limited in distribution. Clearings and openings should have a minimum of 400-600 kg/ha of herbaceous biomass with an ideal herbaceous biomass of 600-1000 kg/ha and herbaceous plants not less than 30 cm in height after grazing. Within clearings distance to forest or shrub cover should be 100 meters or less. Openings created by management should not exceed 150-200 m in width and preferably be irregular in shape. Openings should make up 15% of turkey habitat and be well dispersed throughout suitable habitat. Such areas usually have abundant insects, an essential part of poult diets (Schemnitz and Zeedyk, 1992).

Stocking levels of livestock should be adjusted to allow a maximum of 35% utilization of herbaceous vegetation. All livestock grazing within regularly utilized brood habitats should be deferred until September 1.

Population Monitoring

Continued extensive surveys are desirable to determine population trends. Several options are available. Monitoring the use of perennial roost sites was suggested as most feasible by Zornes and Schemnitz (1993).

Other Practices

Access Roads

A Forest Service road to provide recreational access was proposed but fortunately was rejected. This unecessary road would have traversed through several heavily used roost sites. Numerous hiking trails exist and several vehicular access roads are present. Gould's turkeys are wary birds and are sensitive to human disturbance. Wherever feasible human activities should be kept to a minimum. Seasonal road closures from June to September through brood habitat are recommended to avoid disturbance.

Fire Management

Prescribed fires in spring are a suggested management tool to thin and invigorate dense, inpenetrable, decadent stands of brushy manzanita and Toumey oaks (*Quercus toumeyi*). Burns should create small openings 3-5 hectares in size (Zornes and Schemnitz, 1993). These openings are an essential component of good turkey habitat and ideally should include 20-25% of the total area well dispersed throughout the habitat. The herbaceous growth in openings harbors more insects, a major summer turkey food, than adjacent forest stands. Robinett (1994) recommended fires at an interval of 8-10 years in nearby southeastern Arizona to keep grasslands vigorous and oak trees at a desirable canopy cover. Use of prescribed burns such as the 4000 hectare ecosystem management project in Baker Canyon is expected to enhance Gould's turkey habitat.

Miscellaneous

Illegal fuelwood harvest especially the cutting of live trees has disturbed and adversely impacted key turkey habitat (Schemnitz et al. 1990). More law enforcement and warning signs are needed to curtail this type of habitat perturbation. Fuelwood harvest should be restricted to dead trees.

Extensive harvest of beargrass (*Nolina microcarpa*) should be discouraged. Dense thickets of beargrass were of particular value as escape cover for turkey broods. Where beargrass harvest is essential, the cutting should be done in late summer (August-September) to minimize nesting and brood disturbance.

Other Management Problems

Competition With Exotics

Feral hogs (*Sus scrofa*) are widespread throughout the Peloncillo Mountains and compete with turkeys and other native wildlife for food. Their rootings in the soil are very noticeable particularly in oak woodland stands and riparian sites. Encouragement of pig hunting on public and private lands is needed. Staunch resistance is essential to the proposal by some Forest Service grazing permittees to include pigs in their grazing allotment.

Miscellaneous Problems

Poaching (illegal hunting) is a threat to Gould's turkeys with several instances documented during our studies. Poaching will be difficult to prevent due to the remoteness of the area.

Eradication of hybrid turkeys is an essential need to minimize genetic pollution. Population levels of hybrid turkeys in Guadalupe Canyon have fluctuated due to limited shooting and predation (Potter et al. 1985). Immediate steps need to be taken with the cooperation of the landowner, New Mexico Department of Game and Fish, and U. S. Forest Service personnel to eradicate these nuisance turkeys.

ACKNOWLEDGEMENTS

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Management and Conservation at the Most Important Sky Island of Baja California Sur

Alfredo Ortega-Rubio[1]

Abstract.— For more than eight years, the Centro de Investigaciones Biológicas authorities and researchers have promoted a formal decree for the protection of the most important Sky Island of Baja California Sur: La Sierra de La Laguna. Although our efforts have had the support of national and international agencies, and universities, such as World Wildlife Fund and the University of Arizona, to date there is no official protection for the zone. To guarantee the protection of the natural resources of the zone and to support the local communities our Research Center has made intensive efforts in the search for specific alternatives for the optimal use of the resources of the zone. The main characteristics of the zone are described in this work, as well as the strategy followed in order to protect its natural resources.

INTRODUCTION

Since 1986 the Centro de Investigaciones Biológicas authorities and researchers, have promoted the formal Decree for the protection of the most important Sky Island of Baja California Sur: La Sierra de La Laguna. For instance, during 1987 WWF convoked to the main Federal Agencies of México Government, to the main NGO'S of México and to the main Mexican Researches (Ramos, 1987) in order to proceed to identify the Mexican Priority Spots for Biodiversity Conservation purposes. After one week of intense work, the priorities sites for the Biodiversity Conservation of all México were identified by consensus (Ramos, 1987).

In the list of places considered as Biodiversity priorities, for all Mexico, it was considered as one of the main priorities the Sierra de La Laguna at Baja California Sur. In many other academic, scientific and politic forums we promote the management and conservation of this region. But also we develop intense studies to adequately advice such activities.

MATERIAL AND METHODS

Study Site

La Sierra de La Laguna is a mountainous complex that runs from north to south at the Cape Region reaching altitudes up to 2,100 m. The vegetation of the zone comprises four main physiognomic-floristic associations (León *et al.*, 1988). The desert scrub, the tropical deciduous forest, the oak-pine forest and the pine forest. The tropical deciduous forest comprises most of the biological diversity of all region (Ortega, 1990) and includes approximately 20,000 hectares (Morelos, 1988).

La Sierra de La Laguna vegetation includes the only forests of all the Baja California Sur State (Arriaga and Ortega, 1988). The Sierra harbors the higher total species number and the higher endemic species number of all the State (Arriaga, *et al.* 1992). Thus, la Sierra de La Laguna represents the more important site for the Biodiversity conservation of all Baja California Sur.

Additionally, La Sierra de la Laguna is the site where Cape Region's underwater re-charge take place (Arriaga and Ortega, 1988). This water is posteriorly extracted by the inhabitants of the region, which includes the bigger cities of all the State. If the forests and soils of La Sierra de la Laguna were disturbed, unpredictable effects will occur in the availability of water. Availability of

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water is, up to the present, the main restrictive factor for the development of the region and State.

Methods

In order to obtain all the necessary information to proceed to justify the Federal Decree as Protected Area and to obtain the necessary information to proceed to determine the alternatives for the rational management of the resources of the zone (Even without Federal Decree), the CIB proceed to integrate a multidisciplinary team to develop the project (Ortega *et al*, 1991).

Project activities were developed by a team composed of climatologists, soil scientist, hydrologists, geologists, botanists, zoologists, ecologists (Ortega *et al*, 1991; 1992; 1993). The multidisciplinary team (MT) accomplished, through this years, 38 stays of works at La Sierra de La Laguna. Each stay of work includes at least five days of field work and there were spent a total of 3200 men/hours of field work at La Sierra de La Laguna.

At the study site our MT gathered all the necessary information to justify the Project Zone Federal Decree and/or the Management Programs for the Sustainable use of the Natural Resources of the Zone.

RESULTS

After these years of work there has been generated all the necessary information, according to the Mexican Legislation, to proceed to formally decree the zone as Biosphere Reserve (Ortega *et al*, 1991; 1992; 1993).

Also, there have been generated all the necessary information to proceed to the sustainable management of the natural resources of the zone (Ortega, 1992).

Additionally, the researches composing the MT have developed 21 papers for Sierra de La Laguna. The topics covered in the CIB scientific production ranging from new species descriptions (Jiménez *et al*, 1989; 1992; Hoffmann and Servín, 1990; Servín et *al.*, 1989) up to specific management plans for the zones (Ortega *et. al*, 1990; 1991; 1992). The information provided in each scientific paper produced, in any case, has been extremely helpful in order to establish the specific programs for the sustainable use of the natural resources of the zone (Ortega *et. al*, 1991; 1992; 1993).

Equally important, CIB with the keystone support of WWF, have developed the necessary executive reports, addressed to the Mexican autorithies in charge of the management of the natural resources of the Sierra de La Laguna (SEDESOL, Government of Baja California Sur) in order to proceed to establish specific measures at the zone (Ortega *et. al*, 1991a; 1991b). Up to the present is our pleasure to inform that it has been obtained the Federal Decree for the establishment of La Sierra de La Laguna Biosphere Reserve (Diario Oficial, 1994).

Thus, the specific recommendations for the sustainable use of the natural resources at this zones searching to promote the biodiversity conservation and the rational use of the renewable resources of the zones, have been developed and approved.

DISCUSSION

After these years of continuous work developed in the Sierra de La Laguna Project, we can observe that the results have been prolific and multiple focused. On one hand, there have been gathered all the required information to proceed to decree as Biosphere reserve, according with the Mexican Legislation, this zone. CIB researches have been spent considerable lobbing-time-efforts in order to promote the necessary political proclivity for these decree. Up to the date we have obtained from the Federal authorities of SEDESOL the corresponding Decree.

On the other hand, CIB have developed the necessary research programs to acquire the required biological and ecological information to proceed to the sustainable management of the main natural resources of the zones. We not only offer specific measures to protect the resources, but also offer the concrete alternatives for the inhabitant of the regions (Ortega, 1992; Ortega and Castellanos, In press).

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Prescribed Burning as a Management Tool For Sky Island Bioregion Wetlands with Reference to the Management of the Endangered Orchid *Spiranthes delitescens*

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Abstract.—Canelo Hills Cienega in southeastern Arizona is a rare middle elevation wetland that is one of only four known habitats for the endangered orchid, *Spiranthes delitescens*. This wetland, a Nature Conservancy preserve, is a rare, remnant, perennially wet, spring-fed marsh in a valley between Sky Island mountain ranges. A potential threat to *S. delitescens* at this site is the accumulation of dried vegetation, which may be inhibiting emergence and sexual reproduction of this species. From 1990 to 1993, we investigated the potential of using prescribed burning as a management tool to remove plant litter at this site. Three burn treatments, varying only in frequency, were randomly applied to nine experimental plots. Height of vegetation and depth of litter, cover of each species, and density of non-graminoid (i.e. other than Cyperaceae, Juncaceae, and Poaceae) species were measured yearly on each plot. Here we report on the results of prescribed burning 15 months following application of the burn treatment.

Accumulated litter was effectively removed by burning but returned to pre-burn levels after one year. Vegetation height was not significantly affected by burning. The treatments also had minor effects on cover and density of plant species. In 1993, there was a dramatic increase in the number of flowering *S. delitescens* in both burn and unburned sites. In 1994, *S. delitescens* increased substantially only on previously burned sites. These results suggest that the effects of prescribed burning on cienega vegetation are subtle, although detectable, and that burning by itself is probably not a satisfactory management technique for *S. delitescens* at this site.

INTRODUCTION

This paper reports the effects of prescribed burning on the Canelo Hills Ladies' Tresses Orchid, *Spiranthes delitescens* Sheviak (Orchidaceae), and the vegetation of its cienega habitat fifteen months following the application of a prescribed burn treatment. The study is being conducted at The Nature Conservancy's Canelo Hills Cienega Preserve. Canelo Hills Cienega is located about 75 km southeast of Tucson, Arizona, at 1500 m elevation in O'Donnell Canyon, in the Canelo Hills. Initial vegetation composition, and discussion of the experimental design and earlier results of this study are reported by Fishbein and Gori (1991, 1992). Background information on the geology, climate, biogeography, and history of the site is available from the Arizona Field Office of the Nature Conservancy, Tucson, Arizona.

Canelo Hills Cienega is notable for two reasons: first, it is one of four known locations inhabited by *Spiranthes delitescens*, a Category 1 candidate for federal listing; and second, it is one of only a few remaining examples of a cienega wetland habitat. The aim of the current study is to

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monitor and explain changes in the structure and composition of cienega vegetation, especially the population size and structure of *S. delitescens,* in response to prescribed fire regimes of different frequencies.

This study was undertaken because of anecdotal evidence of the positive role fire has played in past population increases of *S. delitescens* at the preserve. *S. delitescens* has exhibited wide fluctuations in population size, but with an overall decreasing trend, since The Nature Conservancy assumed management in 1969. Our method was to directly monitor changes in density of *S. delitescens* in response to fire and to test hypotheses about the role of competition from dominant graminoid species in the suppression of *S. deltescens,* by measuring the effects of fire on model non-graminoid species.

METHODS

Vegetation was sampled for height and density of living and dead biomass and percent cover of each species present each August, 1990-1992. Vegetation sampling was conducted in nine experimental plots that served as the basis for statistical analysis of the burn treatments and in two plots that recently supported flowering individuals of *S. delitescens* (hereafter referred to as "experimental" and "*Spiranthes* monitoring" plots, respectively). Cover in each plot was sampled in 30 0.5 m^2 quadrats. The quadrats were located along two permanent transects that were established centrally in each plot to minimize edge effects. Density of non-graminoid species (those in families other than Gramineae, Cyperaceae, and Juncaceae) was sampled in 0.25 m^2 quadrats located within each of the 0.5 m^2 cover quadrats. The height of vegetation and accumulated litter was sampled at three points within each cover quadrat.

Three treatment levels were applied to the experimental plots and the *Spiranthes* monitoring plots in the spring of 1991 and 1992: no burn or control (equivalent to very low natural burn frequencies), high frequency burn (prescribed burns conducted every 2-3 years), and medium frequency burn (prescribed burns conducted every 5-7 years). Treatments were assigned randomly to nine experimental plots within the cienega, yielding three replicate vegetation samples for each treatment. Because both high and medium frequency burn plots were burned in the first year and remained unburned in the second year, these treatment levels are grouped together and contrasted with the low burn frequency treatment level in the analyses presented here (see below). One of the *Spiranthes* monitoring plots was burned with the same prescription as the experimental plots; the other served as an unburned comparison.

Depth-to-water was monitored biweekly in 34 wells (27 of which were established for a previous study (Davis 1993). Annual "mean", "maximum", "minimum", and maximum "drop" (annual maximum difference of maximum and minimum) in depth-to-water were used as covariates in analyses of the response of vegetation to the burn treatments. The 3-5 wells per plot were averaged to produce biweekly mean depth-to-water measurements from which the annual measures were calculated.

The vegetation response variables (height of vegetation, depth of litter, and cover and density of each species) were each analyzed separately by repeated measures analysis-of-covariance (ANCOVA) using each of the covariates described above in separate analyses. Height measurements of vegetation and litter were used as untransformed dependent variates. Prior to analysis, angular transformation (arcsine of the square root) was applied to measurements of percent cover; density measurements were log transformed. In order to facilitate biological interpretation, only untransformed values are presented in this report. If none of the covariates in a given analysis accounted for a significant amount of the variation in the response variable, the analysis was rejected, and the data were reanalyzed by analysis-of-variance (ANOVA) without the covariate. If a covariate did account for a significant amount of variation, but there was a significant interaction between the effect of the covariate and the burn treatment, the analysis failed the homogeneity-of-slopes test and was similarly rejected in favor of an analysis without a covariate. For the analyses of cover and density, only the results of ANCOVAs that pass these criteria are reported here. If an ANCOVA did not pass the criteria, the appropriate ANOVA is reported. All analyses reported here have within group error structures that do not differ significantly from a normal distribution.

In addition to the analyses described above, the *Spiranthes* monitoring plots were compared to test directly for the response of the orchid and its associated vegetation to the same burn prescription that was applied to the experimental plots, although statistical analysis is limited by lack of replication. The experimental plots were closely monitored for the emergence of new or dormant individuals of *S. delitescens*. Although *S. delitescens* has recently only been observed in the *Spiranthes* monitoring plots, it has been observed in patches throughout the cienega in the past, including a census following a prescribed burn in 1976 (Geoffrey Babb, pers. comm.).

Data were analyzed using the GLM and ANOVA procedures of SAS System (SAS Institute 1987) and SAS System for Windows, Release 6.08 (SAS Institute 1992).

RESULTS

Effects of the Burn Treatments on Vegetation

The burn treatment was applied to the high and medium frequency burn plots on April 2, 1991. The environmental conditions and fire behavior were relatively constant during the burn period.

Mean vegetation height in both burn and control plots decreased from 1990 to 1991 and increased to higher levels than those of 1990 in 1992 (fig. 1). There was a greater increase in vegetation height in burn plots relative to control plots (fig. 1), however the effect of burning on vegetation height was not statistically significant (Tables 1-3). This effect was non-significant in ANOVA without the use of a covariate (Table 1) as well as in ANCOVA using appropriate covariates. There was a nearly significant relationship between greater annual minimum depth-to-water and decreasing vegetation height (Table 2), but even with the inclusion of this covariate, ANCOVA did not uncover a significant effect of the burn treatment (Table 3).

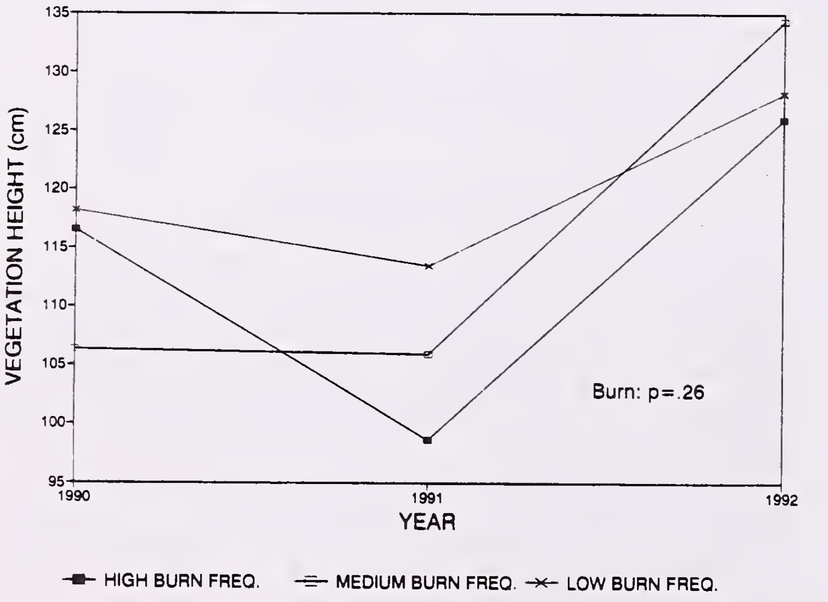

Figure 1.—Mean vegetation height (cm) in three burn treatments, 1990-1992. High and medium frequency treatments were both burned in 1991 prior to sampling and remained unburned in 1992.

Table 1.—Results of repeated measures ANOVA of the effect of prescribed burning on the height of vegetation ($\alpha=0.05$).

Source	Wilks' λ	F	Num. *d.f.*	Den. *d.f.*	p
YR	0.089	25	2	5	0.002
BURN[a]*YR	0.58	1.8	2	5	0.26

[a] BURN is a prior contrast between the high and medium burn frequency levels of treatment and the low frequency treatment as "high" and "medium" were equivalent treatments in the first two years of the study.

Table 2.—Results of repeated measures ANCOVA of the effect of variation in annual minimum depth-to-water on the height of vegetation, independent of burn treatment ($\alpha=0.05$).

Source	df	SS	MS	F	p
MIN	1	1053	1053	7.1	0.08
Error	3	446	148		

Table 3.—Results of repeated measures ANCOVA, using minimum depth-to-water as a covariate, of the effect of prescribed burning on the height of vegetation ($\alpha=0.05$).

Source	Wilks' λ	F	Num. *d.f.*	Den. *d.f.*	p
YR	0.10	9.0	2	2	0.1
BURN[a]*YR	0.28	2.5	2	2	0.28

[a] See Table 1.

Mean litter depth in both burn and control plots decreased in 1991 relative to 1990 and increased in 1992 to near the pre-burn (1990) levels (fig. 2). There was a much greater decrease in litter depth in burn plots compared to control plots in 1991, but this effect was almost entirely removed by reaccumulation in 1992 (fig. 2). The burn effect was statistically significant in ANOVA (Table 4) and was also detected using annual minimum depth-to-water as a covariate (Table 5), as this variable had a nearly significant relationship to litter depth (Table 6).

The relationship of each measure of hydrologic variation used in ANCOVA to the cover of each species is reported in Table 7. The cover of most species did not significantly vary with variation in hydrology. Variation in cover of *Bidens ferulaefolia* (Asteraceae), *Poa pratensis* (Poaceae), and *Ranunculus macranthus* (Ranunculaceae) was significantly accounted for by variation in at least one measure of hydrologic variation in separate ANCOVAs (Table 7). The overall effect of available moisture on the percent cover of *B. ferulaefolia* and *P. pratensis* was negative; on percent cover of *R. macranthus* the effect was positive.

Changes in the percent cover of plant species could be categorized in four ways: increase on both burned and unburned plots, decrease on both types of plots, or increase on one type of plot and decrease on the other (Table 8). Most graminoids decreased on both types of plots. *Carex* spp. (Cyperaceae), *Eleocharis rostellata* (Cyperaceae), *Muhlenbergia asperifolia, M. utilis,* and *Poa pratensis* decreased in cover on both burned and unburned plots (fig. 3). Of these species, *Carex* spp., *E. rostellata,* and *P. pratensis* decreased in cover more on burn plots than control plots, whereas the others had similar decreases on both types of plots. Repeated measures ANCOVA detected no significant effect of the burn treatment on *P. pratensis* using either annual mean depth-to-water as the covariate (F=0.53, p=0.65) or annual maximum depth-to-water (F=0.12, p=0.89). Repeated measures ANOVA also detected no significant effect of the burn treatment on cover of *Carex* spp., *E. rostellata, M. asperifolia,* and *M. utilis* (F=0.26, p=0.78; F=0.54, p=0.61; F=0.27, p=0.78; and F=0.90, p=0.46; respectively). For *E. rostellata, M. utilis,* and *P. pratensis* the analyses demonstrated a significant decrease in cover over

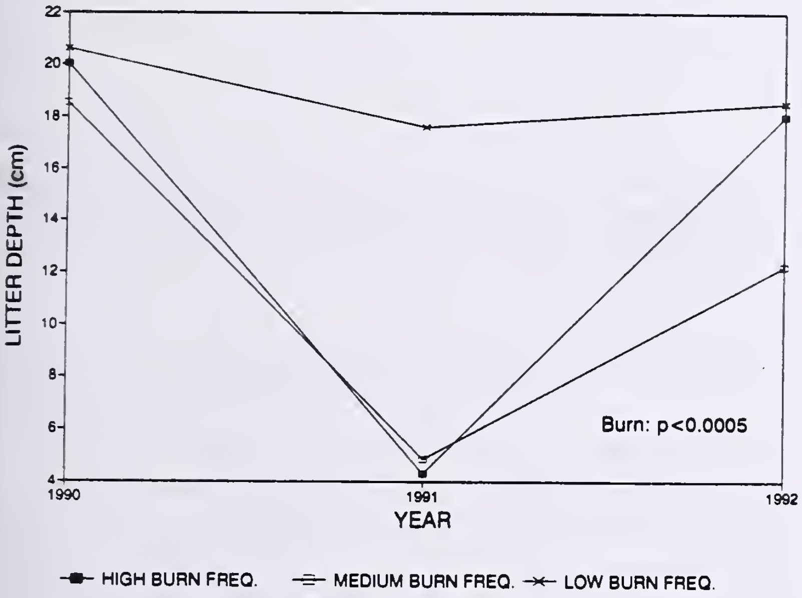

Figure 2.—Mean litter depth (cm) in three burn treatments, 1990-1992. High and medium frequency treatments were both burned in 1991 prior to sampling and remained unburned in 1992.

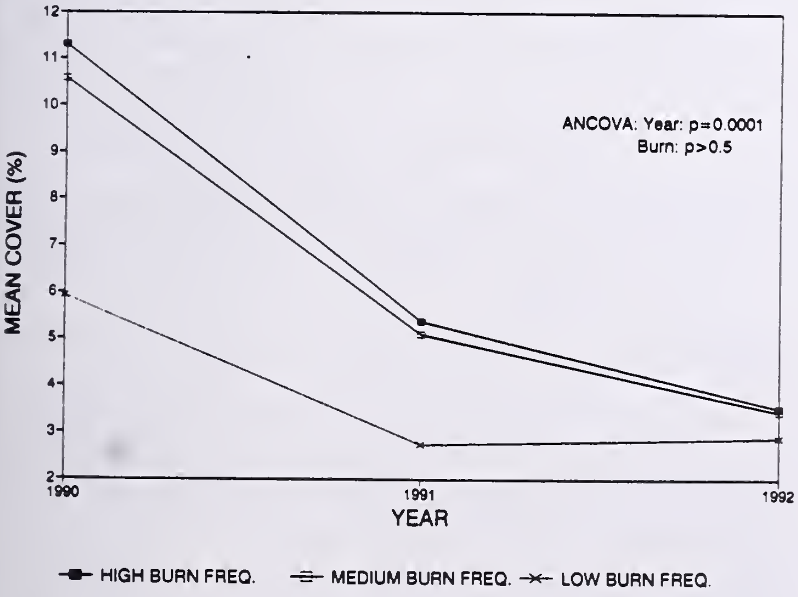

Figure 3.—Mean percent cover of *Poa pratensis* in three burn treatments, 1990-1992. High and medium frequency treatments were both burned in 1991 prior to sampling and remained unburned in 1992.

Table 4.—Results of repeated measures ANOVA of the effect of prescribed burning on the depth of litter (α=0.05).

Source	Wilks' λ	F	Num. *d.f.*	Den. *d.f.*	p
YR	0.011	218	2	5	0.0001
BURN[a]*YR	0.044	54	2	5	0.0004

[a] See Table 1.

Table 5.—Results of repeated measures ANCOVA, using minimum depth-to- water as a covariate, of the effect of prescribed burning on the height of vegetation (α=0.05).

Source	Wilks' λ	F	Num. *d.f.*	Den. *d.f.*	p
YR	0.024	39	2	2	0.02
BURN[a]*YR	0.061	15	2	2	0.06

[a] See Table 1.

Table 6.—Results of repeated measures ANCOVA of the effect of variation in annual minimum depth-to-water on the height of vegetation, independent of burn treatment (α=0.05).

Source	df	SS	MS	F	p
MIN	1	23.9	23.9	6.1	0.09
Error	3	11.8	3.9		

Table 7.—Significant effects ($p<0.05$) of four measures of hydrology (annual mean, maximum, minimum and difference between maximum and minimum depth-to-water), independent of treatment effects, on percent cover of each species in separate ANCOVAs; direction of relationship indicated by + (increasing cover with increasing moisture) or - (decreasing cover with increasing moisture).

MEAN Poa (-), Ranunculus macranthus[a] (+)
MAX Poa (-)
MIN Bidens ferulaefolia[b] (-)
DROP
NO COVARIATE SIGNIFICANT Apocynum, Aster coerulescens, A. commutatus, Carex, Eleocharis, Equisetum, Juncus longistylus, J. mexicanus, Lythrum, Mentha, Mimulus[c], Muhlenbergia asperifolia, M. utilis[d], Scirpus[e]

[a] For MAX, p=0.07

[b] For MAX, p=0.09

[c] For MEAN, p=0.08; for MAX, p=0.07; for DROP, p=0.10

[d] For MIN, p=0.08

[e] For DROP, p=0.07

Table 8.—Direction of change in percent cover from 1990 to 1992 of species present in both burn and control plots (Graminoids, Non-graminoids)[a].

	Burn Plots	
Control Plots	Increase in Cover	Decrease in Cover
Increase in Cover	*Apocynum suksdorfii* *Aster coerulescens* *Lythrum californicum* *Mimulus guttatus* *Ranunculus macranthus*	*Juncus longistylus* *Juncus mexicanus* *Mentha arvensis*
Decrease in Cover		*Carex spp.* *Eleocharis rostellata* *Equisetum laevigatum* *Muhlenbergia asperifolia* *Muhlenbergia utilis* *Poa pratensis*

[a] *Bidens ferulaefolia* and *Scirpus americanus* exhibited almost no change of cover in burn plots but decreased in control plots

time, independent of the burn treatment (F=11.2, p=0.01; F=10.0, p=0.02; and F=111, p=0.0001; respectively). For *Carex* spp. there was a nearly significant among year decrease in cover (F=5.47, p=0.06).

Juncus longistylus and *J. mexicanus* increased in cover on control plots, but decreased on burn plots (fig. 4). Repeated measures ANOVA demonstrated a significant effect of the burn treatment on cover of both *J. longistylus*, and *J. mexicanus* (F=9.6, p=0.02 and F=36.3, p=0.001; respectively). *Scirpus americanus* remained nearly constant in cover on burn plots, but decreased slightly on control plots (fig. 5). Repeated measures ANOVA detected no significant effect of the burn treatment on percent cover of this species although the probability level was nearly significant (F=4.44, p=0.08), but did detect a significant change in cover over time independent of burn treatment (F=6.8, p=0.04).

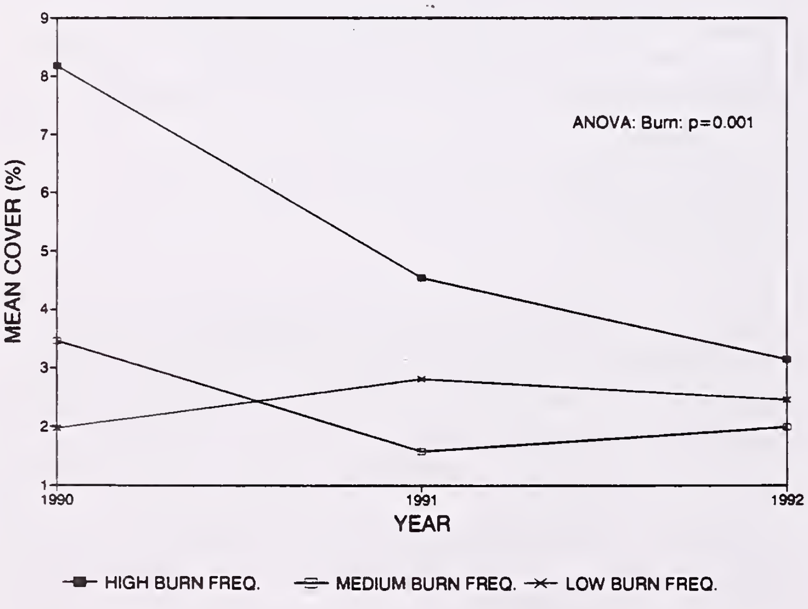

Figure 4.—Mean percent cover of *Juncus mexicanus* in three burn treatments, 1990-1992. High and medium frequency treatments were both burned in 1991 prior to sampling and remained unburned in 1992.

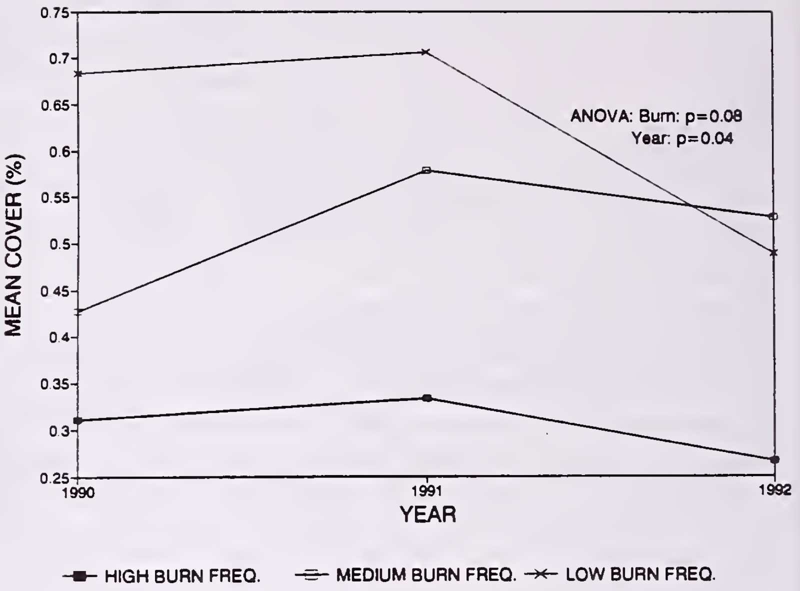

Figure 5.—Mean percent cover of *Scirpus americanus* in three burn treatments, 1990-1992. High and medium frequency treatments were both burned in 1991 prior to sampling and remained unburned in 1992.

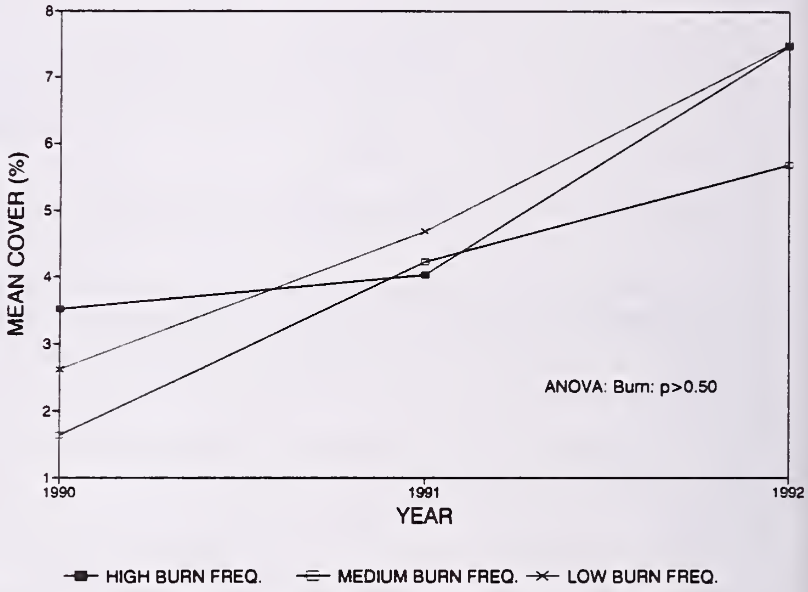

Figure 6.—Mean percent cover of *Apocynum suksdorfii* in three burn treatments, 1990-1992. High and medium frequency treatments were both burned in 1991 prior to sampling and remained unburned in 1992.

To summarize the effect of the burn treatment on percent cover of graminoid vegetation: 1) the three dominant species of the cienega (*Carex* spp., *E. rostellata*, and *P. pratensis*) showed no effect of burning on percent cover, although all three significantly (nearly so for *Carex*) decreased in cover between years, independent of burn treatment; 2) *S. americanus* (which increased slightly in cover on burn plots and decreased on control plots) showed a positive effect of the burn treatment on percent cover; and 3) *J. longistylus* and *J. mexicanus* (which increased in cover on control plots and decreased in cover on burn plots) showed a negative effect of the burn treatment on percent cover. Only the negative effects of burning on *J. longistylus* and *J. mexicanus* were statistically significant, although the positive effect of burning on *S. americanus* was nearly significant.

Of the non-graminoid species, *Apocynum suksdorfii* (Apocynaceae), *Aster coerulescens*, *Lythrum californicum* (Lythraceae), *Mimulus guttatus*, and *Ranunculus macranthus* increased in percent cover on both burn and control plots (fig. 6). *A. coerulescens*, *L. californicum*, and *R. macranthus* increased more on the burn plots, whereas *A. suksdorfii* and *M. guttatus* increased to a similar extent on both. Repeated measures ANOVA failed to demonstrate a significant effect of the burn treatment on cover of *A. suksdorfii*, *A. coerulescens*, *L. californicum*, and *M. guttatus* (F=0.38, p=0.70; F=1.0, p=0.42; F=1.1, p=0.39; and F=0.34, p=0.73; respectively). Repeated measures ANCOVA using annual mean depth-to-water failed to demonstrate a burn effect on cover of *R. macranthus* (F=0.29, p=0.78).

Mentha arvensis (Lamiaceae) decreased in percent cover on burn plots, but increased on control plots. Repeated measures ANOVA failed to demonstrate an effect of the burn treatment on this species (F=1.4, p=0.32). *Bidens ferulaefolia* and *Equisetum laevigatum* decreased on both types of plots. *B. ferulaefolia* decreased more on control plots than on burn plots, but repeated measures ANCOVA using annual minimum depth-to-water did not demonstrate a significant effect of the burn treatment (F=4.0, p=0.20). *E. laevigatum* decreased to a similar extent on both types of plots and repeated measures ANOVA demonstrated no significant effect of the burn treatment (F=2.6, p=0.16); however, a significant decrease in percent cover over time was detected (F=6.4, p=0.04).

To summarize the effect of the burn treatment on percent cover of non-graminoid vegetation: 1) *A. coerulescens*, *L. californicum*, and *R. macranthus* (which increased in percent cover more on burn than control plots) and *B. ferulaefolia* (which decreased in percent cover more on control than burn plots) showed a positive effect of the burn treatment on percent cover; 2) *M. arvensis* and *M. guttatus* (which decreased on burn plots and increased on control plots) showed a negative effect of the burn treatment on percent cover; and 3) *A. suksdorfii* (which increased to a similar extent on control and burn plots) and *E. laevigatum* (which decreased to similar extent on control and burn plots) showed no effect of the burn treatment, although *E. laevigatum* did exhibit a significant among year decrease in cover. None of the burn effects discussed above, however, were statistically significant.

The relationship of each measure of hydrologic variation used in analyses-of-covariance to the density of each species is reported in Table 9. The density of most species did not significantly vary with variation in hydrology. Variation in density of *Bidens aurea*, *Mimulus guttatus*, and *Ranunculus hydrocharoides* was significantly accounted for by variation in at least one measure of hydrologic variation in separate ANCOVAs (Table 9). The overall effect of available moisture on the density of these species was positive.

As with changes in percent cover, changes in density of non-graminoids could be categorized in terms of relative changes on both burn and control plots (Table 10). Most species increased in density on both burn and control plots (fig. 7-8). *Berula erecta* (Apiaceae), *Mimulus guttatus*, and *Ranunculus macranthus* increased in density

Table 9.—Significant effects (p<0.05) of four measures of hydrology (annual mean, maximum, minimum and difference between maximum and minimum depth-to-water), independent of treatment effects, on density of each species in separate ANCOVAs; direction of relationship indicated by + (increasing cover with increasing moisture) or - (decreasing cover with increasing moisture).

MEAN
Mimulus (+)
MAX
Mimulus (+)
MIN
Bidens aurea (+), *Ranunculus hydrocharoides* (+)
DROP
NO COVARIATE SIGNIFICANT
Apocynum, Aster coerulescens, Berula, Bidens ferulaefolia, Equisetum, Lythrum, Mentha

Table 10.—Direction of change in density (stems/.25m2) of non-graminoids present in both burn and control plots from 1990 to 1992[a].

	Burn Plots	
Control Plots	Increase in Density	Decrease in Density
Increase in Density	*Apocynum suksdorfii* *Mentha arvensis* *Mimulus guttatus* *Ranunculus hydrocharoides* *Ranunculus macranthus*	
Decrease in Density	*Bidens ferulaefolia*	

[a] *Aster coerulescens* and *Berula erecta* increased in burn plots but exhibited no change in density in control plots; *Bidens aurea* and *Equisetum laevigatum* decreased in control plots but exhibited no change in burn plots; *Lythrum californicum* exhibited no change in either burn or control plots.

more on burn plots than on control plots (fig. 7). Repeated measures ANOVA failed to demonstrate a significant effect of the burn treatment on the density of *B. erecta* (*F*=0.28, *p*=0.77). Likewise, repeated measures ANCOVA using either annual mean or maximum depth-to-water as the covariate failed to demonstrate a significant burn effect on the density of *M. guttatus* (*F*=1.5, *p*=0.40 and *F*=0.91, *p*=0.52; respectively). Repeated measures ANOVA did, however, detect a significant burn effect on the density of *R. macranthus* (*F*=6.7, *p*=0.04). *R. macranthus* also exhibited a significant increase in density over time, independent of burn treatment (*F*=14.0, *p*=0.009). *Apocynum suksdorfii, Mentha arvensis,* and *Ranunculus hydrocharoides* increased moreútrol plots than burn plots (fig. 8). Repeated measures ANOVA failed to demonstrate a significant effect of the burn treatment on the density of any of these species (*F*=0.19, *p*=0.84; *F*=0.77, *p*=0.51; and *F*=0.31, *p*=0.75; respectively). *Equisetum laevigatum* and *Lythrum californicum* decreased in density on both types of plots (fig. 9). *E. laevigatum* decreased in density more on burn than control plots, but repeated measures ANOVA failed to demonstrate a burn effect (*F*=1.3, *p*=0.36). The analysis did, however, detect a decrease in density of *E. laevigatum* over time, independent of burn treatment (*F*=11.1, *p*=0.01). *L. californicum* decreased in density to the same extent on both types of plots, and repeated measures ANOVA failed to demonstrate a burn effect on this species (*F*=0.86, *p*=0.48). *Aster coerulescens* increased in density on burn plots, but did not change on control plots. Repeated measures ANOVA failed to demonstrate a significant burn effect on the density of this species (*F*=1.1, *p*=0.39). *Bidens aurea* decreased on control plots and did not change on burn plots. Repeated measures ANCOVA using annual minimum depth-to-water as the covariate did not detect a burn effect on the density of this species, although the probability level approached significance (*F*=11.3, *p*=.08). *Bidens ferulaefolia* in-

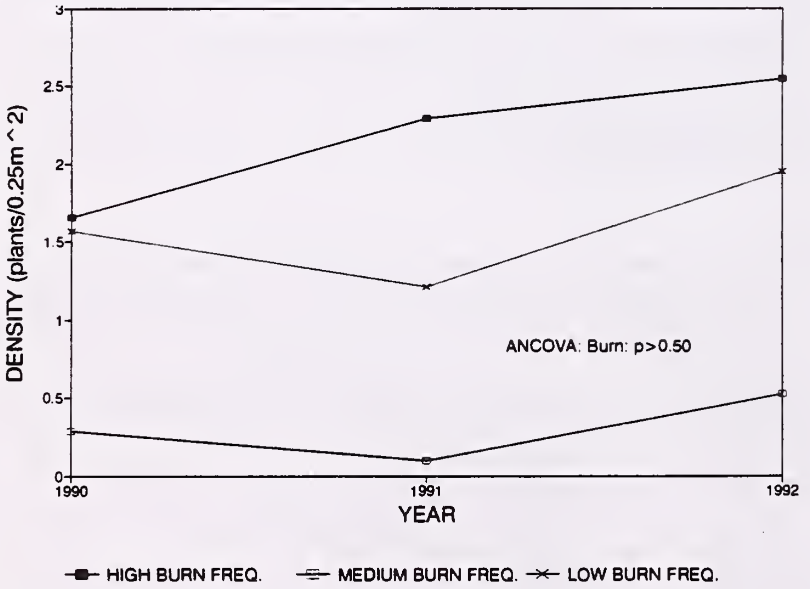

Figure 7.—Mean density (individuals/0.25 m^2) of *Mimulus guttatus* in three burn treatments, 1990-1992. High and medium frequency treatments were both burned in 1991 prior to sampling and remained unburned in 1992.

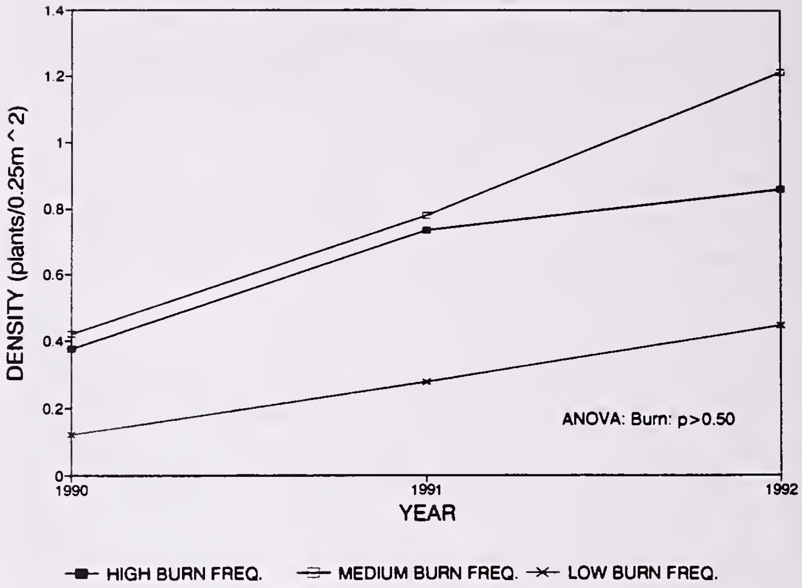

Figure 8.—Mean density (individuals/0.25 m2) of *Apocynum suksdorfii* in three burn treatments, 1990-1992. High and medium frequency treatments were both burned in 1991 prior to sampling and remained unburned in 1992.

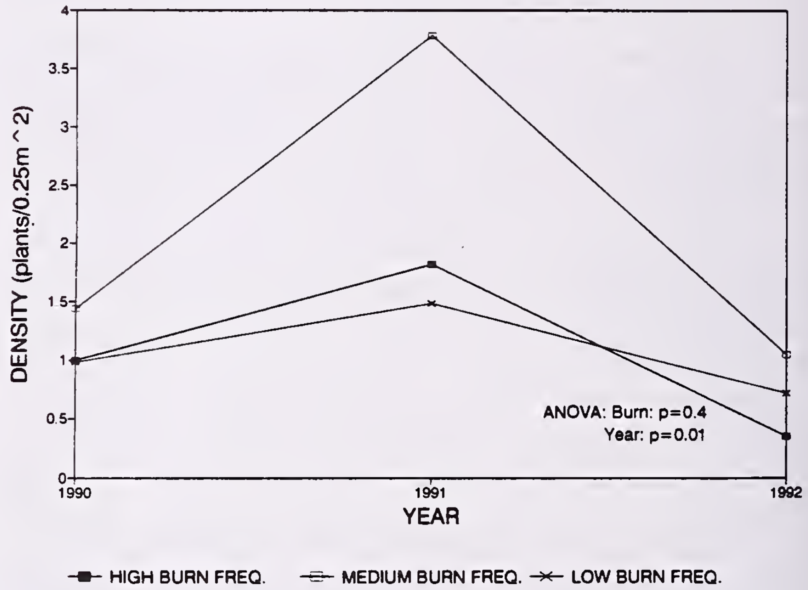

Figure 9.—Mean density (individuals/0.25 m^2) of *Equisetum laevigatum* in three burn treatments, 1990-1992. High and medium frequency treatments were both burned in 1991 prior to sampling and remained unburned in 1992.

creased in density on burn plots, but decreased in density on control plots (fig. 10). Repeated measures ANCOVA using annual minimum depth-to-water failed to demonstrate a significant burn effect on the density of this species (F=0.66, p=0.60).

To summarize the effect of the burn treatment on the density of non-graminoid vegetation: 1) *B. erecta, M. guttatus,* and *R. macranthus* (which increased in density more on burn plots than control plots), *A. coerulescens* (which increased in density on burn plots and did not change on control plots), *B. aurea* (which decreased in density on control plots and did not change on burn plots, and *B. ferulaefolia* (which increased in density on burn plots and decreased in density on control plots) all show a positive effect of the burn treatment on density; 2) *A. suksdorfii, M. arvensis,* and *R. hydrocharoides* (which increased in density more on control plots than burn plots) and *E. laevigatum* (which decreased in density more on burn than control plots) show a negative effect of the burn treatment on density; and 3) *L. californicum* (which decreased in density to the same extent on both types of plots) showed no effect of the burn treatment on density. Only the effect of greater increase in density of *R. macranthus* on burn plots was statistically significant. Also, the increase in density of *R. macranthus* and decrease in density of *E. laevigatum,* independent of burn treatment, were statistically significant.

No *Spiranthes delitescens* were observed in the experimental plots either prior to or following application of the burn treatments.

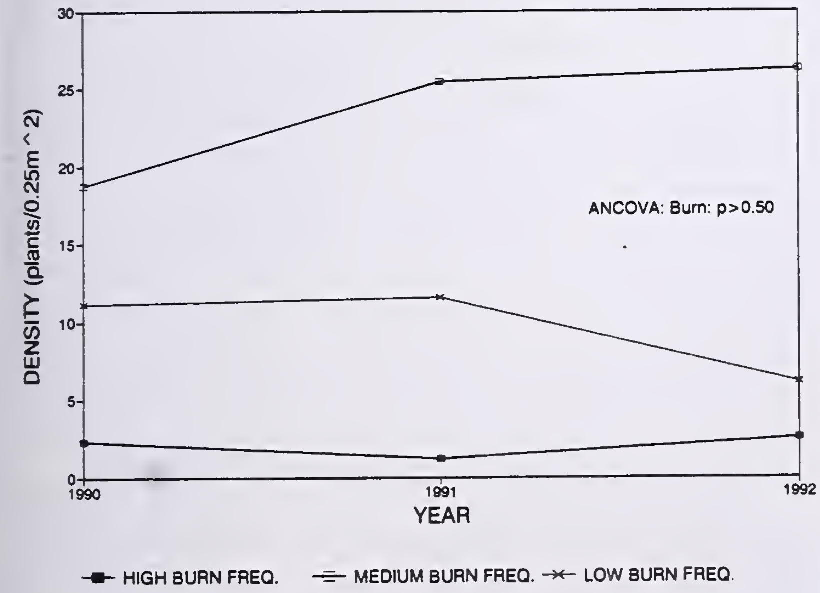

Figure 10.—Mean density (individuals/0.25 m^2) of *Bidens ferulaefolia* in three burn treatments, 1990-1992. High and medium frequency treatments were both burned in 1991 prior to sampling and remained unburned in 1992.

Table 11.—Vegetation and litter height (s.d.) in centimeters on *Spiranthes* monitoring plots, 1990-1992[a].

		Treatment			
Variable	Year	Burned		Unburned	
Vegetation	1990	89.3	(19.2)	145.6	(48.7)
	1991	65.6	(8.9)	123.0	(29.1)
	1992	74.0	(16.3)	147.0	(51.0)
Litter	1990	15.1	(6.6)	20.2	(13.3)
	1991	1.6	(1.0)	20.0	(12.1)
	1992	5.1	(3.7)	15.8	(9.8)

[a] Variables measured at three points in each of 10 0.50m2 quadrats per plot.

Effects of Burn Treatments on *Spiranthes* Monitoring Plots

As in 1991, no *Spiranthes* were observed along the transects in the monitoring plots in 1992. There was no systematic survey for *Spiranthes* in 1992, but it appeared that there were fewer flowering individuals in this year than in the previous two years of the study. In 1993, we observed a dramatic increase in the number of flowering *Spiranthes.* In order to document this increase, we surveyed extensively for the orchid and censused each patch. We succeeded in relocating one previously known patch in an unburned location and discovered a previously unknown patch along the east side of the creek in an unburned location. The total number of individuals recorded from each patch were 55 in the burn plot, 31 in the unburned plot, and 29 along the creek. In 1994, we observed a substantial increase only for the patch in the previously burned area. The total number of individuals recorded in each patch in 1994 were 155 in the burn plot, 33 in the unburned plot, and 18 along the creek.

Vegetation height on the *Spiranthes* monitoring plots decreased from 1990 to 1991 and increased from 1991 to 1992 (Table 11). The increase on the unburned plot was greater than that on the burned plot, in contrast to the results obtained on the experimental plots (see above). The response to burning of the depth of accumulated litter on *Spiranthes* plots also differed from that observed on the experimental plots. Unlike the experimental burn plots, the burned *Spiranthes* plot did not recover to pre-burn litter levels in 1992 (Table 11).

The percent cover of the most important species found on the *Spiranthes* monitoring plots is reported in Table 12. Of the dominant graminoids, *Eleocharis rostellata* decreased in cover on the unburned plot (it was not present in the burned plot). *Poa pratensis,* however, decreased on both plots. *Juncus mexicanus* remained relatively constant in cover on the unburned plot and returned to pre-burn levels on the burned plot following an increase in 1991 (the year of the burn). This result is paradoxical in light of the negative response of this species to burning on the experimental plots. *Carex* spp. were not abundant on the *Spiranthes* plots.

Of the common non-graminoids, *Bidens ferulaefolia* increased in cover on the burned plot and decreased in cover on the unburned plot. *Ranunculus macranthus* increased in cover on the unburned plot, as it did on the burned plot following a decrease in the year of the burn (1991).

The density of the most abundant non-graminoid species found on the *Spiranthes* monitoring plots is reported in Table 13. *Ranunculus macranthus* increased in density on the burned plot and also on the unburned plot in 1991, dropping somewhat in 1992. *Bidens ferulaefolia* increased in density on the burn plot following the burn in 1991, then decreased somewhat in 1992, and decreased in density on the unburned plot. Likewise, *Equisetum laevigatum* followed the same pattern on the burned plot and increased slightly in density on the unburned plot, where is was uncommon.

DISCUSSION

The most striking effect detected in 1992, 15 months following burning of the experimental plots, was the rapid reaccumulation of plant litter. Litter depth nearly returned to pre-burn levels in both burn treatments in the year between the 1991 and 1992 vegetation samplings. This result is important because of the hypothesized relationship between litter accumulation and suppression of *Spiranthes delitescens.* If litter suppresses *S. delitescens* and burning is to be used as a management tool for this species, then burns must be conducted very frequently in order to significantly effect litter depth. Consequently, it seems unlikely that natural patterns of burning in the cienega have been responsible for maintaining populations of *S. delitescens.* Notably, we observed no individuals of *S. delitescens* emerging in cienega locations following burning where they had previously been observed.

Table 12.—Percent cover[a] (s.d.) of important species on Spiranthes monitoring plots, 1990-1992.

		Treatment	
Species	Year	Burned	Unburned
Aster commutatus	1990	4.4 (4.0)	0.2 (0.3)
	1991	1.9 (1.6)	0.2 (0.4)
	1992	7.5 (6.7)	0.5 (1.1)
Bidens ferulaefolia	1990	18.6 (16.0)	20.5 (8.3)
	1991	21.7 (17.4)	11.8 (6.0)
	1992	26.4 (27.6)	12.5 (4.6)
Eleocharis rostellata	1990	0 (0)	41.0 (12.2)
	1991	0 (0)	13.5 (4.9)
	1992	0 (0)	11.9 (4.3)
Juncus mexicanus	1990	2.8 (1.3)	2.3 (0.7)
	1991	3.2 (1.7)	2.8 (1.7)
	1992	2.6 (0.7)	2.7 (2.1)
Poa pratensis	1990	5.3 (3.4)	1.0 (1.2)
	1991	8.5 (5.6)	1.8 (1.8)
	1992	8.5 (4.4)	3.3 (3.6)
Ranunculus macranthus	1990	4.8 (3.9)	0.4 (0.8)
	1991	2.9 (2.0)	1.0 (1.9)
	1992	6.6 (4.5)	1.1 (1.4)
Salix lasiolepis	1990	0 (0)	3.6 (6.4)
	1991	0 (0)	5.8 (7.5)
	1992	0 (0)	12.1 (15.6)

[a] Mean of 10 0.5m^2 quadrats.

Table 13.—Density[a] (s.d.) of abundant non-graminoid species on Spiranthes monitoring plots in 1990 and 1991.

		Treatment	
Species	Year	Burned	Unburned
Aster commutatus	1990	5.6 (5.5)	0.1 (0.3)
	1991	4.7 (6.3)	0.6 (0.4)
	1992	11.8 (14.3)	1.3 (3.5)
Bidens aurea	1990	0.7 (1.3)	0.3 (0.9)
	1991	1.5 (2.3)	0.4 (1.3)
	1992	1.0 (1.7)	0 (0)
Bidens ferulaefolia	1990	38.2 (31.7)	42.6 (20.3)
	1991	47.3 (33.5)	37.2 (21.8)
	1992	42.7 (38.9)	33.2 (19.4)
Equisetum laevigatum	1990	6.9 (4.2)	0.1 (0.3)
	1991	7.3 (3.5)	0 (0)
	1992	6.5 (3.9)	0.5 (1.3)
Ranunculus macranthus	1990	3.8 (2.4)	0.3 (0.7)
	1991	4.0 (3.1)	1.0 (1.6)
	1992	5.2 (3.5)	0.6 (1.0)
Salix lasiolepis	1990	0 (0)	1.5 (2.8)
	1991	0 (0)	2.0 (2.4)
	1992	0 (0)	1.7 (2.3)
Sisyrinchium demissum	1990	0 (0)	0 (0)
	1991	0.1 (0.3)	0 (0)
	1992	3.7 (2.8)	0 (0)

[a] Mean number of stems on 10 0.50m^2 quadrats per plot.

Prescribed burning had subtle, but demonstrable effects on vegetation structure and composition. Vegetation height increased more rapidly in burned plots in the year following burning than in unburned plots (although this trend was not statistically significant). Again, this result challenges the hypothesis that prescribed burning could be an effective management tool to control vegetation competing with *S. delitescens*; burning apparently *stimulated* the growth of the dominant graminoid vegetation of the cienega.

On a species-by-species basis, burning showed little effect on the dominant graminoids. On burn plots, the sedge *Scirpus americanus* did not exhibit the decrease in cover exhibited by other graminoids on burn and unburned plots alike. Conversely, the two common rushes of the cienega (*Juncus mexicanus* and *J. longistylus*) were negatively effected by burning, suggesting that different families of graminoids might respond differently to burning. The overall decrease in cover of dominant graminoids, independent of burn treatment, detected earlier (Fishbein and Gori 1992) continued in 1992, suggesting that other factors such as climatic conditions may have stronger effects on cienega vegetation than burning.

Non-graminoid species tended to be favored by burning as measured by changes in both percent cover and density, although one species, *Mimulus guttatus*, increased in density on burn plots, yet decreased in cover. This sort of result is not surprising; if burning stimulated recruitment of *M. guttatus*, then intraspecific competition might result in a negative effect on cover in burn plots. Whether or not one concludes that burning "favored" *M. guttatus*, however, is dependent on the life history of this species and the relative importance of recruitment and later life stages to population growth. Conclusions about the effects of burning on these non-graminoid species are limited because no statistically significant or otherwise compelling trends were detected.

Although it appears that prescribed burning at Canelo Hills Cienega has not resulted in changes in vegetation commensurate with predictions concerning the management of *S. delitescens*, it is too early to conclude that the technique is ineffective. In 1994, we observed a considerable increase in the number of emergent stems of *S. delitescens* in the burned plot that was not exhibited by the two unburned patches. Further study is required to determine whether this increase represents a delayed direct response to the burn treatments, an interaction between burning and some other factor, a response to some other factor unrelated to burning, or simply a chance increase in that patch. The response of *S. delitescens*, in addition to the more subtle effects on cienega vegetation generally, warrants further investigation in the role of fire as a management tool.

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A Conservation Agreement for the Wet Canyon Talussnail, Graham County, Arizona

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Abstract.—The Wet Canyon talussnail *Sonorella macrophallus* is a land snail whose total range apparently is restricted to talus slopes in a 1 mile reach of Wet Canyon in the Pinaleno Mountains, Graham County, Arizona. The species appears to require a somewhat wetter and possibly a lower elevation habitat than other talussnails in this mountain range. The U.S. Fish and Wildlife Service (USFWS) placed the species on its candidate list in Category 1, i.e., taxa for which the USFWS has sufficient information on vulnerability and threats to support a proposal to list them as threatened or endangered under the Endangered Species Act. To obviate listing, USFWS and Coronado National Forest, in cooperation with Arizona Game and Fish Department, are developing a Conservation Agreement that outlines methods to remove threats and maintain stability of the species and its ecosystem. Conservation agreements may be appropriate for species whose range is finite and naturally limited, that have threats to their existence that are relatively simple to resolve, and whose habitat is under the control of a single landowner. Conservation agreements may not be applicable to species with less tractable problems.

INTRODUCTION

About 1,900 vertebrate and invertebrate animals, and a similar number of plants native to the United States are being reviewed by the U.S. Fish and Wildlife Service (USFWS) for possible addition to the list of endangered or threatened wildlife under the Endangered Species Act of 1973, as amended (ESA). The U.S. Forest Service (USFS) includes ca. 600 animals on its national sensitive species list. Many of these species have small, finite ranges with modest threats to their existance that can be easily resolved. Accomplishing recovery actions for these "candidate species" before they are listed may lower their listing priority, or entirely eliminate the need to list them. Refraining from accomplishing recovery actions while waiting for a species to be listed, with a subsequent recovery plan prepared, is shortsighted because it can result in the species spiraling further into extinction, and reducing options for management and recovery.

Since the enactment of the ESA, the process required to reach a listing decision has become increasingly burdensome and encumbered with political and legal complexities. In spite of good efforts, USFWS routinely has not met required deadlines for reaching listing decisions (U.S.General Accounting Office [USGAO] 1993). The backlog of unlisted species is so great that a lawsuit against the Department of Interior was filed in 1992, charging the agency with unreasonable delays in listing species (Fund for Animals v. Lujan). The parties reached a court-approved settlement agreement that requires USFWS to make listing determinations for ca. 400 species (USGAO 1993). One avenue that USFWS is pursuing in meeting the terms of that agreement is the development of Conservation Agreements (CA) for selected species, documents that can make their listing unnecessary.

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THE DOCUMENTS

A CA is a formal written document agreed to by USFWS and another Federal agency, tribe, State agency, local government, or the private sector to achieve conservation of a species through voluntarily actions. The agreement documents the specific actions and responsibilities for which each party agrees to be accountable. An effective CA may lower listing priority or entirely eliminate the need to list a species (USGAO 1993).

Conservation agreements are supported by conservation assessments, defined as a comprehensive, state-of-knowledge technical document that describes life history, habitat requirements, and management considerations for a species or group of species throughout its/their occupied range on the lands managed by the cooperating agencies. A conservation assessment recommends specific management practices for the recovery of the species or group. It is developed by an interagency, interdisciplinary team of specialists and land managers familiar with the species and its/their habitats.

The employment of CA in lieu of listing has been used infrequently by the USFWS. In 1981, USFWS proposed that CA could be used in lieu of listing, provided that all known threats to the species that would otherwise warrant listing were removed. Policy directed that careful monitoring would be done to ensure that the agreements' objectives were achieved and that any corrective actions, including listing, were instituted as necessary. But in 1985, USFWS discontinued using CA in lieu of listing because it felt that the narrowly-defined legal applicability of a CA did not warrant their pursuance. The USFWS noted that between 1981 and 1985 only seven situations had been identified where CA were appropriate, and that funds and personnel could be more effectively and efficiently utilized for evaluating candidate species and processing proposed and final rules.

In 1992, USFWS resurrected CA as "an appropriate mechanism to use to maximize the protection of a candidate endangered or threatened species when...(the agreement) effectively removes known threats ...." Draft guidance for CA emphasized the value of early conservation efforts to stabilize and recover species and their ecosystems before they are listed. The USFWS noted that by addressing the conservation of candidate species, management flexibility could be retained, conflict with development avoided, costs of recovery minimized, and the potential need for restrictive land use policies alleviated.

A Memorandum of Understanding (MOU) between USFWS, USFS, Bureau of Land Management, National Park Service, and National Marine Fisheries Service in 1994 encouraged the development of CA. Purpose of the MOU is to "... establish a general framework for cooperation and participation in the conservation of species that are tending toward federal listing as threatened or endangered under the ESA." The MOU provided that the cooperators would work together and participate in the conservation of selected plant and animal species and their habitats to reduce, mitigate, and possibly eliminate the need for their listing under the ESA by developing habitat conservation assessments leading to CA. The five-member federal agency MOU was later amended to include the International Association of Fish and Wildlife Agencies as a cosigner, thus bringing representation from state wildlife agencies into the development and implementation of these documents.

The Wet Canyon talussnail *Sonorella macrophallus* is a species included in the Fund for Animals settlement. Accordingly, USFWS began preparing documents to propose its listing under the Endangered Species Act. The Southwestern Region of USFS requested that the agencies work together to develop a conservation assessment and CA for the talussnail in order to remove the need for its listing. Work on the documents began in spring 1994[3].

THE SPECIES

Wet Canyon talussnail is a pulmonate land snail whose total range apparently is restricted to a 1-mile reach of Wet Canyon in the Pinaleno Mountains. There it occupies talus slopes composed of rocks high in calcium carbonate along the north-facing banks of the perennial stream. This species appears to require a somewhat wetter and possibly a lower elevation habitat (range 6,050 to 6,900 feet) than other talussnails in the mountain range. The rock slides have a high soil

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[3] *At the time of this conference (September 1994) the CA for the Wet Canyon talussnail was still in draft form. It had not been approved by any of the cooperators, nor had any of the directions for management been accepted. It is likely that technical and agency review will result in changes or alterations of the management direction referred to in this paper. Suggestions in this paper for management of the Wet Canyon talussnail are solely those of the authors.*

content, but retain sufficient interstitial spaces required by the talussnail for living space. A factor that may have contributed to its restriction is the general drying trend since the Pleistocene, which has led to desert expansion and a contraction of southwestern forest communities, and isolation of species on the sky islands of the "Madrean Archipeligo". Whether the distribution of Wet Canyon talussnail has changed in response to climatic variations cannot be stated with certainty, but there is evidence that suspected limiting environmental factors of high temperature and low moisture were more relaxed during pluvial periods.

Above-ground emergence of the Wet Canyon talussnail appear dependent on local moisture conditions. The life span of land snails is dependent on their cycle of activity, and talussnails in the Pinaleno Mountains are active for a much greater number of days per year than are land snails inhabiting the desert below. Most Pinaleno Mountain talussnails reach maturity in from two to three years and their life span is approximately six years (Hoffman, 1990).

Hoffman's (1990) survey provided the basis for USFWS to include Wet Canyon talussnail on the Federal Notice of Review as a Category 1 species. Reasons for inclusion included the extremely limited range, the amount of recreational development within that range, and the uncertainty of knowledge regarding the status and population trend of the species and its habitat (USFWS 1990, S.E. Stefferud, USFWS, pers. comm.).

Although Hoffman (1990) noted that the population appeared stable, and was probably in no danger unless local conditions changed considerably, the strength of his assertions was disconcerting given the minimal information on past and present status of the talussnail. If for no other reason, natural wasting of slope soils that clog and fill talus interstices in the limited habitat, combined with the probable existing fragmentation of its range by roads and trails, portended an uncertain future for the species.

THE SETTING

The eastern slopes of the Pinaleno Mountains have a history of human occupation and use, and present land uses near the habitat of the talussnail are typical of multiple-use USFS lands. Wet Canyon, along with other canyons on the eastern slopes of the Pinaleno Mountains, was logged extensively during the late 1800's to early 1900's. In the upper reaches of the canyon, about a mile upstream from occupied habitat, pieces of a cast iron stove and other evidence of human habitation and development have been found. In addition, several old logging skid trails run directly into the canyon bottom. To what extent logging and other activities may have altered the canyon or affected the range of the talussnail is unknown.

Currently, saw timber or fuelwood harvest may be done only to enhance recreation, visual quality, and wildlife values, or to reduce hazards. Any harvest of standing trees is limited to individual tree selection, and is done under permit. Some gathering of firewood for campfire use in Arcadia and Wet Canyon recreation sites occurs.

Arizona Highway 366 (Swift Trail) crosses Wet Canyon near the lower end of the habitat for the talussnail, and has been in place since the exploration and settlement period. The bridge at Wet Canyon was constructed in the 1930's. Grazing by domestic livestock is not permitted in the Wet Canyon area. There are no diversions of surface water from Wet Canyon, but a well provides drinking water for the recreation sites. Facilities for recreation include the three-unit Wet Canyon Picnic site (day-use only) where Swift Trail crosses Wet Canyon, and Arcadia Campground with 26 family units available for overnight use on the slopes above Wet Canyon. No data are available on amount of use at the recreation sites.

Trails, both developed and user-built, connect the two recreation facilities with other recreation trails in the vicinity. A self-guided nature trail developed and maintained by a local school teacher leads from Arcadia Campground to Wet Canyon. An extension of that trail leads downstream along Wet Canyon to intersect with a user-built trail back to the campground. Another trail extends along Wet Canyon from the picnic area upstream about one mile to Arcadia National Recreation Trail. This user-built trail passes over and through talus slopes occupied by the talussnail, and its construction and use may have caused disturbance and fragmentation of the habitat. It is not part of the USFS trail system and is being recommended for removal, closure, or re-alignment out of the canyon bottom. If re-aligned, it will be rerouted so that it will not disturb habitat of the talussnail. No data are available on extent of use of trails in the vicinity.

THE PROBLEM

Based on our current understanding of the needs of the talussnail, its habitat appears intact and in sufficiently good condition to continue to support the species. However, the range of Wet Canyon talussnail is extremely limited and naturally fragmented. The species is vulnerable to any disturbance that would remove talus, increase interstitial sedimentation, open forest canopy, alter stream discharge or otherwise change moisture conditions in Wet Canyon, or increase fragmentation. Primary human-caused threats to it include degradation, destruction, and fragmentation of the habitat by trails, potential for wildfire exacerbated by a build-up of fuels as a result of past fire-suppression efforts, and potential for diversion of water from Wet Canyon.

THE SOLUTION

An effective and proactive CA for the Wet Canyon talussnail and its habitat can effectively remove human-caused threats, maintain stability of the population, and protect the watershed containing the habitat. Protection of the Wet Canyon talussnail and its habitat through a CA is particularly relevant because of the following factors:

- The habitat is entirely under the control of a single landowner, i.e., the USFS.
- There is rudimentary understanding of the relationship between proper habitat management and maintenance of the species, and of the specific management actions that will be needed for its conservation.
- Habitat of the talussnail appears intact and in sufficiently good condition to continue to support the species.
- Conservation actions mostly involve refraining from some activity that would lessen the value of habitat for the talussnail, rather than undertaking corrective or restorative action.

Existing on-the-ground activities, except for the trail system, do not appear to be causing impact to the habitat of the talussnail. Therefore, direction in the CA primarily addresses changes in standards and guidelines that coordinate land uses in the area. The opportunity to establish a special resource management area in Wet Canyon will be explored, a fuels treatment plan for Wet Canyon developed, a water right for instream flow in Wet Canyon applied for, and guidelines for habitat protection during any maintenance or improvement of the Swift Trail specified. On-the-ground project activities call for removal of the user-built trail from the talussnail's habitat, and restrictions on campfires in the picnic area. Other project activities are relatively minor and inconsequential in terms of economic or public use impact.

A plan is only as effective as its implementation. The CA for Wet Canyon talussnail provides direction to not only establish monitoring of the talussnail and its habitat, but also to evaluate annually the effectiveness of the agreement. Most importantly, it directs that the Land Management Plan for the Coronado National Forest be amended to incorporate the direction provided, thus institutionalizing the agreement.

If actions prescribed in the CA are carried out successfully, the need to list the species as threatened or endangered may be obviated. However, the CA provides that if there are threats to the survival of the Wet Canyon talussnail that are not or cannot be resolved through the CA, then action may be initiated to list the species under Section 4 of the ESA, through either a proposed rule or an emergency rule. Events that could require the USFWS to initiate listing of the species include, but are not limited to: failure to amend the Coronado Forest Plan to incorporate management direction for the species, failure to develop a monitoring plan acceptable to all signatory parties, or loss of funding or inability to implement protective actions.

THE FINE PRINT

The use of CA to remove threats to candidate species whose range is finite and naturally limited, that have threats to their existence that are relatively simple to resolve, and whose habitat is under the control of a single landowner is appropriate and convenient. Many candidate species fall under these criteria, and early efforts to conserve them via a less bureaucratic procedure than formal listing as threatened or endangered should enhance their potential for recovery.

However, species with less tractable problems (e.g., wide-ranging species occupying lands with multiple ownerships, or those with threats whose resolution may entail significant economic or sociologic burdens) may not accrue recovery benefits meaningful enough to justify going through the CA process. For those species, listing as threatened or endangered under the ESA may be warranted. Finally, agencies that assume CA will replace all proposals for listing, or that believe existence of a document is a surrogate for action, are likely to be disappointed. Many species are so close to the brink of extinction, or have threats that are so all-encompassing that listing under the ESA will be their only chance for survival. In addition, if meaningful actions are not applied USFWS will likely pursue listing for the species, even though a CA is in place.

The ESA is perhaps the best and most provident piece of wildlife legislation ever passed in this country. Application of its authority to accomplish meaningful recovery through CA is auspicious and timely.

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The Formation and History of the Malpai Borderlands Group

Bill McDonald[1]

Abstract.—A working group of landowners in Hidalgo County, New Mexico and Cochise County Arizona has joined together as the Malpai Borderlands Group, Inc. whose goal is to restore and maintain the natural processes, including fire, that create and protect a healthy, unfragmented landscape to support a diverse, flourishing community of human, plant, and animal life in our Borderlands Region. They encourage profitable ranching and other traditional livelihoods which will sustain the open space nature of the land for generations to come. Active cooperation has begun among the Malpai Borderlands Group and several Federal, State, and conservation organizations.

The Malpai Borderlands Group is attempting to implement ecosystem management on nearly a million acres of virtually unfragmented open space landscape in Southeastern Arizona and Southwestern New Mexico. The area involved is roughly pyramid-shaped, with the base of the pyramid running just east of Douglas, Arizona into New Mexico to the far eastern boundary of the 500 section Gray Ranch. The apex is just south of Rodeo, New Mexico on the Arizona-New Mexico state line and runs south to the Mexican border.

The elevation for this area ranges from 4500 feet, which is characterized by desert scrub and tobosa grasslands, up to 8500 feet which features Arizona Ponderosa Pine and Douglas fir. Within this diverse area of mountains, canyons and valleys are numerous riparian corridors with Sycamores and Cottonwoods. Several rare, threatened or endangered plant and animal species are found here. In addition, it is the only area in the United States where Gould's turkey and white-sided jack rabbits naturally occur. It is also home to such popular big game species as Coos deer, mule deer, pronghorn and Desert Bighorn sheep. But perhaps the most remarkable thing about this huge landscape is that less than 100 human families reside on it. Except for two small wildlife preserves, this is cattle ranching country.

The diversity of the land ownership is nearly as great as the country itself. The patchwork of ownership includes 53% private and 47% made up of state trust land in New Mexico and Arizona or public land managed by the U.S. Forest Service or the Bureau of Land Management.

On the surface, little has changed since the homestead days of the turn of the century when my family established our ranch in the area. It was a time when a regime of survival of the fittest established the carrying capacity of the land for people and their livestock, although not without cost to the land. Since that time, it might appear that not much has changed, but change is in the works.

About 4 years ago, in 1990, several of the area ranchers met at the Malpai Ranch in the San Bernardino Valley. The ranch is so named after the volcanic malpai rock which is prevalent in the area. We met to discuss what we saw as a deteriorating situation. Cattle ranching in the West, especially grazing on Public Lands, is under attack and on the defensive. Additionally, we were concerned about the future of the resource we depended on for our livelihood. The grasslands with some shrubs were moving inexorably to shrublands with some grass. As individuals living on our remote ranches, we felt ill equipped to deal with all this. It seemed as though the "dig in your heels" approach was doomed to failure, so we decided to embark on a different approach, to reach out to our critics and find common ground.

For two years, a small group of ranchers and environmentalists, together with scientist Ray Turner, met to discuss our mutual concern for the health and the open space future of our land. We called ourselves the Malpai Group and after two

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years, we drafted a Malpai Agenda. It addressed two major concerns. One was the threat of fragmentation of the landscape. Already some ranches on the fringe of our area had been subdivided. Fragmentation would permanently limit future options for a desired sustainable condition for the land. The second concern was for the declining productivity and loss of biological diversity accompanying the encroachment of woody species on grasslands. The consensus of the group was that more government regulation was not going to help. At best, it would replace one set of problems with another. The inevitable result of the free market would seem to be 20 acre ranchettes. This was not the future we wanted to see for this land.

We were not sure what we needed, but we felt, whatever it was should be driven by good science, should contain a strong conservation ethic, be economically feasible and be initiated and led by the private sector with the agencies coming in as our partners, rather than with us as their clients.

Two subsequent events took us to the next step. One was the suppression of a small brush fire just inside our area. The fire was suppressed by the land management agency in authority over the objection of the private landowner whose land intermingled with that managed by the agency. The fire was burning in some three-awn grass interspersed with creosote brush. The fire was bounded on one side by a road and on all other sides by bare ground and creosote brush. It wasn't going anywhere. The ranchers felt strongly that this fire should not have been put out. Fire suppression was believed to be a major factor in the encroachment of brush which has accelerated in this century and many ranchers, as well as others, felt it was time for fire to regain at least some of its naturally occurring role in the ecosystem. Another meeting was held at the Malpai Ranch, this time with some 30 ranches represented. Out of that meeting came a request for the land management agencies to work with the ranchers on a Comprehensive Fire Plan for the area. The response from the agencies was quick. A followup meeting with the Coronado Forest Service, the Bureau of Land Management in Safford, Arizona and Las Cruces, New Mexico, and the State Land Departments of New Mexico and Arizona represented, was held at the Gray Ranch. This two day meeting with representatives from the ranching community produced a commitment by all parties to work toward coordinated ecosystem management for the whole area. After all, fire crosses land ownership boundaries and fire is just one tool in managing landscapes. Clearly, it was time to figure out how to work across political boundaries to improve the land. The second event which transformed our group was the purchase of the huge Gray Ranch by the Animas Foundation from The Nature Conservancy. The Conservancy had purchased the ranch from a Mexican National who was willing to subdivide part of it in order to maximize its worth. Following the purchase, TNC began to look for a buyer. The community, fearful that the buyer might be the federal government, went to the Hadley family, twenty year owners of the Guadalupe Canyon Ranch, and asked them if it might be possible for them to purchase the Gray. The Hadleys, who have substantial resources beyond their cattle operation, were able to create a private organization, the Animas Foundation, with which to purchase and manage the Gray. It was important to TNC that the Gray be sold to a party which would keep it in open space and preserve and maintain its natural beauty. The ranch was purchased, therefore, with conservation easements on the private land guaranteeing that it would never be subdivided and with conditions establishing monitoring procedures to record the health of the range and habitats. To help manage the Gray, the Animas Foundation has invested in a Geographic Information System and has offered to extend its use to ranches involved with the Malpai Group. It has also provided some seed money to the group to help start up its operations. The Nature Conservancy became interested in the group and its goals and assigned a senior vice-president, the same man who negotiated the Gray Ranch purchase with the Animas Foundation, to work with the group and the Foundation at the request of the ranchers.

The upshot of these events was the establishment of the Malpai Borderlands Group as a 501(c)(3) nonprofit organization, capable of accepting tax-deductible contributions and of holding conservation easements. Our nine member board includes local ranchers, a scientist and a venture capitalist. Our cooperators include those ranchers in our planning area in Cochise and Hildago Counties, the State Land Departments of Arizona and New Mexico, the Coronado National Forest; U.S. Forest Service, the Soil Conservation Service in two states, the Bureau of Land Management in two states, the Hidalgo Soil and Water Conservation District, The Whitewater Draw Natural Resource Conservation District, the Game and Fish Departments in two states, the Desert Laboratory of the University of Arizona, The Nature Conservancy and the Animas Foundation. The goal statement of the group reads as follows:

Our goal is to restore and maintain the natural processes that create and protect a healthy, unfragmented landscape to support a diverse, flourishing community of human, plant and animal life in our borderlands region. Together, we will accomplish this by working to encourage profitable ranching and other traditional livelihoods which will sustain the open space nature of our land for generations to come.

We are in the process of putting together a five year plan for ecosystem management of our area. It will target three things: number one, conservation and land protection, including such things as on the ground projects, use of fire, holding of conservation easements, etc. Number two would be sustaining rural livelihoods which would include grass banks and other innovative approaches to grazing, possibly cooperative marketing of beef, and exploring of other economic opportunities with low impact on the environment. Number three is science and education which includes a comprehensive resource inventory of the area including threatened and endangered species, game and nongame and archaeological. We are offering our area as a laboratory for research with our emphasis being the merging of theoretical science with applied science.

All of this sounds wonderful, but will this ship float? We've been at this about a year now and here's what we have accomplished so far: We have had assigned to us a senior range conservationist from the Soil Conservation Service, the only field-level SCS individual who can work in two states. The Forest Service also has allotted much of the time of their senior range conservationist for the Coronado Forest to our project. The BLM District Manager in Safford, AZ and Las Cruces, NM regularly attend our meetings and have our project as their highest priority.

We have completed the first approved fire prescription ever for the Borderlands Region. It involved two states, four private landowners, two BLM Districts, two State Land Departments, the Forest Service, the Game Departments in two states, the U.S. Fish and Wildlife Service in two states, and coordination with Mexico. It included a Wilderness Study Area and needed to comply with the National Environmental Policy Act, the Endangered Species Act, and the Antiquities laws. We did it in eight months.

We have completed a brush removal and native reseeding project. There is much debate and controversy surrounding the use of exotic grass species on range restoration projects. The cost and difficulty of reestablishing natives with native reseeding exacerbates the situation. There has been limited success in using exotics as nurse plants to establish an environment in which natives can return. We intend to tackle this issue head on.

The Geographic Information System is going in at the Gray Ranch. This will make inventory, monitoring and mapping information readily available to those who need to use it. Confidentiality of information on private lands, access issues, etc. will be handled on a case by case basis.

We were fortunate in getting a grant through the Rocky Mountain Forest Research Station of the U.S. Forest Service for research in our area. This will include a literature review of what is already known, field research including remote sensing and ground truthing to attempt to determine the landscape trajectory and the development of an integrated model of vegetative response to various factors such as fire, grazing and climate change. The significant findings of this research will be published, subject to peer review, and available for those who might be interested in using them. This project will be a coordinated effort between the Research Work Unit and the Malpai Group. While some might find this type of research threatening to current land uses, we recognize that mankind is the only species capable of considering the consequences of his actions on the land and of making an effort to modify them. In order to do that, we need some kind of baseline against which we can measure.

The Animas Foundation is co-sponsoring a Chair for an Arid-Lands Ecologist with the Desert Laboratory of the University of Arizona. That individual would head up the research effort in our area. A nationally renowned scientist is very close to accepting this position. We have, in our area, an ongoing project involving the threatened Chiricahuan Leopard Frog. A rancher has been hauling water to one of his stock ponds to save the frogs which reside there. Some scientists feel that isolated stock ponds are the frog's best chance for survival. Ponds fed by active acquifers usually contain bullfrogs, an introduced species, which prey on the Leopard Frogs. We intend to complete a project which will provide permanent water in the stock pond for the frog and also help the rancher in his overall management. Ranch management and the needs of endangered or threatened species can be coordinated. Our private landowners would like to be proactive on this issue.

Perhaps the most exciting thing we have become involved in is grass banks for easements. A grass bank is a concept we came up with whereby grass on one ranch would be made available to another rancher's cattle in return for an equal conservation value for the land. In the two grass banks we have negotiated so far, the value received for the grass has been as easement on development rights to be held in perpetuity by the Malpai Group in return for our paying for the rancher's use of the grass. This accomplishes conservation in two ways: one, the rancher's own grass resource is rested and two, his land will never be subdivided and developed. There are two caveats attached to these easement agreements. One is that should our group disband sometime in the future and be unable to maintain the easement, the easement would revert back to the landowner if no acceptable substitute holder could be found. The second caveat involves change in the status of surrounding state and federal lands which would make an open space livelihood on the private lands impossible. Under these circumstances, the easement would revert back to the landowner. This puts the onus on the state and federal governments to make a commitment equal to the private landowner's to an open space future for the area. We have three more grass banks and five more easements in negotiation.

In conclusion, the success of this effort so far has resulted from the local community, the landowners, being the drivers. The participation in this effort is voluntary for individuals as well as agencies. The enthusiasm, support and participation at this point exceeds our expectations. In a political climate where the traditional position on this issue of land use is usually to be at one end of the spectrum or the other, we find ourselves in the "radical center." We invite you to join us right there.

Sky Islands: Gloom Or Glory

Ervin H. Zube[1]

Abstract.—This paper addresses the question of values attributed to mountain landscapes, how they have evolved historically, and what factors have influenced that evolution. As the title suggests, mountains have sometimes been preserved in less than favorable fashion. Furthermore, values have been conflicting. Among the values explored are those of scenery, recreation, wilderness, timber harvest, and watershed protection. Gloom and glory perceptions and values are illustrated with both historic and contemporary examples from diverse geographic settings, but with specific emphasis on the Southern Arizona Sky Islands.

INTRODUCTION

When the invitation was extended to submit an abstract for a paper on landscape values, and particularly on values related to mountain landscapes, the first thought that came to mind was of a book written by Marjorie Hope Nicholson. It has the intriguing title, Mountain Gloom and Mountain Glory (1959). That provocative title seemed to fit the conditions that prevailed around the concept of the Sky Islands National Recreation Area in Southern Arizona that had been discussed for more than two years.

Nicholson traced the perceptions of and attitudes towards mountains from the classical era of Greece and Rome to the mid-Nineteenth Century and William Wordsworth. Her sources of information included literature, theology, philosophy, and geology. While her book still stands as the major scholarly work on this topic, others provide additional insights and, collectively present a fascinating chronicle of the diversity and changes in perceptions of and attitudes towards nature and mountains over time. The following presents a sampling from that chronicle.

Nicholson suggests that the Greeks, living in a mountainous region, "accepted them as an integral part of life, . . ." (1959:38). Architectural historian, Vincent Scully (1979) augments her interpretation and, in discussing the Hellenic Period (8th to the 4th Centuries BC), adds the attribute of sacredness to mountain and landscape when he notes relationships between temples and specific elements in the landscape, including mountains, that were considered sacred.

Writing about the Medieval Era, English art historian Kenneth Clark (1979) suggests that "The average layman would not have thought it wrong to enjoy nature; he would have simply said that nature was not enjoyable . . . The fields meant nothing but hard work" . . . "the sea coast meant danger of storm and piracy . . ." (1979:3). Furthermore, until about 900 A.D., the landscapes of Europe underwent a significant transformation as the cleared fields converted to forests because of the uncertain social conditions that prevailed and caused people to gather in protective communities (Darby, 1956:202-203; Mumford 1961:248-253).

Nicholson also describes the conflicting arguments advanced by Calvin and Luther in the Sixteenth Century about the origin of mountains. She suggests that Calvin, having spent many years in the Swiss Alps, believed that all nature that God had created was beautiful. In contrast, she suggests that Luther, being a lowlander for whom mountains presented a sense of terror and the unknown, believed that mountains were a product of the flood that God had sent to punish Adam and Eve and all others who had sinned. In 1592, the question of whether mountains had been a part of the creation of the earth was considered at the Jesuit College in Coimbre. It was concluded that they were because mountains were both utilitarian and beautiful. Their utility was defined primarily in terms of their role in providing water; as the instruments that caused the moisture-laden air to rise and then produce rain which was carried by streams and rivers to the valleys where humans used it (Glacken, 1967:376). This interpretation of all nature existing to satisfy hu-

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man wants and needs was also evident in the Doctrine of Signatures that prevailed in England until the late seventeenth-century. That was the belief that every plant, by virtue of its' color, shape, or texture indicated its use for humans. Plants with spotted leaves would cure diseases that created spots, perhaps measles, and yellow leaved plants would cure a disease such as jaundice (Thomas, 1983:84).

Another factor that added to the prevailing "mountain gloom" perception was the basic concept of landscape beauty that prevailed well into the eighteenth-century, particularly in England. Beauty was associated with "the tamed and fertile landscape over which man had asserted control" (Thomas, 1983;258). Beauty was found in neat orderly geometric landscapes, the kinds of landscapes that were defined by hedge-rows and stone walls, and that were associated with their beliefs about good agricultural stewardship, and not with mountains (Zube, 1986).

Mountain gloom was also present in New England. William Bradford, who was the governor of Plymouth Plantation for 33 years, wrote in 1630, a history of his early experiences and perceptions of the New England landscape. In one description he invoked the symbol of Pisgah, the mountain from which Moses viewed the Promised Land. He wrote, "Besides what could they see but a hideous & desolate wilderness, full of wild beasts & wild men? and what multitudes there might be of them they knew not. Neither could they, as it were, goe up to the top of Pisgah, to view from this wilderness a more goodly countrie to feed their hopes: for which way soever they turned their eyes (save upward to the heavens) they could have little solace or content in respecte of any outward objects" (Bradford, 1630).

Mountain glory took a long time to surface and replace mountain gloom. Nicholson suggests, however, that "If the Mountain Glory did not shine full splendor in the earlier eighteenth-century, the Mountain Gloom was gone"(1959:345).

Mountain gloom of a sort prevailed in the United States until the second-half of the nineteenth century. Much earlier, in the eighteenth century, mountains, primarily the Appalachian Chain provided the first major barrier to western expansion. Once that barrier was overcome, there were the Rocky Mountains farther to the west to be conquered. One can make an argument that it was the recognition of the beauty of Yosemite Valley in 1865 and yellowstone National Park in 1872 that marked the beginning of the demise of mountain gloom in the United States, a demise that was aided and abetted by the dramatic landscape paintings of Bierstadt, Moran, and others from the Hudson River Valley School of painting who traveled to the west, captured the dramatic mountain landscapes on canvas, and introduced them to a receptive audience in the East (Truettner, 1991).

Nevertheless, the Mountain Gloom—Mountain Glory concept can provide a useful metaphor, albeit, defined somewhat differently than Nicholson did, for discussing landscape values related to the sky islands of southern Arizona.

LANDSCAPE PERCEPTION

In a provocative essay entitled, "The beholding eye Ten views of the same scene" geographer Donald Meinig suggests, "Take a small but varied company to any convenient viewing place overlooking some portion of city and countryside and have each, in turn, describe the landscape . . . It will soon be apparent that . . . we will not — we cannot — see the same landscape" (1979:23). Landscape perception research tends to support Meinig's assertion, but with one important caveat. The individual differences alluded to by Meinig have not been the focus of most landscape perception research which has most often focussed on the collective perceptions of groups rather than of individuals. Of interest has been the levels of agreement among groups defined by occupation, place of residence, and/or orientations to nature, for example, farmers, professional resource managers, real estate sales-persons, picnickers, canoeists, motor-boat riders, off-road vehicle recreationists, and hikers. Frequently, there have been important differences found among these groups, or sub-sets of them. The differences have not been expressed in terms of whether the landscape is valuable or beautiful, but rather in terms of for what purposes it is valuable or in terms of how its' value or beauty should be exploited (Pitt and Zube, 1986).

WORKSHOPS AND PRECEDENTS

In Searching for information about values associated with the Sky Islands of the Coronado National Forest, I have focussed on the recorded comments from workshops organized by the Forest to engage the public in discussions about a proposed Sky Islands National Recreation Area (NRA) (USDA Forest Service, Southwestern Region, 1992a,1992b) and on a file of newspaper clippings and newsletter articles made available to me by the Coronado National Forest. Workshops were held in Tucson, Sierra Vista, Green Valley, Safford, and Douglas on March 23 through 26 and on the 28th. Participant comments were recorded in response to discussions about such topics as: reasons for and against the NRA, results/impacts/effects of designation, and management implications of designation. Three hundred and thirty-six persons participated in small groups of eight to ten persons. A total of 1,193 comments were recorded.

For this analysis a systematic sample was drawn of ten percent of the comments. That sample was then analyzed and sorted into five content categories, two of which relate directly to the topic of this paper. Before presenting the results of that analysis, however, a brief review of the series of events within which the workshops took place provides a useful introduction for better understanding of the outcomes of the workshop.

As suggested in Table 1, the Sky Islands NRA proposal was a newsworthy topic of interest for approximately 16 months and introduced, or, at least reinforced the concept of biodiversity into the local media. During that period of time, the NRA was a topic of discussion in newspapers, newsletters and various mailings throughout the region at least 25 times. In addition, an announcement of the workshop discussions appeared on the "Across USA page of USA Today.

An important event that followed announcement of the NRA proposal was the creation of the Sky Island Alliance and the issuance of a proposal for a Sky-Island National Biodiversity Conservation Area, the objective was to have, "the Forest Service and Congress designate the most ecologically rich mountain ranges of the Coronado national Forest as a biodiversity area that included "all ranges in Southeastern Arizona with elevations over 8,500 feet (supporting large areas of conifer forest at their summits), plus two additional ranges that provide habitat for rare species and crucial international migration corridors for wildlife . . ." (1992,3). In addition, there were, and still are strong negative feelings among environmentalists about the University of Arizona being responsible for the construction of several telescopes on Mount Graham, a sky island that is habitat for an endangered red squirrel and that is sacred to the San Carlos Apache Indian Tribe. It is possible, but not easily confirmed at this time, that these events had some effect on the responses of participants in the workshops. Both of these activities probably influenced public attitudes about the proposed NRA.

Table 1.—Significant events in the evolution in the evolution and demise of the sky island proposal.

May 29, 1991	Announcement of consideration of the Sky Islands National Recreation Area proposal by the Coronado National Forest
Fall, 1991	Formation of the Sky Island Alliance, an organization of conservationists and scientists
January 15, 1992	Sky-Island National Biodiversity Conservation Area Proposal (draft) completed by the Alliance
March, 1992	Five workshops held throughout the region to elicit public discussion and comment on the NRA proposal
March 24, 1992	Tucson Citizen (newspaper) headline, Public saying no to the Forest Service (Sorenson)
October 2, 1992	Tucson Citizen headline, "Forest Service grounds "Sky Islands" plan (Sorenson) Arizona Daily Star (newspaper) headline, The nays have it (Kreutz)

FINDINGS FROM THE WORKSHOPS

Collectively, workshop participants generated a wide array of values or special qualities (Table 2) which were categorized as: activities and opportunities, aesthetic resources, cultural resources, and natural resources. There were few surprises in the list and they suggest that the discussions led to a reasonably comprehensive listing of the special features and opportunities that exist in those areas. There was notable exception, however, and that was the single word "home", which, one could assume was written by someone who has a home on leased land in the forest.

The concerns and questions category turned out to be more provocative and informative. This category produced four sub-categories: biodiversity, increased use, self interest, and other.

As indicated in Table 3, primary emphasis appears to have been on issues of self-interest, on what an NRA designation means to the individual participating in the workshop, whether it was their personal use of the area, "my cabin on leased land", or the continuation of ranching. These are both understandable and unsurprising. In some respects the comments reflect the kinds on concerns that are frequently associated with the uncertainties of impending change (Zube and Sell, 1986). It is probable that the concerns about increased use also reflect concerns about impacts on personal environments in the forest and on biodiversity. At this point in time there is no way to parcel out the relative emphases. The catch-all "other" category suggests that there was some uncertainty or suspicion about Forest Service procedures and motivations as indicated by comments such as "What are the Supervisor's intentions? and How available will the information be on the process for the NRA?

DISCUSSION

Where does mountain gloom and mountain glory enter into this narrative about the Coronado National Forest Sky Islands? In the simplest of interpretations, one can say that one persons glory is the other persons gloom. Perceptions of mountain gloom or mountain glory today is not dependent upon beliefs about the creation of the earth or the extent of human dominion over the earth. It is, however, about conflicting perceptions of how the sky islands should be managed, for what purposes, and to serve whom.

During the sixteen month time period in which the Sky Island NRA proposal was a news item, there were three primary interest groups: the Forest Service, the Sky-Islands Alliance, and the interested public, which included at least the 336 persons who participated in the workshops and others who wrote letters. The primary vehicle that the public had available to voice their opinions was the workshops that the Forest Service sponsored. Nevertheless, within the region the activity was clearly of broad interest as indicated by the news coverage. And, some level of national interest apparently continued as the National Geographic News Service issued, from their Washington, D.C. office, a News Feature that was distributed across the country on May 3, 1993,

Table 2.—Special qualities and values identified at the workshops.

ACTIVITIES

- * Access and natural resources are special.
- * Birding, biological.
- * Dirt roads and back-country.
- * Recreation, extreme change, climatic relief.

AESTHETIC RESOURCES

- * Beautiful and inspirational.
- * Incredible scenery.
- * Escape.
- * Quietness, no parties
- * Wilderness, solitude.

CULTURAL RESOURCES

- * Archaeological areas.
- * Sacred to Indians.
- * Pinaleno Mountains contain rich cultural, historic, educational, and scientific value as they relate to the Gila and Sulphur Springs Valley
- * History and multiple-use, diversity meets needs of people.
- * Multiple-use concept is what makes it special, why do we need a change? amen.
- * Scientific value i.e. telescopes (Mt. Graham).
- * Home

NATURAL RESOURCES

- * Biodiveristy
- * Hummingbirds.
- * Primitive areas.
- * Streams and riparian areas.
- * Two bioregions, two deserts.
- * Vegetation
- * Weather
- * Wildlife in general.
- * Wildlife migration routes

Table 3.—Concerns and questions raised at the workshops.

BIODIVERSITY.

- * Advertising and designating of this area (Chiricahuas) will cause great havoc to the special biodiversity.
- * No one wants to see these unique and biodiverse mountains changed in any way that would promote more use and development.
- * Destruction and degradation

INCREASED USE

- * How much will use increase if this proposal (NRA) is implemented?
- * Are seeing more use now.
- * More development, potential for increased use, maybe overuse.
- * Danger in attracting more people, are we ready for that?
- * Will NRA designation increase development?

SELF INTEREST

- * Our cabin is safe under the current plan, designation could force us out.
- * Ways to make ranching compatible with other uses: practices that encourage biodiversity by ecological repair, like gabions in dried out washes.
- * Let Graham County decide what's best for Mt. Graham.
- * Will leased land be renewed?
- * Do all of us as citizens have a basic right to recreate an public land?
- * Is the NRA taking into consideration the current users of the National Forest System?
- * Don't fix it if it ain't broke.
- * Will the NRA accommodate the needs/uses of the people using the (National) Forest System?
- * We would like information on impacts to specific user groups and resources, will: leases change, skiing change, hunting access change, wildlife and flora be affected?

OTHER

- * Money should not be basis of decision.
- * The impression among some of the publics is that public input exercises are a are just a pacifier, that the Service goes ahead and does what they want to do anyway
- * Where can people find the Forest Plan?
- * What are the Supervisor's intentions?
- * Does designation give Forest Service all the power to manage the area?
- * How could this possibly improve recreation in the areas?
- * Why not expand wilderness areas?
- * How would designation effect management?
- * How available will the information be on the process for NRA?
- * Will there be more money for rangers and enforcement?
- * Why do it?

nearly one year after the issue had been dropped from the local newspapers. The release was given an eye-catching headline, "Controversy Looms Over Arizona's Sky Islands" (Gross,1993). That article reduced the disagreement to a two-sided affair, the Forest Service and the Sky-Island Alliance. My interpretation is that they left out the powerful voice of the local people who can, in the long run, influence who experiences a sense of gloom and who experiences a sense of glory, and therefore, what the probable future is for the forest. Clearly, For many who voiced opinions about the NRA at the workshops, or in letters, the NRA represented a specter of gloom. Those for whom it might have represented a sense of glory, however, were conspicuously quiet.

NOTE: *The assistance of Steve Plevel, Coronado National Forest (Ret.) in the use of records relating to the Sky Islands NRA proposal workshops and clipping files is gratefully acknowledged.*

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From Casas Grandes to Casa Grande: Prehistoric Human Impacts in the Sky Islands of Southern Arizona and Northwestern Mexico

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Abstract.—Cultures, past and present, like ecosystems, are dynamic entities, and the relationships between them must be carefully considered. The relationship between people and the natural environment has been a topic of archaeological investigation for many years. Faunal, floral, and climatological data recovered from archaeological sites can be used to reconstruct important aspects of past ecosystems and to determine how they have changed through time. The picture that emerges is one of interaction between a constantly changing environment and a constantly changing human system. This paper summarizes our current knowledge of the prehistory of the Sky Islands, in terms of potential human impacts to the environment and discusses strategies for gaining a better understanding of past relationships between people and their environment in the southwestern United States and northwestern Mexico.

INTRODUCTION

"The human impact on environment is not simply a process of increasing change or degradation in response to linear population growth and economic expansion. It is instead interrupted by periods of reversal and ecological rehabilitation as cultures collapse, populations decline, wars occur, and habitats are abandoned. Impacts may be constructive, benign, or degenerative (all subjective concepts), but change is continual at variable rates and in different directions. Even mild impacts and slow changes are cumulative, and the long-term effects can be dramatic (Denevan 1992:381)."

The belief that New World peoples, for many thousands of years, lived in harmony with nature without causing significant alterations to their environment has been a long standing and popular notion (Denevan 1992; Sale 1990). Contrary to this traditionally held viewpoint, the North American landscape was not a sparsely populated and "pristine" environment when discovered by Columbus in 1492 (Butzer 1990; Denevan 1992). Archaeological research is becoming increasingly important in demonstrating that human activities such as hunting animals and gathering plant foods, clearing land for agricultural fields, cutting wood for fuel and to construct dwellings, and many other endeavors resulted in both intentional and unintentional changes to the natural landscape (Cartledge and Propper 1993). The landscape we see today is the result of a lengthly and dynamic history of interaction between humans and their environment, an interaction that began long before the arrival of European explorers and settlers.

Humans also have been an important component of the Madrean Archipelago, or Sky Islands, landscape, for least 10,000 years (Figure 1). Evidence of past human use is found virtually everywhere one looks; from the high peaks of Mt. Graham, to the inner canyons of the Chiricahuas, to the flanks and ridges of most of the lower mountain ranges. And of course, substantial evidence exists in major river valleys and their tributaries such as the Gila, Santa Cruz and San Pedro. People have used the sky islands in a variety of ways; from short-term hunting, plant gathering, and mining, to seasonal or nearly permanent occupation and plant cultivation. Some of the sky island mountain ranges are among the most rugged in the Southwest, yet they contain an

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abundance of stone resources and minerals, large and small game animals, and were a source of spiritual power to peoples living in and surrounding them. Prehistoric adaptation to these areas involved a range of land use patterns that were as diverse as the environments being exploited, while surrounding river valleys provided important riparian resources and served as natural corridors for communication and transportation.

An awareness of earlier occupations has existed at least since Spanish explorers traveled northward from central Mexico. Abandoned ruins served as landmarks for the first major entrada into the area, that of Francisco Vasquez Coronado in 1540 where the mysterious Red House, or Chichilticale, near the base of Mt. Graham marked the route (Udall 1991). Other ruins such as Casas Grandes, located in northern Chihuahua, Mexico and Casa Grande, the Hohokam Great House located on the banks of the Gila River, may have been abandoned for less than a century prior to exploration of the region by Spaniards.

We believe that archaeological reconstructions can contribute valuable information to our understanding of the historical development of ecosystems in the sky islands. It is generally recognized that humans have had a significant impact on flora, fauna and climatic conditions within the last century, however we know very little about the impacts that prehistoric inhabitants undoubtedly made to the landscape (Bahre 1991). Human activities may affect all the major aspects of biotic communities including composition, biomass, diversity, density and productivity (Dinacauze 1987:283). Modern ecosystems have histories of which humans are a part and knowledge of this history is essential to an understanding of ecosystem dynamics (Crumley 1993). Here we review current knowledge of prehistoric occupation in southeastern Arizona, southwestern New Mexico and northern Mexico in terms of effects past lifeways may have had on the environment. Archaeological and paleoenvironmental data are used to consider the changes that occurred in the prehistoric environment as a result of human impacts. This information is then used to emphasize the importance of documenting and understanding the interactions of humans and ecosystems through time.

Figure 1.—Sky island region of the southwestern United States and northwestern Mexico.

PREHISTORY OF THE SKY ISLANDS

Little archaeological research has been conducted in the sky islands region in comparison with other parts of the Greater Southwest. In the 1920s, geographer Carl Sauer and archaeologist/geographer Donald Brand, early proponents of a cultural-historical approach to man-land relationships, conducted archaeological surveys in southern Arizona and northern Mexico, and referred to the area as "a neglected corner" (1930). With the exception of a few excavated sites, and even fewer large scale surveys, the area still remains poorly known archaeologically (Dean and Ravesloot 1993). This is particularly true of northern Chihuahua and Sonora. For all practical purposes, our only information about the prehistory of northern Chihuahua comes from the site of Casas Grandes (Figure 2) (Di Peso 1974; Ravesloot 1988; Minnis 1989; Woosley and Ravesloot 1993). A more detailed summary of previous archaeologial research is presented elsewhere; for example, see Phillips 1989, Gumerman 1991, Woosley and Ravesloot 1993, and Fish and Fish 1994.

Humans have been present in the area for at least 10,000 years and are perhaps best known in association with Pleistocene mammoths found in the San Pedro Valley (Haury et al., 1959). Semi-nomadic peoples who relied on hunted and gathered plant and animal resources and probably made seasonal rounds between the uplands and lowlands occupied the region for many centuries, in what is termed the Archaic Period. A shift to cultivation of domesticated plants near the end of the Archaic is evident from excavated sites in the northern Santa Rita Mountains (Huckell 1984), Empire Cienega, and the San Pedro and Sulphur Springs valleys (Huckell 1988, Huckell and Huckell 1988).

The biodiversity documented for the sky islands is matched by the cultural diversity evident in the archaeological record after around A.D. 700 (Doyel 1993) when cultivation of domesticated plants became a major component of the subsistence strategy. Minor cultural traditions, regional variants, and a blending of cultures have all been proposed since the material culture does not fit neatly into the three major traditions defined for the Greater Southwest (i.e. Anasazi, Mogollon and Hohokam). The only general agreement appears to be that this "International Four Corners" area (Minnis 1989) lies south of Anasazi territory and north of Mesoamerica (Fish and Fish 1994). Thus, we have an array of terms such as Dragoon Culture, O'otam, Chihuahua frontier, Trincheras Culture, Salado, Hakataya, perhiperhal Hohokam, San Simon Mogollon, Anasazi migrants, and others to describe the variability observed in the archaeological record. The sheer number of these terms illustrates the material culture differences documented within small geographic areas of the sky islands. There is little apparent comparability between valleys and across mountain ranges.

The various cultural traditions became well established by about A.D. 1000 with distinctive material traits, subsistence patterns, and evidence of substantial regional interaction (Doyel 1993:58). Considerable changes are evident in material culture, architecture and settlement patterns during the next century. The thirteenth and fourteenth centuries saw the development of massive structures such as Casa Grande and the large trading center of Casas Grandes. By the mid 1400s, however, a major cultural devolution and/or abandonment had occurred.

Figure 2.—Casas Grandes, Chihauhua, Mexico. Photgraph by John Ravesloot.

Traditionally, environmental conditions have been the most common explanation for these cultural changes. As Gumerman and Gell-Mann (1993:30) have stated:

> *"There can be no question that perturbations in the environment affected the cultural history of both small drainages and large provinces. The close correlation of only a few variables (such as the numbers, density, and distribution of population) with environmental conditions underscores the important role of environment in most schemes of culture changes."*

What needs further consideration, which we do here, is the role that human activities and long-term settlement had on environmental conditions rather than viewing the environment as the major causal factor in cultural change.

We focus on the later prehistoric time periods, when people became agriculturalists, because it was during this time that inhabitants of the sky Islands had the most profound impact on the landscape. As stated by Wills (1988:1),

> *"Farming is an economic strategy predicated on the manipulation of plant biogeography and productivity. In contrast to foraging strategies, which respond largely to natural resource availability, the use of domesticates signals an investment in actually managing the availability of future resources by controlling plant ecology and physiology."*

We ask the question: To what extent did prehistoric agriculturalists modify the natural environment by culturally affecting distributions of plants and animals? Impacts from farming practices, as well as from hunting strategies, fuelwood harvesting, and purposeful burning are examined to determine how each contributed to the creation of distinctive anthropogenic landscapes. Because of a lack of excavation data, the examples we use come mainly from the larger, well-known sites located mainly in river valleys (Figure 3).

AGRICULTURAL STRATEGIES

A wide variety of farming techniques including irrigation, floodwater, and dry farming were employed to grow food within this geographically diverse region (Fish and Nabhan 1991; Masse 1991). Each required a considerable investment of labor that resulted in substantial cultural modifications to soils and landforms, plant diversity, animal populations and habitats. Corn, beans, and squash, introduced from Mexico and now considered native to the region were the major crops cultivated.

Remnants of ancient canal systems have been documented in northern Chihuahua at Casas Grandes (Doolittle 1993), in the the floodplain of the Santa Cruz River near Tucson (Bernard-Shaw 1987), along the Gila River in the vicinity of Casa Grande ruins (Crown 1987) and Snaketown (Haury 1976), and along the Salt River in metropolian Phoenix (e.g., Ackerly, Howard and McGuire 1987; Nials and Gregory 1989; and Nicholas and Feinman 1989). In terms of scale and complexity, the Hohokam irrigation system along the Salt River in the Phoenix Basin is the most sophisticated. For this system alone, archaeologists have reconstructed over 500 kilometers of main canals from excavation data and aerial photography. This figure does not include additional components of the system such as distribution canals, field laterals and irrigated fields. During the Classic period, between approximately A.D. 1200 and A.D. 1400, roughly 150 square kilometers may have been irrigated on the south side of the Salt River (Nicholas and Neitzel 1984:168). Clearly, the construction and maintenance of these systems altered the landscape of the river valleys.

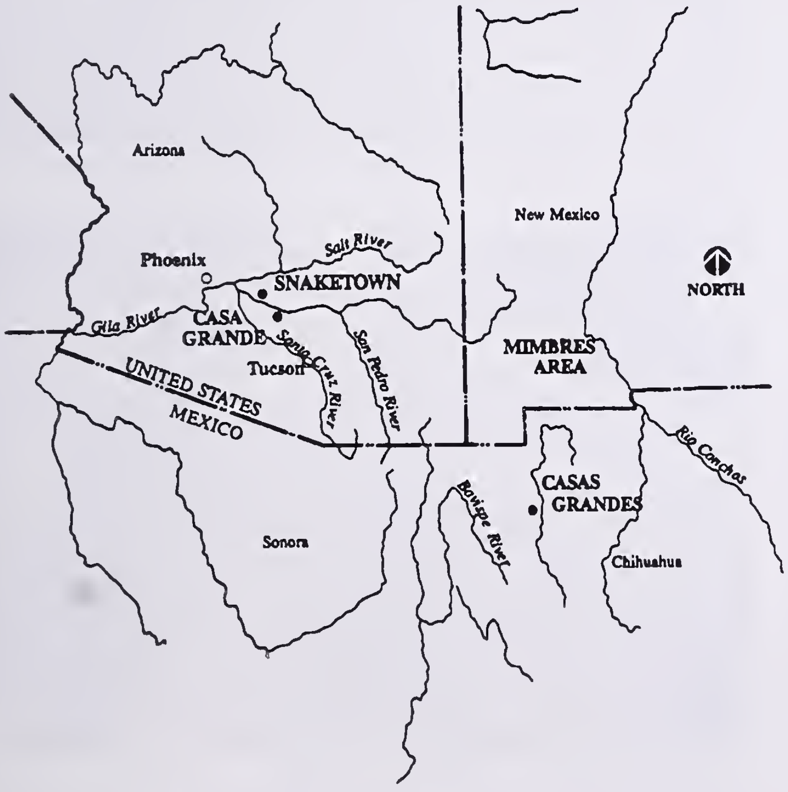

Figure 3.—Major archaeological sites of the Sky Island region.

The timing and availability of water was critical to the operation of these systems and to ensuring a successful harvest of crops. Tree-ring information has been employed to reconstruct paleoclimatic conditions and streamflow histories for the Salt and Verde rivers (Graybill 1989, Graybill and Nials 1989). This research has revealed that Hohokam canal irrigation systems were extremely vulnerable to periodic events such as drought, snowmelt, and rainfall, and that flood rather than drought conditions may have been a major factor in agricultural failures. Similar studies need to be conducted in other major river valleys.

Floodwater farming systems, both floodplain inundation and ak-chin, are associated with a variety of features that include linear rock alignments, earth berms, and small ditches or canals to capture runoff. Recent geomorphological studies of the Santa Cruz River near San Xavier have established a possible link between hydrological events such as episodes of flooding, channel entrenchment, and erosion with prehistoric human modifications of the floodplain and settlement pattern changes through time (Waters 1987, 1992). Waters (1992:179) suggests,

> *"Although there is no direct evidence to support the hypothesis that human actions on the floodplain resulted in entrenchment, the temporal correlation between the occupation of the Santa Cruz River by Hohokam agriculturalists and the increased frequency of floodplain entrenchment is striking. It appears that the Hohokam agriculturalists may have made the same mistakes that historic farmers made in the late nineteenth century."*

Dry farming systems comprise another important component of agricultural strategies. They typically consist of rock piles, linear alignments, or other features designed to capture rainfall runoff. These systems were used for cultivation of domesticated plants as well as for enhancement of native vegetation. A major drawback of their investigation is that these generally nondescript features have only recently been recognized and recorded with any consistency in archaeological surveys (Figure 4). Over 1,200 acres of contiguous fields have now been documented in the foothills of the Tortilla Mountains at the Marana complex of late prehistoric sites (Fish et al. 1992), and similar rock pile sites are being investigated in the northern Santa Rita Mountains (Coronado National Forest site files).

Native plant species were also cultivated, some of which could be grown during the cool season in fallow fields or in dry farming fields in the uplands. These semi-domesticated plants include barley, chenopods, amaranth, devil's claw, cholla, and agave (Nabhan et al. 1978; Fish et al. 1985; Gasser and Miksicek 1985; Bohrer 1991). Cholla and agave appear to have been grown prehistorically outside their known native habitats (Bohrer 1991:228), often associated with rock piles or alignments. Long-term affects on species composition and distribution are unknown. All methods of cultivation appear to have modified uncultivated plant species density and distribution within the vicinity. Pollen samples from agricultural contexts include a variety of weedy flora in response to soil disturbance situations (Fish and Fish 1992:274). Vegetation disturbance communities have been mentioned in archaeological reports but rarely examined from an ecological perspective.

FAUNAL SPECIES AND HABITATS

Animal species and their habitats were affected by vegetation modifications that occurred as a result of agricultural practices (Fish 1984; Minnis 1978, 1985; Szuter 1991). Evidence from excavated sites within the sky island region indicates that small and medium sized mammals were much more common than artiodactyls such as deer, presumably because they were more readily available as a result of alterations the inhabitants made in fields surrounding villages. The creation of disturbed areas near agricultural fields, houses and villages also was favorable to rodent populations which were then exploited (Szuter 1991:285). There is evidence for differential exploitation of cottontails and jackrabbits through time as agricultural practices intensified. Jackrabbits generally prefer less vegetative cover, or open habitats, such as fields while cottontails prefer more shrubby vegetation. With an increase in land clearing for settlement and farming, the exploitation of cottontails relative to jackrabbits decreased through time in the archaeological record (Szuter 1991).

Figure 4.—Rock Pile Agricultural Features, Marana Site complex. Photograph by Paul Fish.

Water control systems created habitat for water-associated species such as fish, a variety of birds, and occasionally beaver and muskrats (Szuter 1991:284). Avifauna collections obtained through archaeological excavations contain numerous bird species that would have been associated with a water habitat including the White Pelican, Mexican Duck, Ruddy Duck, Marsh Hawk, Sandhill Crane, the Great Blue Heron, Canada Goose, White-fronted Goose, and Snow Goose. Their occurrence in archaeological collections reflects the presence of nearby streams, reserviors, and cienegas (McKusick 1974:280; McKusick 1976:377).

At the University Indian Ruin in Tucson, 15 species of birds have been identified (Ferg 1985:120). All species except the Indian Domestic Turkey can be found today although in small numbers and they are more common in grassland areas. Examination of the prehistoric distribution of avian species across the sky islands has yet to be undertaken but could provide intriguing information regarding species diversity and patterns of exploitation.

Fish have never been considered particularly important as a prehistoric food source in the sky islands although this may be more a reflection of archaeological techniques than actual use. Fish bones are extremely small and fragile and will pass through 1/4 inch mesh screens typically used in archaeological excavations. During recent excavations at the Pueblo Grande site near Phoenix 1/8 inch mesh screens were used. Analysis of the recovered faunal remains found that fish comprised almost 30 percent of the bone material and appears to be second in importance only to rabbits (James 1994).

Among the larger mammals there are some indications that deer and bighorn sheep distributions were influenced by human alterations to the environment (Szuter 1991:282) although again, data are limited. Bighorn sheep petroglyphs are commonly found at rock art sites throughout southern Arizona and northern Mexico (Coronado National Forest site files; Schaafsma 1980)(Figure 5). Their image was also painted on pottery by Hohokam and Mimbres peoples, and has been carved on bone implements and modeled in clay. However, this species, while consistently occurring in the archaeological record,(e.g., sites in the Phoenix and Tucson areas, the Santa Rita Mountains, and Casas Grandes) has not been recovered in substantial quantities (McKusick 1974:253; Greene and Mathews 1976:376). For example, at Snaketown, only 31 bones representing 19 individuals were excavated from features that cover a temporal span of roughly 1,000 years (Greene and Mathews 1976:376). Archaeological speculation is that bighorn sheep may have been scarce prehistorically, or people may have not relied on this species as a food source (McKusick 1974), or that the limited use may reflect religious practices or taboo (Haury 1976:114).

Casas Grandes data provide another example of changes in animal species distribution. Excavations indicated that pronghorn sheep was a dietary mainstay at the site along with heavy reliance on mule deer and bison (McKusick 1974:253). The presence of bison indicates that Casas Grandes was within bison habitat around A.D. 1200. Today, only a few remnant herds are reported in northern Chihuahua (DiPeso 1974: Vol 8:243). The archaeological evidence suggesting that the American Bison was a primary meat source during prehistoric times indicates "... that the once-available bison was probably hunted out of this portion of its natural habitat, not by nature, but by some outside force such as man (Di Peso et al., 1974,Vol. 8:250-251).

Some faunal species were used for reasons other than food. This exploitation can not be overlooked in examining the amount of ecological influence that humans had on their habitat. At Casas Grandes thick-billed and lilac-crowned parrots, scarlet and military macaws and the common turkey were raised and traded, presumably for their feathers and for ceremonial offerings (Figure 6). Specialized breeding pens have been located, and ninety percent of the bird remains found during Casas Grandes excavations were macaws and turkeys (McKusick 1974:273; Breitburg 1993). Most of the macaws were approximately one year of age when death occurred, suggesting ceremonial or commerical use. The implications for species distribution relevant to intentional breeding and trading still remains to be investigated. We do know, however that today thick-billed parrots inhabit the forests of the Sierra Madres near Casas Grandes, while the northern range of lilac-crowned parrots are southwestern Chihuahua and southeastern Sonora (McKusick 1974:279). Neither scarlet macaws nor military macaws are native to the area and are believed to have been taken at an early age from nests in other regions of Mexico and transported to Casas Grandes.

Mountain lion and American Black Bear also were well represented in the Casas Grandes faunal collections, however they were only found in ceremonial contexts. This indicates the specialized nature of their use as well as the fact that people used the higher elevations of the nearby Sierra Madre Mountains on a regular basis.

Figure 5.—Bighorn Sheep Petroglyphs in the Santa Catalina Mountains. Photograph by Jim McDonald.

Figure 6.—Mccaw Pens at Casas Grandes. Photograph by John Ravesloot.

FUELWOOD HARVESTING AND SETTING FIRES

Additional human activities affected the landscape for which there is no direct archaeological evidence. Two activites which must have had a significant effect at various times during prehistory are woodcutting and deliberate setting of fires.

Wood was cut for use in houses, cooking, warmth, cremating the dead and a variety of other activities relevant to everyday life. Only indirect information is available to estimate the problems prehistoric peoples may have had regarding fuelwood. An analogy has been made for the Mogollon Rim area regarding prehistoric fuelwood use. Fuelwood availability has been estimated at 3.4 cords per acre (by the USDA Forest Service). An average rate of consumption prehistorically has been estimated by Plog (1982) to be 2.7 cords per person. Using these figures and an average population of 20 people per square mile, trees would be depleted over an entire square mile area before there was a chance for them to regenerate. Population density frequently reached this average after A.D. 1100 when numerous Southwestern settlements contained over 1,000 people. Under this sccenario, a 3.5 mile radius around a village would be cleared of trees within one generation. This radius would increase to 6 miles before any real regeneration occurred (Plog 1982).

Even if these figures are not accurate, a good case can be made for fuelwood shortages near major settlements. If prehistoric people did experience fuelwood shortages that may have led to the abandonment or relocation of villages, this situation should be reflected in the use of less desirable fuels (Plog 1982:27). Archaeologists believe that exhaustion of local fuelwood may have been a factor in village abandonment in a number of cases (Bahre:1991:30).

The purposeful use of fire is probably one of the oldest anthropogenic factors affecting the landscape. Aboriginal burning is often assumed to have been accidential, however fire served a variety of purposes useful to survival (Dimbleby 1977; Williams 1994), many of which have been documented historically for Native Americans. These include: to clear forested areas for agriculture, to attract game animals or drive them from cover for hunting, to improve grass cover to attract game animals, in warfare as defense from enemies, to protect settlements, for cooking, for cremating the dead, for breaking stone for took-making, for firing pottery, and to provide warmth. Conrad Bahre (1991:30) has suggested that in southern Arizona aboriginal burning of grasslands may account for the large expanses of brush and shrub-free grasslands prior to Anglo-American settlement. Ethnobotanist Vorsila Bohrer (1991:233) also suggests that large tracts of desert were burned by the Hohokam to promote grasses and cool seasons herbs as important subistence resources. Overall, it has been proposed that American Indians also burned to promote a "diversity of habitats" for their use, while European settlers burned to create greater "uniformity in ecosystems" (Williams 1994). Archaeological data to support intentionial use of fire to modify the land is obviously difficult to obtain, however we should proceed with the assumption that fire has played a role in ecosystem development over hundreds of years rather than continuing to assume that fire management has only had an effect in modern times.

CONCLUSIONS

In conclusion, archaeology, because of its use of a diachronic perspective, and the analytical techniques available, provides researchers and managers with the tools to explore the human role in changing environments and to reconstruct the history of complex ecosystems. To date, the ecosystem concept in archaeological research has been used primarily as a hueristic device, and the majority of archaeological work has focused on the collection of environmental data (e.g., geomorphological, palynological, and dendroclimatic) relevant to examining the impact of a changing environment on long-term cultural evolution (e.g., Dean et al. 1985; Gumerman 1988). Nevertheless, archaeological studies can contribute significant information to our understanding of the changes that occurred through time as a result of both natural events and impacts caused by humans, along with the strategies employed by prehistoric populations to adapt to their natural and culturally modified environments.

A thorough understanding of the evolutionary history of ecosystems is attainable only by employing a long-term diachronic perspective which archaeology provides. Such a perspective is necessary to ensure that we develop management strategies that accurately maintain and conserve the biodiversity of unique ecosystems such as those in the Madrean Archipelago. Otherwise, it will be easy to perpetuate the myth of a "pristine environment" and underestimate the long-term role that humans have played in the biodiversity observed today.

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Ethnoecology of the Lone Mountain/San Rafael Valley Ecosystem

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Abstract.—This paper will present an overview of the results of research conducted for the Coronado National Forest on the Lone Mountain/San Rafael Ecosystem Project Areas. The project research goal is a history of land use and ecosystem change within the project area. The research methodology includes conventional archival research, examination of historic photographs of the area, and extensive oral history interviews with long-term residents of the study area. The overview presented at the conference will be illustrated by slides of historic photographs and historic maps which offer insights into land use and into ecosystem changes which resulted from specific uses. The paper will include a brief description of historic human occupation by the study area's major ethnic groups (Native American, Spanish, Mexican, and Anglo-American) with a summary of each group's settlement pattern, land-use activities, perceptions of the local ecosystem, and possible environmental impacts. The paper will focus on evaluating comparative impacts by the area's ethnic groups according to the specific subsistence and economic activities in which they engaged. It will conclude with a general analysis of the evidence of vegetation and landscape changes within specific ecosystem components of the project area, including Plains Grassland, Oak Woodland, Riparian Habitats, and Coniferous Forests.

INTRODUCTION

Today, we are going to be talking about one of the grassland and woodland seas surrounding the sky islands of southeastern Arizona. This is appropriate, because most human settlement and land use has been concentrated in the alluvial valleys and foothills of the Madrean Archipelago of the southwestern United States and northwestern Mexico. People have climbed the sky islands to hunt, to worship, to escape the heat, and to cut timber from precolumbian times to the present. But they have built most of their communities, cultivated most of their food, run most of their livestock, cut most of their fuelwood, and dug most of their minerals in the basins or lower slopes. In order to understand human impact upon the Madrean Archipelago, we must begin with the desert or grassland oceans and work our way upward.

Our particular study focuses upon the Lone Mountain/Redrock Canyon Ecosystem. That ecosystem encompasses 130,000 acres within the Sierra Vista Ranger District of the Coronado National Forest. Located in Santa Cruz and Cochise counties in southeastern Arizona, the ecosystem stretches from the crest of the Huachuca Mountains on the east to the crest of the Patagonia Mountains on the west. Its southern boundary is the international border with Mexico. Its northern border is formed by the Canelo Hills. The Lone Mountain/Redrock Canyon Ecosystem is drained—and defined—by the upper Santa Cruz River, which arises within it and flows south into Mexico before looping west and north into the United States again. From precolumbian times to the present, the Santa Cruz was a magnet for human settlement and the major avenue of transportation and communication linking the ecosystem with the larger regions, both ecological and political, within which it was embedded.

Forest Service personnel have further divided the ecosystem into three major landscape units:

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Lone Mountain, the San Rafael Valley, and Redrock Canyon. Lone Mountain in the eastern portion of the ecosystem consists primarily of Madrean oak woodland grading into coniferous forests. Elevations range from 4500 feet at the Mexican border to nearly 9400 feet at Miller Peak in the Huachucas. The southeastern portions of the Lone Mountain landscape unit drain into the San Pedro watershed to the east. Major recreational features include Parker Canyon Lake and the Miller Peak Wilderness. Recreation and cattle grazing constitute the major land uses today, but intensive mining and logging, particularly in the Sunnyside district, had a significant impact upon local vegetation and wildlife populations as well.

The San Rafael Valley dominates the central portion of the ecosystem. Drained by the headwaters of the Santa Cruz, the valley consists of broad, gently rolling hills of plains grassland that extend south into Mexico. For much of its human history, in fact, the most important settlement in the region was the Jesuit mission of Santa Mara Soamca, which later became the presidio of Santa Cruz. Santa Cruz is approximately 10 miles south of the international border. Elevations in the San Rafael Valley rise from 5,000 feet at the Mexican border at Lochiel to nearly 7,000 feet at the Canelo Hills. Along its borders, the plains grassland intergrades with encinal, chaparral, and Mexican pine oak woodlands. Cattle ranching has been the most important economic activity since the late 17th century, but most of the agriculture in the study area has taken place along the Santa Cruz or the lower stretches of its tributaries as well.

The final landscape unit identified by the Forest Service is Redrock Canyon in the northwestern portion of the ecosystem. Redrock Canyon drains into Sonoita Creek, a tributary of the middle Santa Cruz. The primary land use was and has been cattle ranching, although recreational use is increasing, as it is throughout the ecosystem itself.

THE RESEARCH STRATEGY OF ETHNOECOLOGY

In terms of historic land use, we further subdivide the ecosystem into additional units, particularly the eastern slopes of the Patagonia Mountains, where the most intensive mining and fuelwood cutting took place during the 19th and 20th centuries. Human occupation, of course, crosscuts vegetation zones, watersheds, and even ecosystems themselves. Before we discuss those patterns of land use, however, we need to describe the goals of our project and the methodology we employed. In September 1993, the Forest Service solicited proposals for an ecosystem study of the Lone Mountain/San Rafael Valley area. The two major objectives of the project were to identify the sequence of human occupation in the ecosystem from late precolumbian times to the present and to investigate the land use activities that may have affected the evolution of Lone Mountain/San Rafael landscape. Among the topics to be addressed were: the chronology of human settlement within the study area; the introduction and development of stock-raising, agriculture, mining, timber and fuelwood harvesting; fire management practices; changes in population numbers and locations; the relationship between settlement patterns, land use, and regional changes in transportation, government, and governmental policies; and specific changes in vegetation cover, landscape, and watershed conditions. Finally the Forest Service requested an assessment of the relationship of land use practices and ecosystem change in order to determine the degree to which the existing landscape evolved in response to either natural or human-induced forces.

In order to answer such questions, we employed a research strategy called ethnoecology. Ethnoecology is the study of the way in which groups of people conceive of and exploit the particular environment they inhabit. The term ethnoecology combines three word roots, deriving from the Greek terms ethnos, oikos[eco], and logos. Ethnos is the word for a group, band, or nation of individuals living together. Oikos is the word for "household" or "dwelling place." Logos is the term frequently incorporated into words which describe discourse, discussion, or logical arguments, and is even etymologically related to the word "gossip." Philosophically, the term "logos" applies to to the regulatory or controlling principles in a system. Therefore, the term ethnoecology refers to the study of groups of people, living in a particular environment, who utilize that environment according to culturally determined sets of principles, regulations, or habitual practices. Ethnoecology examines the ways in which people perceive the landscape and the ways in which they adapt to and exploit it. It also explores the ways in which their perceptions change through time and are forever incomplete. The landscape is always more complex than peoples' conceptions of it. Moreover, their impact upon the landscape almost always has consequences they neither intended nor foresaw.

The research strategy of ethnoecology is interdisciplinary. It combines method and theory employed by archaeologists, ethnographers, geographers, historians, biologists, geoscientists, ecologists, and climatologists. In theory, this constellation of disciplines should allow researchers to generate a chronological history of land use along with a chronology of changes in the land that may or may not be human-induced. Distinguishing between human-induced and "natural" changes in the landscape is an extremely difficult task — one that requires the collaboration of both social and natural scientists. We do not pretend that we have all the skills to make such determinations, and we are only beginning to analyze the data we have collected in order to address the questions involved. Nonetheless, we hope that this brief summary of land use history in the Lone Mountain/San Rafael ecosystem reveals the complex interplay between humans and the land in one small area of the Southwest over the last 500 years.

NATIVE AMERICAN OCCUPATION

During that half a millenia, we pay particular attention to the impact of O'odham, Chiricahua Apache, Spanish, Mexican, and Anglo American populations upon the study area. Even though archaeology was not a focus of the Forest Service proposal, we began the study by reviewing the site files of the Arizona State Museum and the Coronado National Forest to determine the precolumbian and historic occupation of the ecosystem by Native Americans. We also consulted relevant secondary sources, including published and unpublished archaeological reports, historical syntheses, and ethnographies, to determine the nature and intensity of Native American land use in the ecosystem.

No formal archaeological survey was undertaken. Nonetheless, the available archaeological data suggest that there were a series of Hohokam sites along the upper Santa Cruz during late precolumbian times. When Europeans first passed through the San Rafael Valley in the late 1600s, however, the study area was within the territories of O'odham groups identified as Sobaipuri Pimas. During one such reconnaissance in 1692, Jesuit missionary Eusebio Francisco Kino noted an O'odham community called Beradeuguachi along the Santa Cruz River north of Santa Mara Suanca (the modern town of Santa Cruz). Five years later, Kino's traveling companion Juan Mateo Manje made no mention of the settlement while traveling between Suanca and the Sobaipuri settlements in the San Pedro watershed. There is no further documentary evidence of any permanent Sobaipuri settlement in the San Rafael Valley during the colonial period.

According to archaeologist Deni Seymour, who surveyed Sobaipuri sites along the San Pedro, the Sobaipuri O'odham frequently abandoned sites and shifted the location of their settlements. Moreover, the density of Sobaipuri artifacts is quite low, even in core areas of settlement such as the San Pedro or Babocmari drainages. It is possible that a comprehensive archaeological survey of the San Rafael Valley will identify more intensive Sobaipuri settlement in the study area.

We suggest, on the other hand, that the O'odham may never have established any permanent settlements there. According to our scenario, the Sobaipuri O'odham were frontier populations colonizing or recolonizing the Santa Cruz and San Pedro drainages after—or during—the collapse of the Hohokam. The San Rafael Valley undoubtedly served as an important corridor of communication between the O'odham communities of the Santa Cruz and those located in the San Pedro watersheds, but the San Rafael Valley simply was too high to attract the desert-dwelling O'odham. The O'odham were sophisticated desert farmers with numerous species of corn, beans, and squash well-adapted to arid and semi-arid conditions. What the O'odham did not have was a major food crop that was frost-tolerant, which would have limited them to one reliable crop a year in an area where frosts can be a danger from late September to late April.

The Sobaipuri O'odham undoubtedly utilized the Lone Mountain/San Rafael ecosystem for a wide range of subsistence activities, including the hunting of large and small game and the gathering of agaves, yuccas, acorns, walnuts, beargrass and other wild plants found in the plains grassland and the evergreen woodlands. Nonetheless, they preferred to locate their settlements at lower elevations in the Santa Cruz and San Pedro watersheds where the number of frost-free days was greater, where mesquite bosques (forests) were more extensive, where stands of prickly pear and cholla were denser, and where important ceremonial plants like saguaros were closer. If Sobaipuri populations had continued to grow, their range might have expanded and they might have adapted their agriculture and their wild plant gathering to the higher altitudes of the study area.

As it was, the increasing intensity of warfare with other Indian groups, particularly the Western and Chiricahua Apaches, halted Sobaipuri expansion and eventually drove them out of the San Pedro watershed altogether by 1762.

The Apaches apparently did not occupy the study area on a permanent basis either. According to the limited archaeological and documentary evidence available, ancestors of the Chiricahua Apaches moved into southeastern Arizona sometime in the 17th century. There they encountered groups identified by the Spaniards as Janos and Jocomes, whom they eventually assimilated. By the 18th century, the eastern slopes of the Huachucas may have become part of the territory of the central band of the Chiricahua Apaches, who called themselves the Chokonens, especially after the Sobaipuri withdrew from the San Pedro Valley. Chiricahua society was fluid and relatively mobile. Some Chiricahua local groups planted plots of corn, beans, and squash, but hunting, gathering, and livestock raiding were more important economic pursuits.

In contrast to the O'odham, the Chiricahua Apaches were upland people who exploited upland resources. Parties of women collected the buds, flowers, and stalks of different species of yucca and the stalks and caudices of agaves in the mid-spring to early summer period known as "Many Leaves." Then they gathered one-seeded juniper berries and other summer plants in the season called "Many Leaves." During late summer, "Large Fruit"—their second most important wild harvest season—began, and they collected chokecherries, walnuts, pion nuts, acorns, and other fruits and nuts, which they mixed with deer meat to make a sort of pemmican.

Until more archaeological research is conducted, it is difficult to assess the environmental impact of either the O'odham or the Chiricahua Apaches. It is possible that Native American hunting practices may have affected deer and antelope populations in the study area, although Forty niners and other Anglo American observers in the mid-19th century describe the San Rafael Valley and the Huachuca Mountains as a "paradise for hunters" with large numbers of deer, antelope, waterfowl, wolves, and even grizzlies. It is probable that frequent fire drives suppressed shrubs and helped maintain the grasslands of the Santa Cruz Valley and the park-like oak woodlands along the lower slopes of the Huachucas, the Patagonias, and the Canelo Hills. Fire drives were a common Apache hunting technique and both Apaches and Northern Pimans such as the Sobaipuris used fire drives as a battle tactic. J. Ross Browne described once such incident in 1863 when the Apaches set fires during an attack on a party of Anglo Americans near the abandoned hacienda of Santa Brbara south of Nogales. It is doubtful, however, that either the O'odham or the Apaches had much of an impact upon the Santa Cruz or its tributaries because little or no evidence of intensive agriculture in the study area has been uncovered from late precolumbian times until the late 19th century.

THE SPANISH AND MEXICAN PERIODS

Land use diversified and accelerated during the Spanish and Mexican periods. But it did so in a sporadic fashion, advancing and retreating according to the intensity of Hispanic-Apache hostilities. After examining secondary historical sources and the primary documents precised by the Arizona State Museum's Documentary Relations of the Southwest Project, we have identified three periods of Hispanic utilization of the study area. The first began in the 1670s, when Jos Romo de Vivar and other Spanish stockraisers occupied the bend of the Santa Cruz below the study area and drove their cattle and horses into the San Rafael Valley and the foothills of the Huachucas as well. Much as we would like to help the Sierra Vista Ranger's District increase its interpretive budget, we believe that historian John Wilson's contention that Francisco Vasquez de Coronado and his troops passed through the San Rafael Valley is speculative at best. In our opinion, Romo de Vivar was the first Spanish pioneer to indisputably visit the study area.

That initial period of utilization ended abruptly in 1688 after Captain Nicols de Higuera massacred the O'odham ranchera of Mototicachi along the Ro Bacuachi and provoked an O'odham revolt against the Spaniards. Romo de Vivar abandoned his ranch at San Lzaro at the bend of the Santa Cruz, and he and other Spanish stockraisers withdrew from the San Rafael Valley. The second period began in the 1720s, when Spanish settlers once again reoccupied the bend in the Santa Cruz they called the San Luis Valley. It is difficult to determine how far their animals ranged, but the presence of a ranch known as Torren within or just south of the study area suggests that, once again, Spanish livestock grazed the lush gramas of the San Rafael.

Between the 1720s and the 1760s, more than a hundred settlers cultivated the San Luis Valley and ran their stock in the surrounding uplands. That occupation came to an end in 1763, when they petitioned Juan Bautista de Anza, captain of Fronteras presidio, to be allowed to abandon their ranches and move downstream, closer to the presidio of Tubac, because of Apache attacks. The year before, the Sobaipuris along the San Pedro had been resettled at Santa Mara de Suanca or San Xavier del Bac. In 1768, Suanca itself was abandoned because of Apache hostilities.

The third and final period of Hispanic occupation began in 1787, when the Spanish presidio, or military garrison, of Santa Cruz de Terrenate was transferred to Suanca. As Apache raids decreased and more and more Apaches settled in peace camps near presidios like Santa Cruz, Spanish settlers once again expanded their herds and also opened a number of mines, particularly in the Patagonias. By 1821, residents of Santa Cruz even petitioned the Spanish authorities for four square leagues of land for the raising of livestock in the San Rafael Valley itself. By the time the San Rafael de la Zanja grant was surveyed and approved, Mexico had won its independence from Spain. For the next two decades, however, Hispanic ranchers made their most concerted effort to occupy the study area and transform its rich grasslands into beef, hides, and tallow.

The grantees were "Ramon Romero and other associated residents" of the presidio of Santa Cruz. The parcioneros, or shareholders, ran their livestock together on the open range. No fences divided the grant into individual pastures, and the animals of the parcioneros utilized the surrounding "overplus" lands beyond the four square league grant as well. According to the testimony of five surviving parcioneros or their descendants in 1880, there were twenty or thirty shareholders and their families on the grant. Between 1825 and 1843, they ran between 2,000 and 5,000 head of cattle and many horses in the San Rafael Valley and the surrounding foothills. The only settlement of note was La Boca de la Noria—present-day Lochiel—just north of the international border. Beginning in 1834, however, Apache raids made it dangerous to occupy the grant. Then, in 1843, Apaches killed at least thirty of the settlers at La Noria and most of the survivors retreated to Santa Cruz. Once again, stockraising and settlement ceased in the San Rafael Valley. Most of the mines were also abandoned. Mining and stockraising did not resume until after the study area became part of the United States under the terms of the Gadsden Purchase, which was ratified by Congress in 1854.

THE ANGLO AMERICAN MINING INDUSTRY

During the seventeenth, eighteenth, and much of the nineteenth centuries, then, the Lone Mountain/San Rafael ecosystem was a political and economic frontier in the most basic sense of the term. By frontier, we do not mean a boundary between civilization and savagery, or civilization and wilderness, because those are little more than the value judgements of the people employing the terms. On the contrary, we use the term "frontier" to signify a zone of contact and conflict where no one group—American Indian, Hispanic, or Anglo American—held uncontested sway. Human settlement in the San Rafael Valley and the surrounding uplands was shifting and ephemeral from late precolumbian times until the 1880s, when the Chiricahua Apaches were confined to reservations or deported to Florida. There was little or no intensive agriculture. Stockraising occurred in three distinct waves and may never have reached the carrying capacity of the ecosystem itself. Whenever Spanish or Mexican ranchers attempted to increase their herds, human and non-human predators preyed upon their animals. Geoscientist Paul Martin evenbelieves that certain keystone predators like wolves and grizzlies may actually have expanded their ranges and increased their numbers during the eighteenth and nineteenth centuries in response to the presence of Spanish, Mexican, and Anglo American livestock. All of these factors limited human impact upon the environment of the study area.

When the first Anglo American Forty-niners passed through the study area in the late 1840s, they described a paradise of lush grasses, abundant water, and enormous cottonwoods in the San Rafael Valley and open, spacious oak woodlands in the surrounding foothills. Two decades later, those conditions still existed. According to journalist J. Ross Browne (1950:211-15), "Groves of cotton-woods of gigantic size fringe the stream at intervals of every few miles; the grass is wonderfully luxuriant, covering the valley and hill-sides as far as the eye can reach with a rich gold-colored carpeting." The Santa Cruz was a series of springs and cienegas during the dry season of late spring and a wide, shallow stream during the summer and winter rainy seasons. The ecosystem flourished because human settlement did not.

All that began to change in the late 1870s, when mining activity intensified. The study area contains three significant mining areas: Mowry and Duquesne/Washington Camp in the Patagonia Mountains, and Sunnyside on the western slopes of the Huachucas. Located slightly north of the study area is Harshaw, the largest of the region's mining camps and the only one which experienced a true mining boom. Harshaw was excluded from the Lone Mountain/San Rafael ecosystem because Harshaw Creek drains into Sonoita Creek rather than the upper Santa Cruz. Nonetheless, Harshaw mines and miners had a tremendous impact upon the vegetation and wildlife of the study area.

Although mining itself may be a localized activity, subsidiary activities associated with mining produce a web of ecological impacts that extend far beyond the mining site itself. These associated activities include: road construction; fuelwood cutting, particularly during the period when smelting was done with charcoal or steam boilers operating machinery; the development of mining camps and nearby towns; the extraction of water from surface and underground sources; the generation of waste dumps; chemical and mineral leakage from both tailing and slag piles; and the creation of markets for local products. Without question, mining in all its manifestations constitutues the single most important human impact upon the Lone Mountain/San Rafael ecosystem.

There were scores of individual mines and mining claims in the study area and the nearby Harshaw district. The area included at least thirty-one mining camps, fifteen concentrators and mills, and eight smelters. Most of the largest mines operated intermittently from the late 1870s until the 1950s, producing millions of dollars of silver, copper, lead, zinc, manganese, tungsten, alunite, and gold. At their height, they employed hundreds of miners, smelter workers, and, at least during the early periods, woodcutters. Both production and employment ebbed and flowed according to mineral prices and the availability of capital. National depressions in the 1890s and the 1930s closed mines. World wars stimulated mineral production. Substantial communities arose at Harshaw, Mowry, Washington Camp, and Duquesne in the Patagonias and at Sunnyside in the Huachucas. In 1880, for example, Harshaw had more than 600 residents from thirty-five states and three territories of the United States, fourteen European countries, China, India, and Mexico. The town had one hotel, two lodging houses, four livery stables, one tailor, several shoemakers, several barber shops, one tobacco shop, and one watchmaker. There were also two lawyers, one musician, one physician, three druggists, one telephone operator, one printer, and four prostitutes. By 1909, on the other hand, only a few residents remained. During the 1960s, the Forest Service destroyed most of the remaining buildings. Harshaw's role in the ecological history of the study area now must be read largely on the landscape itself, and those changes are often subtle and hard to see.

Mining booms and busts played an enormous role in the land use history of the Lone Mountain/San Rafael ecosystem, and we are just beginning to try to estimate the size of the impact of the mining industry upon the study area's vegetation and hydrology. Nonetheless, a few tentative conclusions can be advanced. Watersheds in most mining districts still exhibit signs of incision and degradation. The Harshaw townsite, for example, is cut by gullies that probably resulted from the overharvesting of fuelwoods in the surrounding areas. Historic photographs from the late 19th and early 20th centuries reveal a landscape with far fewer trees and much less grass. Such a landscape would have encouraged both sheet and gully erosion. The impact of mining upon subsurface aquifers in the study area is, unfortunately, a topic we are unable to address at present.

The composition of the oak woodlands and coniferous forests in the study area were undoubtedly affected by mining and its attendant fuelcutting as well. Both contemporary accounts and oral histories attest to the preference for certain types of wood above others. Juniper, in particular, was a preferred wood for both smelting and fenceposts. Oak was also a popular fuelwood for both mining and domestic consumption. We have not carried out any vegetation transects, but we are struck by the relative absence of either large junipers or large oaks. Several consultants have told us that it is still possible to find the stumps of enormous junipers in the evergreen woodlands of the study area. We also wonder whether scrub species such as manzanita were as extensive in the past as they are now. Travelers' accounts rarely provide the level of detail allowing for a sophisticated reconstruction of past vegetation. Nevertheless, we are struck by the consistent emphasis upon the parklike nature of the evergreen woodland, at least along its lower borders where it integraded with the plains grassland. It is possible that longterm overharvesting of oaks and junipers, combined with the suppression of fires around mining camps and ranches, may have stimulated the invasion of shrubby species.

We do know that timber cutting for the mines decimated the small stands of ponderosa pine and other conifers in the Patagonia Mountains and reduced those stands in the Huachucas. In 1914 and 1915, Rex King made an initial, or "extensive" classification of lands in the Coronado National Forest. He reported that the only saw timber on the forest were light stands in the Santa Rita and Huachuca Mountains. "The Patagonia Mountains also once had a scattering stand but it was practically all cut before the Forest was created, to supply the mines in the vicinity," King (1915:6) observed. "The Huachuca stand...has been extensively culled over and there are places which were clear cut." King concluded that the evergreen woodlands were recovering well, but King conducted his study during the Mexican Revolution when the mines were inactive and demand for fuelwood was low. Perhaps more detailed studies of the composition of the study area's vegetation, combined with fire histories and repeat photography, may reveal other enduring effects of timbercutting, fuelwood cutting, and other activities related to mining in the Lone Mountain/San Rafael ecosystem.

ANGLO AMERICAN LIVESTOCK GRAZING

During the late nineteenth century, the territory of Arizona changed from a frontier to an extractive colony of the industrialized world. The military conquest of the Chiricahua Apaches allowed settlers unimpeded access to the natural resources of Arizona including the study area. The presence of the military and the creation of Indian reservations provided the first major local markets for the goods those settlers produced, particularly agricultural produce, mutton, and beef. After two transcontinental railroads were completed across Arizona in the early 1880s, however, Arizona's resources could suddenly be transported to national and even international markets. One result was the mining of low-grade copper ore, which did not play a major role in the Lone Mountain/San Rafael ecosystem. The other was a spectacular boom in the range cattle industry. With its lush grasslands, the San Rafael Valley quickly attracted the attention of both large and small stockraisers, including Arizona's prototypical cattle baron, Colin Cameron.

We do not have time today to discuss Colin Cameron's two decade struggle to establish uncontested control over the San Rafael Valley and the surrounding mountains, including the areas where major mining districts like Duquesne, Washington Camp, Mowry, and Harshaw were located. Cameron, who purchased the San Rafael de la Zanja land grant in 1883, argued that the grant gave him title to four leagues square rather than four square leagues.

In 1899, the Court of Private Land Claims confirmed the land grant but not the so-called "overplus" lands, leaving Cameron with 17,474 acres rather than the grandiose 152,889 acres he claimed. For nearly twenty years, however, Cameron ran off or burned out small farmers and stockraisers and kept any large outfits from moving into the San Rafael Valley. Cameron also introduced a series of innovations into the Arizona range cattle industry, including a reliance upon purebred Herefords and the development of artificial sources of water. Cameron used Mexican longhorns as instruments of occupation to keep others off San Rafael ranges, but he also reduced his herds during the disastrous drought years of the 1890s when 50 to 75 percent of the cattle in Arizona died. Cameron may have been ruthless, but his actions also may have kept the San Rafael Valley from becoming as degraded as other desert grassland ranges in southeastern Arizona during the late nineteenth century.

Cameron sold the San Rafael de la Zanja to Colonel William C. Greene in 1902. Thereafter, the grant served as one relatively small part of Greene's enormous land holdings in southern Arizona and Sonora. Greene made no claims to the rest of the San Rafael Valley, so other stockraisers quickly moved onto every portion of the Lone Mountain/San Rafael ecosystem that could support cows. By then, however, the federal government was forcing its way into the Western livestock industry by creating its Forest Reserves, the forerunners of our national forests. The federal government did not begin to regulate the rest of the public domain until 1934, when Congress passed the Taylor Grazing Act. But many of that act's provisions, including the creation of grazing districts and the collection of grazing fees, were pioneered in the national forests themselves.

Because most of the study area fell within the Huachuca Forest Reserve, which was established by presidential proclamation in 1906, regulation came early to the Lone Mountain/San Rafael ecosystem. That regulation continued and grew as the reserve became a national forest in all its various administrative permutations between 1907 and 1953. Ranchers in the region therefore became accustomed to at least some federal interference in their lives. Settlers had removed some well-watered stretches of bottomland along tributaries of the Santa Cruz from the public domain; we are currently analyzing the timing and extent of filings under the provisions of the General Homestead Act and the Desert Land Act. In 1906, Congress also passed the Forest Homestead Act, which allowed settlers to homestead up to 160 acres within the forest reserves themselves. The legislation was designed to removed potentially arable lands from the public domain and transfer them to private owners. Its passage coincided with a dry farming boom in the Western United States that peaked during World War I and the early 1920s. Between 1910 and 1924, 91 forest homesteads were filed and proved up in the Coronado National Forest. The majority of those claims—51 of them—fell within the study area or the mountains bordering it. And while some of the homesteaders actually did try to make a living as dry farmers, most used the forest homesteads as their lever into smallscale stockraising on national forest lands.

Largely because of the Forest Homestead Act, a mixed agropastoralist economic strategy of smallholder ranching and farming played a major role in the development of the Lone Mountain/San Rafael Valley ecosystem until the late 1930s and World War II. Small ranchers congregated in such well-watered areas as Parker Canyon east of the Santa Cruz. Many miners continued to run a few head of cattle in the Patagonias. According to Hugh M. Bryan, who prepared a detailed grazing plan for the Coronado National Forest in 1917, "The rough and broken nature of this Range [Harshaw] complicates the handling of stock for the owner in this vicinity. In most cases the stock are just turned loose on the range and rarely seen except on the Range. There are very few corrals and salting places except at the home ranches and the stock is none too tame."

A few large outfits continued to run their stock in the study area as well. Vail & Ashburn dominated the Red Rock Range, which they utilized as a southern extension of their holdings around Patagonia and Cienega Creek. A few large permittees also moved onto the Lone Mountain Range, which Bryan (1917:27) called "the far away, little known, and little used area of the Division." We have tabulated data on total animals and total animal months from grazing permits in the study area between the mid-1920s and the mid-1940s, but our analysis is not yet complete. Nonetheless, a few general trends can be identified. First of all, the number of allotments increased as huge ranges such as the Parker Canyon Range were broken into smaller and more manageable grazing units. Secondly, the number of permittees declined as smaller outfits were consolidated into larger ones. The San Rafael de la Zanja remained the largest private operation in the study area, but other large outfits such as the Heady Ashburn Ranch, started by Greene's foreman Tom Heady, and the Vaca Ranch, founded by Clyde McPhearson, took shape as well.

By the time we complete our analysis, we should be able to provide some reasonably accurate estimates of grazing intensity on the different ranges of the study area during this crucial period. We should also be able to trace the evolution of the cattle industry during the first half of the 20th century as ranchers had to improve both their herds and their ranges. Because the Lone Mountain/San Rafael Valley ecosystem contains both a large private spread and national forest lands, it offers an interesting opportunity to compare private tenure with the management of grazing on public lands.

CONCLUSIONS

At this stage in our project, we have collected an enormous amount of data on mining, grazing, fuelwood cutting, and agriculture in the study area. Now we need to carry out our final analyses of that data and draw some more precise conclusions. When we do so, we should be able to provide at least ball-park quantitative estimates of the intensity of grazing and fuelwood-cutting at certain times in the study area's history during the past 100years. We will also attempt to correlate our findings with regional climatic trends in order to make some informed guesses about the nature and extent of human impact upon the Lone Mountain/San Rafael Valley ecosystem. At this time, however, a few broadbrush observations can be made. In the San Rafael Valley itself, the main channel of the Santa Cruz has been considerably modified. Most of its bogs and cienegas have been drained to keep cattle from becoming mired and to elimate breeding grounds for mosquitoes. Large cottonwoods still line the banks, but there are probably fewer now than there were when the Forty-niners trudged through the valley. Moreover, many stretches of the channel are also incised, and flow may have decreased. We need to be careful about those observations, however, because the upper Santa Cruz was an intermittent stream before the cattle boom of the late 19th century—one with surface water along perhaps half its length during dry times of the year. There are also reports of local incision in the early accounts;

the name San Rafael de la Zanja itself may indicate the presence of an ancient irrigation ditch, or zanja, predating the land grant, or it may reflect the presence of a naturally formed arroyo.

We have already suggested some possible changes in the composition of the study area's vegetation, particularly in the evergreen woodlands and the conifer forests. There were also changes in the ecosystem's wildlife, including the extermination of resident populations of grizzlies, wolves, and antelope. When we complete our analysis, we may be able to say more. Above all, however, our study should serve as a baseline for more sophisticated ecological and hydrological studies that take human impact upon the ecosystem into account in order to achieve a true ethnoecology of the Lone Mountain/San Rafael region.

Ecotourism and the Madrean Archipelago

David A. King and Brian Czech[1]

Abstract.—Ecotourism is promoted as both a means to achieve community development and to preserve natural environments. Our intent in this paper is to identify the issues that would need to be addressed if ecotourism were used as a tool for maintaining biodiversity in the Madrean Archipelago. We discuss concepts related to tourism and ecotourism, review case studies of nature tourism, and then use those ideas and experiences to identify and comment on the important issues regarding ecotourism in the Madrean Archipelago.

TOURISM

A discussion of general concepts in relation to tourism and rural communities is a necessary prelude to defining and understanding the concept of ecotourism. In this section we discuss tourism as a tool for rural community development, the concept of hosts and guests, and the concept of scale in relation to the impacts of tourism.

Tourism is a means to develop rural communities that can provide jobs, incomes, and tax revenues while having relatively less impact on the natural environment and public services and infrastructure than most other industries. Thus, there is a motivation to use tourism to accomplish not only community development, but preservation of natural environments as well. When tourism serves both of these objectives, a symbiotic relationship is formed in which the natural environment is the attractant for tourists, and the tourists provide the means for community development and for preservation of the natural environment. However, this relationship is fragile and breaks down when tourism serves one of the two objectives at the expense of the other.

Hosts and Guests

The concept of host communities and guest societies is useful for discussing the social impacts of tourism (Smith 1989). For rural host communities, urban communities are the primary sources of the guests. Through their high productivity, the guest communities have created leisure time and the income to use it for travel. Their high productivity also makes them more economically powerful than the rural host community. This power relationship led Nash (1989) to see tourism as a form of imperialism.

Tourism brings to the host community a new socio-cultural reality (Nash 1989). The guests expect and need to be served, and the service sector expands in response. Members of the host community shift from production activities to service activities that, in rural societies, may be perceived as socially inferior to traditional production activities.

The socio-cultural consequences of tourism are an important aspect of community development. A sense of economic inferiority can reduce the sense of self-worth of members of the host community. A shift in economic activity from the production to the service sectors can change the distribution of income within the community. New, and perhaps unsettling, social relationships can result from changes in relative economic status. These changes can lead to social and psychological conflicts within and between members of the host community. Tourism can change the rules of access to, and utilization of, the land and resources. These changes also can have important cultural, as well as economic, implications.

Scale

Scale is important in addressing the ecological and socioeconomic consequences arising from tourism. Similar to the biogeographic approach to species diversity that Whittaker (1972) introduced, the ecological consequences of tourism may be viewed as occurring on at least two levels,

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alpha and gamma. Changes at the alpha level are changes in ecological qualities, processes, or functions that occur in a local ecosystem. Changes at the gamma level are those that may occur on a regional or global scale. A gamma consequence is not simply a summation of widespread alpha consequences (although summation may be appropriate in some cases). The ecosystem qualities and functions that we are concerned with at the gamma level are rarely considered on the alpha level.

In general, alpha consequences, such as soil erosion, and the processes that cause them, such as hiking, are directly related to the tourist's onsite activity. Gamma consequences, such as air pollution, occur on a regional/global scale, and the causal processes, long distance automobile travel to natural sites, may be incidental to the tourist activity, or they may be related to cumulative or synergistic alpha impacts.

Similarly, scale is important in looking at the economic consequences of tourism. For example, increased income in Cochise County of Arizona is a benefit to that local economy. However, at a higher level, say the state or national economies, some of that income is simply a transfer from one part of the larger economy to another and is not a benefit. In large economies, such as those of the United States and Mexico, the national economic impact of tourism is small (Boo 1990a).

Scale also is important when looking at the social consequences of tourism. What may be considered socially good at a national level in the host country may cause great social disruption at the community level.

Cultural diversity tends to increase with scale and is, according to Durning (1992), inextricably linked to biological diversity. Distinct human cultures have distinctive ecological relationships that often "fit" best with the lands that gave rise to them.

ECOTOURISM

Recognition of the potential symbiotic relationship of tourism, community development, and the natural environment, led to the ecotourism concept. Tourism, if carefully planned and implemented, came to be seen as a way to further community development and the preservation of natural environments. The two objectives of community development and preservation of natural areas, in turn, are means to achieve the respective goals of improving social welfare and of maintaining biodiversity. The ecotourism idea also arose from a recognition of: 1) the social and economic injustices that occurred when natural environments were set aside, opened to tourists, and closed to traditional uses by native peoples, and 2) the ecological impacts of excessive levels of tourism activity. So ecotourism is different from other forms of tourism because it attempts to build and maintain a symbiotic relationship with community development and preservation of natural areas.

Indeed, Lee and Snepenger (1991) see ecotourism as an ideal; a concept of integrated conservation and development in which tourism is planned and managed in such a way as to protect or restore environmental settings, to improve the socioeconomic conditions of local residents, and to provide educational experiences for the tourists (Johnston and Edwards 1994).

Johnston and Edwards (1994) point out, however, that ecotourism attempts to sell the exotic. It commodifies nature and human/nature relationships. Commodification is "the process by which objects and activities come to be evaluated primarily in terms of their exchange value in the context of trade, in addition to any use value that such commodities might have (Watson and Kopachevsky 1994:645)." When this process occurs, the allocation of resources to the provision of the objects and activities becomes driven by the market, an imperfect institution for the allocation of natural and environmental resources (Randall 1987).

Viewing ecotourism in the context of other forms of tourism is helpful in understanding it (fig. 1). Because it involves touristic use of natural environments, ecotourism is a form of nature tourism. It differs from recreational nature tourism in its emphasis on education as opposed to entertainment. In opposition to hunting and gathering, it takes nothing physically from the environment. Most importantly, however, it differs from all other forms of tourism in its emphasis on social justice and its concern for preservation of the natural environment.

Figure 1 also points out that most tourism experiences are bundles of the tourism types shown. For example, ecotourists may engage in ethnic and recreational nature tourism as well as ecotourism.

In summary, ecotourism is an evolving concept, an ideal. The objectives of ecotourism are community development and environmental preservation. These objective, in turn, serve the goals of improving social welfare and maintaining biodiversity.

TOURISM, COMMUNITY DEVELOPMENT, AND ENVIRONMENTAL PRESERVATION

Numerous case studies of nature tourism have been done (Whelan 1990, Boo 1990b, West and Brechin 1993). In this section we review case studies of nature tourism that were selected for their relevance to identifying the issues arising from the concept of ecotourism in relation to the Madrean Archipelago. A common shortcoming of these studies is the lack of baseline data to evaluate the consequences of tourism relative to either the pre-existing situations or alternative resource uses and development schemes.

Kenya

Kenya is well known for its wildlife oriented tourism. It abolished hunting in 1977, set aside wildlife parks, and implemented a policy to encourage tourist visits to the them. Olindo (1991) states that Kenya's wildlife resources are seriously threatened due to mismanagement of protected areas, illegal hunting, and lack of local support. One of the important areas of mismanagement is a lack of control on numbers of visitors. Tourist visitation is so high that it is having negative impacts on the wildlife resource. Local landowners, feeling they were treated as less important than animals, fenced their lands and waterholes to prevent access by wildlife causing a decline of wildlife populations on the reserves.

Kenya's wildlife oriented tourism is often cited as an economic success. However, the economic benefits were obtained at the international and national levels while many of the costs were borne at the local level (Olindo 1991). As a result political pressure grew and, in response, the national government agreed to share revenues with local residents (Olindo 1991, Sherman and Dixon 1991).

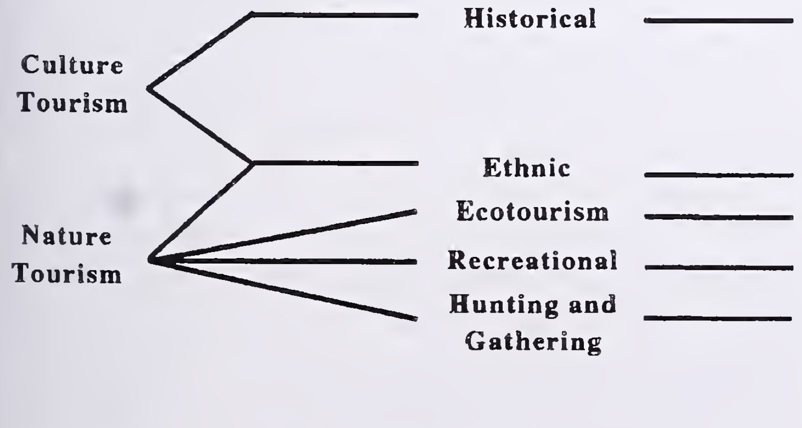

Figure 1.—Tourism Types (Based on Smith 1989).

Recent reports from Kenya indicate that the government now recognizes that the game parks cannot sustain wildlife and are in fact losing biodiversity (Baskin 1994). Kenya's population rose from 6 million in 1957 to 20 million in 1987. The resulting need to devote more land to crops put pressure on the wildlife resource. As a consequence, new policies are being put in place to help private landowners to establish wildlife oriented economic enterprises, thereby encouraging them to protect wildlife. In addition, the government is considering a proposal to lift the ban on hunting. The new policies show a recognition of the importance of the community development objective and that the previous policies placed too much emphasis on natural area protection.

Australia

Uluru National Park, containing Ayer's Rock, is "the place that white Australians and international tourists feel they must visit to capture the 'outback experience', which shaped the national character of Australia" (Bosselman 1978:83). The Park contains an abundance of rock art, paintings by the ancestors of the Aborigines, but, when the Park was first established, managers were unable to satisfy the tourists' interest in aboriginal art and interpretation of the land.

The passage of the Northern Territory Lands Rights Act in 1976 provided a means to satisfy that interest. The Act enabled local Aboriginal tribes to regain rights to portions of parks, but with the stipulation that they lease the land back to the government for 100 years. Under the terms of the Uluru lease, the Uluru Katatjuta Board of Management was established with an Aboriginal majority membership that provided the Aborigines with considerable influence on Park planning and management. (Alanen 1992). According to Alanen (1992), the Aborigines' involvement has renewed their interest in their culture and strengthened its integrity.

The Aborigines influence, however, stops at the Park boundaries. During the 1970's, various tourist development enclaves were removed from the Park and a new, compatibly designed development was built outside the Park boundaries. Pressures, however, exist for the location of incompatible land uses, such as a golf course, on lands near the Park over which the Aborigines have no control.

Costa Rica

Costa Rica is well known for its emphasis on nature tourism. This emphasis results from Costa Rica's unique environmental resources and a general lack of infrastructure to support other forms of tourism (Chant 1992).

The Monteverde Cloud Forest Reserve in Costa Rica is a private reserve established in 1972 by North Americans, who settled in the area in the 1940's, and the Tropical Science Center of San Jose. Visitation to the Monteverde Cloud Forest Preserve grew from 300 in 1973 to 15,000 in 1989. Up to that time the area of the Preserve was 2,000 hectares. In 1990 the Preserve was enlarged to 10,000 hectares. Rovinski (1991) reported that visitor facilities were inadequate and tourist trails were suffering serious erosion. In response, an educational center and new tourist trails were planned. Local residents have reported changes in animal behavior within the Preserve and wildlife now stays away from the tourist trail during the heavy use season (Rovinski 1991).

The Reserve seems to have had positive economic effects, although the benefits have not been shared equally (Chant 1992, Rovinski 1991). Tourism is now the second largest source of income in the local economy. The North American settlers had the capital to take advantage of the tourism investment opportunities and they, not the local residents, reap most of this income. A total of 17 employees were permanently employed by four lodging places with a seasonal high of twice that number (Boo 1990b). Their salaries were higher than the national average (Boo 1990b). The settlers encouraged the local residents to continue their craft work (Chant 1992), and a cooperative was established to sell the articles to tourists (Boo 1990b). Boo stated that the shop "recently" had annual sales of US $50,000. Given the 70 members of the cooperative, that is a gross revenue of about US $700 per member annually. Land prices were among the highest in Costa Rica and were having a negative impact on the local agricultural sector (Boo 1990b). According to Boo (1990b:47), the local residents consider the tourism boom to be a "mixed blessing."

Mexico

Izta-Popo National Park in Mexico is located 80 kilometers from Mexico City and centers on the second and third highest peaks in Mexico, Iztaccihuatl (5,386 m) and Popocatépetl (5542 m). Seventy-four percent of the visitors engaged in mountaineering. Ecotourism activity consisted of botanical study (23 percent) and bird watching (9 percent) (Boo 1990b).

At Izta-Popo National Park negative environmental impacts have been reported that could grow to become serious if action is not taken (Boo 1990b). Garbage is increasing in the area. The quality of the water in a spring is being degraded by the discharge of wastewater from the Park lodge. Deforestation is resulting from the cutting of trees for tourist campfires.

According to Boo (1990b), the greatest economic impact of the Park may arise from expenditures for local taxis to bring tourists the 22 kilometers from the bus terminal in Amecameca, to the Park. The restaurant in the lodge at the Park employs nine people during the week and 15 on weekends. There are 35 Park employees. The importance of the Park in the local economy is unknown (Boo 1990b).

Arizona

A recent study was made of the local economic impacts of ecotourist visits to the Ramsey Canyon Preserve and the San Pedro Riparian National Conservation Area in Southeastern Arizona (Crandall, Leones, and Colby 1992). The Ramsey Canyon Preserve, about ten miles from Sierra Vista, Arizona, is owned and operated by The Nature Conservancy. The area of the preserve is about 130 hectares. It is a nationally renowned bird watching spot because of the presence of a variety of hummingbirds, as well as the Eared and Elegant Trogons (Euptilotis neoxenus and Trogon elegans, respectively). Additionally, three rare and protected species of rattlesnakes are found within the Preserve.

The San Pedro Riparian National Conservation Area is located along the San Pedro River near Sierra Vista. Its area is approximately 22,600 hectares. With 60 percent of North America's inland bird species present at various times of the year, the area is also a national favorite of bird watchers.

Visitors to these two areas spent an estimated US $1.2 million in the Sierra Vista economy in the 1991-1992 fiscal year, about 1 percent of the US $122.5 million spent by the Fort Huachuca military base in the local economy. The visitors' expenditures produced 26 jobs, US $475,000 in local employee compensation, and US $271,000 in income to property in the local economy (Crandall, Leones, and Colby 1992). The distribution of these impacts across sectors of the local economy was as expected, about 41 percent of the employee compensation and 45 percent of the jobs were in the retail trade sector with about 23 percent of the compensation and 25 percent of the jobs in the lodging sector (Crandall, Leones, and Colby 1992).

ECOTOURISM ISSUES IN THE MADREAN ARCHIPELAGO REGION

In identifying these issues, we emphasize the U.S. portion of the Madrean Archipelago region because of our relatively greater knowledge and experience in that portion. Many, if not most of the issues, will be common to both portions of the Archipelago, but their resolution may differ. In this section we present the characteristics of the Archipelago in relation to ecotourism and then present those issues that need to be addressed in considering an ecotourism policy for the U.S. portion of the region.

The Madrean Archipelago

The Madrean Archipelago is a corridor of mountain ranges, Sky Islands, extending north from the Trans-Mexican volcanic belt to the Colorado Plateau. The east and west boundaries are approximated by the Davis Mountains on the east and the Santa Catalina Mountains on the west. (Peet 1998:64)

The corridor is rich in plant and animal species. The number of plant species in the mountain ranges of southeastern Arizona ranges from 663 to 1199 (Bennett and Kunzmann 1992). Preliminary results of a study of avian species (Block and Severson 1992) in these ranges showed numbers of species ranging from 52 to 78, with a combined total of 117. Lowe and Zweifel (1992) reported 12 amphibian and 72 reptilian species in the Chiricahua Mountains. Various studies show that this biodiversity is a significant attractant for tourists (Crandall, Leones, and Colby 1992; Richards and King 1982).

Four Native American Indian reservations, with an area slightly greater than 2 million hectares, are located in the U. S. portion of the Archipelago's region. Approximately, 2 million hectares of the U.S. portion of region are in national forests with the Coronado National Forest comprising most of the mountain ranges in the southeastern Arizona. Saguaro National Monument, East, includes the Rincon Mountains, another of the Sky Islands of the area. The total area of natural areas administered by the Nation Park Service in the region is about 174,000 hectares (USDI 1991). The Bureau of Land Management and the Arizona State Land Department are responsible for most of the lower elevation lands not in reservations. The important points regarding land ownership in the U.S. portion of the region are that 1) public and Native American lands predominate, and 2) most of the mountain ranges are in public ownership.

The major resource uses in the Archipelago region are tourism, mining, agriculture, and livestock grazing. The most vulnerable to competition from ecotourism is livestock grazing.

Issues to Be Addressed

Obviously, nature tourism exists in the region of the Madrean Archipelago and, if it is to be guided towards the ecotourism ideal, certain issues need to be addressed. As noted, ecotourism strives to achieve the two objectives of rural community development in order to improve social welfare and preservation of natural environments in order to maintain biodiversity.

These are not easily achievable goals. As Pigram (1992), points out, achieving them requires reconciliation of ethics and economics, a difficult task. To address that task in the Archipelago region, policies and planning processes should be appropriately designed to fit its culture, market driven economy, landownership patterns, and governmental structures.

Regional Planning

It is now clear that maintaining biodiversity requires a landscape or ecosystem approach, not just the simple setting aside of a disconnected series of preserves, whether they are opened to tourist visitation or not. The Kenyan experience demonstrates this need. Isolated preserves may work temporarily at the alpha level, but their lasting influence at the gamma level is marginal.

Regional planning for maintaining biodiversity focusing on ecosystems requires taking into account the economic and socio-cultural effects over the relevant geographical area in which they occur. In such a planning effort, ecotourism should be given consideration as a tool for maintaining biodiversity. If ecotourism is among the tools chosen, then planning for it should also be done from a regional perspective.

In this regional planning, ways must be found to promote cooperation among landowners having different ownership objectives. Although the large proportion of land in public or Native American Indian ownership in the Madrean Archipelago may make this task seem easier region than where private ownership is a much larger element, significant differences in mandates and objectives do exist among the responsible public agencies.

The announced shift to ecosystem management by the Forest Service and the Bureau of Land Management is a recognition that a more holistic land management approach is necessary. Federal lands are those most likely to form the core of lands open to and managed for ecotourism. Thus, this change could have positive effects for maintaining biodiversity and could incorporate ecotourism as a management instrument. Can this shift to ecosystem management be made by other land ownerships?

State lands in Arizona are managed to provide revenue to support public education. Maintaining biodiversity could become an alternative land use objective for state lands if the management goal for these lands were broadened so that the indirect benefits of ecotourism to the state's economy could be considered. State lands can be leased for commercial uses, including tourist facilities. Because these lands frequently are near federal lands, their potential for tourist facility development should be considered in planning for ecotourism on the federal lands.

Profit-oriented private landowners may not be interested in maintaining biodiversity on their lands, but may be interested in providing ecotourism accommodations and services. On the other hand, private, non-profit conservation organizations, such as The Nature Conservancy, own lands for the purpose of maintaining biodiversity. Still other private landowners, who value biodiversity, will maintain it and still others might be encouraged to do so through conservation easements.

County and local governments play important roles in land use decisions on private lands and must be brought into the process of planning for ecotourism and maintaining biodiversity. For these governments, the objective of community development will be particularly important and they must be educated to the symbiotic relationship between that goal and preservation of natural environments.

Public Involvement

Regional planning for ecotourism will not only require cooperation among landowners and local governments to fulfill its potential, but the public must participate in the planning effort. Participation by the local public can help avoid situations, such as those in Kenya, where local residents take actions directly counter to the biodiversity goal. It can also provide for the inclusion of native peoples and their knowledge of the ecosystems in the planning process, as was done in Uluru National Park.

Education

Successful ecotourism requires the education of guests and hosts. The tourist must be educated about the environmentally appropriate behavior. And, to provide educational experiences, on-site, environmental interpretation programs should be a high management priority for agencies managing natural areas. Education of guests can also build public support for the goal of maintaining biodiversity. Hosts need to be educated and trained to invest and to be employable in the ecotourism industry. Ecosystem planners and managers need to be educated about the knowledge that native peoples may have of the ecosystems in which they have lived for many centuries. The incorporation of such knowledge at Uluru National Park has provided the opportunity for an improved ecotourist experience to Park visitors.

Investment Capital

Local residents may lack capital to take advantage of the investment opportunities provided by ecotourism, as was true in the Monteverde and Kenya examples. Capital must be made available to residents of the local community to ensure that a majority of the economic benefits of ecotourism remain in the community. In addition to providing greater local economic benefits, local ownership of facilities may reduce the imperialistic nature of tourism and the socio-cultural conflicts arising from it. Therefore, serious consideration should be given to providing low interest loans for such investments.

Control of Tourist Activity Levels

One of the conundrums of ecotourism is that economic success carries the seeds of failure to preserve the natural environment upon which it depends. This conundrum ensues from the fact that ecotourism depends, typically, on both private facilities and services and public natural areas and facilities. Therefore, coordination of the efforts of the private and public sectors is very important. It is also a very difficult task. For example, the levels and kinds of tourist activity that would maximize private net returns may be higher than natural areas can withstand, destroying the symbiotic relationship and subverting the goal of maintaining biodiversity.

Controlling tourist visitation to public natural areas is necessary but very difficult where the economy is market driven and where public access to public lands is considered an individual right. Visitation levels at public natural areas are partially determined by the capacity of privately owned facilities and services. At the same time, however, visitation limits at the natural areas are factor in private ecotourism investment decisions. Therefore, there is a need, at the very least, for communication between the public and private sectors to avoid over or under investment in ecotourism facilities.

Further coordination may require greater cooperation between the public and private sectors in planning for ecotourism than now exists. The degree of cooperation needed may require new institutional approaches to ensure that the social goals of ecotourism are not subordinated to the private goal of profit.

CONCLUSION

Given the many things that must go well for nature tourism to become ecotourism and the present and potential strength of the regional economies, we conclude that a public policy endorsement of ecotourism in the region of the Madrean Archipelago to maintain biodiversity is premature without further study. We do suggest, however, that the natural area preservation objective of ecotourism be emphasized over the community development objective in the U.S. portion of the Madrean Archipelago region.

In particular situations, however, the ecotourism approach could be useful. These are situations in which commercial land uses threaten natural areas that are essential to maintaining the region's matrix of biodiversity.

Finally, we wish to emphasize that ecotourism is a special kind of nature tourism that is directed to the two objectives of community development and natural area preservation.

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Fuelwood Harvesting in the Sky Islands of Southeastern Arizona

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Abstract.—Fuelwood harvesting has occurred in and around the "sky island" mountains of southeastern Arizona for centuries. Native Americans utilized the woodlands as a source of food and a source of fuel for cooking and heating. Spanish explorers, Mexicans, and American settlers later expanded utilization to include such uses as mine timbering, coal production, and fencing. Utilization of the woodlands had minimal impacts on woodland resources until the local mining boom which took place in the late 19th century, and more recently from fuelwood harvesting in the late 20th century. This paper reviews the recent history of fuelwood harvesting on the Sierra Vista Ranger District of the Coronado National Forest and the changing demand for fuelwood in southeastern Arizona from the early 1970's to 1994.

INTRODUCTION

Throughout the settlement of the Southwest, the oak woodlands have been used as a source of energy for heating and cooking, for food, and for building materials. Fuelwood harvested in the woodlands has provided heat for both comfort and cooking. Oak, which has a high caloric content, was plentiful and created a hot, long lasting fire. Juniper, although faster burning, was also used for its quick ignition and high heat content. Other species, including mesquite and manzanita, were also widely utilized.

Acorns, from the woodland oaks, were a staple food for the Native Americans and were harvested in the late summer and fall, roasted, ground into flour, and cooked into a bread. Some well preserved archeological sites still contain remnants of oak seeds harvested centuries ago. Mexican and American settlers in the area, learning from the indigineous people, also harvested acorns for food (Spoerl, 1988). Today, many people, especially the local Mexican-American population and Apache people from San Carlos and Whiteriver, Arizona, continue to harvest acorns for either personal consumption or for minor commercial sales.

Woodland tree species also have been utilized as a source of building material for crude shelters, fencing, mining, and miscellaneous ranch and home construction (Ffolliott, 1988). During the mining boom of the 1800's, the woodlands of southeastern Arizona were cut heavily to support the mining industry. Wood was used to fuel the ore processing smelters and as support timbers inside mine shafts, tunnels, and adits. Miners preferred the native oak and juniper to imported species, especially when the work area was wet or subject to frequent flooding (Bahre & Hutchinson, 1985).

Utilization of the oak woodlands began to decline in the late 1880's when mining activity decreased in the area. Many small mines "played out" while several profitable mines became flooded at the lower levels as a result of a strong 1887 earthquake centered in northern Sonora, Mexico. This decline in fuelwood utilization continued for the rest of the 19th century and on into the first-half of the 20th century. Paralleling this decline, consumption of fuelwood in the United States also had dropped from an estimated 140 million cords in the 1870's to 16 million cords by 1960 (Skog & Watterson, 1986).

The energy crisis of the early 1970's was credited with playing a major role in reversing the downward trend of fuelwood consumption in the United States. As prices of major energy sources (natural gas, electricity, and heating oil) increased, the public turned to cheaper, alternative energy sources. Once again people began burning fuelwood to supplement home heating. It was

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estimated that by 1981, one-fourth of all households in the United States burned fuelwood, and in the rural west it was estimated that two-thirds of all households burned fuelwood. Annual fuelwood consumption in the United States was estimated to be 42 million cords by 1981, however, it was estimated that this amount only supplied 2 to 3 percent of home heating requirements for that year (Skog and Watterson, 1986).

FUELWOOD HARVESTING ON THE CORONADO NATIONAL FOREST

In the oak woodlands of southwestern United States and northern Mexico, low precipitation and high temperatures result in slow growing, low density forest stands. These slow growing stands, however, are a highly utilized fuelwood resource. Some fuelwood species harvested in southeastern Arizona take from 60 to 100 years to grow from seed to desirable harvest size, that is, 6 to 8 inches in diameter at the root collar (Callison, 1988). Ffolliott (1989) notes that the oak woodland vegetation type has an annual growth rate of less than one percent. Long rotation age, limited resource, and high demand for fuelwood were three of the ingredients that combined in the late 1970's. This mixture alerted area land managers to a pending resource problem. At the current rate of harvesting, demand would soon exceed supply (Tolisano, 1984; Frank, 1982). To solve the problem, several questions needed to be answered, for example, what was the volume of accessible fuelwood, what rate of harvesting could be tolerated to assure a sustained yield, and what was the current and foreseeable demand for the resource.

On the Coronado National Forest fuelwood demand rose dramatically between 1973 and 1981. All of the five District offices reported increased requests for fuelwood. On the Sierra Vista Ranger District, sales of fuelwood permits for one cord of fuelwood prior to 1976 were less than 500 cords annually. However, in 1977, over 3,000 cords of wood were sold, and in 1978, after a cold winter, sales topped 5,100 cords. Forest officials wondered how long this rate of cutting could continue before the supply would become depleted.

Nearby towns and cities continued to grow, as did the number of homes with fireplaces or wood stoves. In 1970, the population of Pima County, Arizona was 351,666; it grew to 531,433 by 1980 (Tucson City Government, 1994). The population of Cochise County rose from 61,918 in 1970 to 85,686 in 1980, and the population of Sierra Vista had risen from 6,689 in 1970 to over 26,000 in 1980 (Sierra Vista Chamber of Commerce, 1984).

The Forest Service noted that, relative to other parts of the country, little was known about the demand for fuelwood in southeastern Arizona. Demand appeared to be related to income. It was estimated that as the personal income level and population of the area increases, so would the demand (USDA Forest Service, 1989). Fortunately, by 1984, energy prices were stabilizing or retreating, and the demand to harvest fuelwood was decreasing. It was estimated that in 1984, 2,700 cords of oak, 2,000 cords of mesquite, and 1,000 cords of juniper were harvested in Cochise County (McLain, 1988).

During the 1970's and 1980's, of the five districts on the Coronado National Forest, the Sierra Vista Ranger District saw the greatest increase in the amount of fuelwood harvested. The other four districts that make up the Coronado, with offices located in Douglas, Nogales, Safford, and Tucson, were either lacking the fuelwood resources to provide or were not located close enough to a populated area to experience that increase in demand.

Green Fuelwood Harvesting

In the spring and summer of 1979, the Forest Service conducted a preliminary inventory of the fuelwood supply on the Sierra Vista Ranger District by aerial photo analysis and field checks. Certain criteria were used in determining which areas could be included in the inventory and which areas could not. These criteria included, but were not limited to, slope, wildlife habitat, visual quality objectives, and accessibility. Areas that exceeded 35 percent slope could not be harvested due to the erosion potential from inexperienced woodcutters driving vehicles within the fuelwood area. Important wildlife habitat areas also were excluded as a fuelwood source. Wildlife constraints were developed through a cooperative effort between the Arizona Game and Fish Department and the Forest Service. (Each year representatives from the two agencies meet in potential fuelwood areas to determine availability of fuelwood and discuss constraints and marking guidelines.) Potential effects to the visual quality of the area were discussed to assure the maintained quality of the viewshed. (Areas with high public visibility, such as the eastern slope of the Huachuca Mountains, have low tolerance to vegetative manipulation, while other viewsheds are better able to withstand some modification.) Fuelwood reserves that had ready accessibility, such as existing roads, flat terrain, etc., were documented and placed on the list of near-future sites to be harvested. Inaccessible areas, such as areas needing road construction, or some type of land modification, were noted as potential sources of fuelwood.

The rotation age of Emory oak (*Quercus emoryi*), the major species utilized for fuelwood during the 1970's and 1980's, was not known. Very little research had been conducted in the oak woodlands, therefore, a preliminary estimate of 150 years was made. (This estimate did not take into account whether the tree came from seed or sprout. Land managers, unfamiliar with the local history, believed that most of the local stands originated from seed rather than sprout. A study by Touchan (1986) found that the biological rotation age of Emory oak, from sprout, is approximately 35 years.) A historical review of the area later showed that nearly all of the woodlands in this part of the state had been harvested nearly a century earlier to support the nearby mining industries, and that a majority of the oak stands were most likely from stump or root sprouts.

Using the data from the inventory and assuming a 150 year rotation, it was estimated that approximately 1,000 cords of green fuelwood could be harvested annually to assure a sustained yield. Therefore, a 1,000 cord limit was incorporated into the fuelwood management program for Sierra Vista in time for the 1979 cutting season. The harvesting limit was imposed only on the personal-use permits offered and did not effect the amount of fuelwood harvested by commercial cutters. Commercial harvesting was a separate program and was allowed to continue temporarily while land managers monitored the demand for personal-use permits. These permits, which previously had allowed the annual harvesting of two cords per family per year, were reduced to one cord per family annually, making the limited supply of fuelwood available to a greater number of families. The price of a permit also increased from $5.00 in the 1970's to $10.00 in the early 1980's.

In 1980, the commercial harvesting program, which to date had amounted to approximately 500 cords of greenwood per year, was eliminated from the district fuelwood plan altogether. The elimination of the commercial program was due to the high demand for personal-use permits in 1979; all 1,000 permits were sold the first week they were available and requests for more permits continued throughout the wood burning season.

In the mid-1980's the demand for fuelwood in southeastern Arizona decreased significantly. This decrease was due in part to several factors: primary energy resource prices had stabilized or lowered, the current tree species being harvested was alligator juniper (*Juniperus deppeanna*) - a less-desirable wood burning species, the distance from towns and cities to the harvesting area was getting greater, and the price of fuelwood permits were increasing. In 1985 the price of a one cord permit rose to $25.00. In 1986, the demand for fuelwood permits dropped below the 1,000 cord mark. Although 1,000 permits were offered, only 720 were sold. That trend continued, and in 1988, only 700 cords were offered.

In 1991, 400 permits for juniper were offered and the amount of fuelwood permitted by each permit was reduced to one-half cord, while the price remained at $25.00. That year only 76 permits sold. Since that time the number of permits sold each year has remained below 100.

It is interesting to note that in 1981, the issuance of free-use manzanita permits, allowing the free harvesting of *Arctostaphylos pungens*, a hard, multi-stemmed plant, surpassed the number of oak and juniper permits sold that year. This was a minor achievement because manzanita was considered a non-desirable species for fuelwood. It is a hard wood that quickly dulls the cutting edge of any saw; it requires hard work to harvest and returns relatively little reward. However, from 1981 through 1985, the number of free-use manzanita permits issued outnumbered oak and juniper permits in each year. In 1986, when fuelwood demand decreased, the demand for manzanita permits almost disappeared. A summary of green fuelwood permit sales for the Sierra Vista Ranger District from the mid-1970's to the present is shown it Table 1.

Downed-Deadwood Harvesting

The sales of deadwood permits parallelled those of the live wood. When the harvesting of live wood included oak, there existed only a moderate demand for deadwood. Deadwood was harvested on a district-wide basis, that is, a permit holder could harvest downed-deadwood anywhere on the district. In 1979, when the number of live wood permits was limited on the Sierra Vista Ranger District, the number of downed-deadwood permits was also limited, to 500 cords personal use per year. From that point to 1985, all downed-deadwood permits were sold out. In

1986, when the demand for live oak decreased below the number of offered permits due to the falling prices of more conventional heating sources, and the increasing prices of a fuelwood permit, the demand for deadwood followed. The district sold approximately 350 deadwood permits that year.

In 1988, when the live wood sales included juniper, the number of deadwood permits increased. The reason for this increase is threefold: people could get seasoned dead oak rather than juniper; harvesting could take place anywhere on the district; and the likelihood of being checked by a forest officer was remote and therefore more than the one cord limit could be harvested. This upward sales trend continued until 1991 when land managers determined that the district-wide policy of gathering deadwood encouraged off-road driving, degradation of the riparian areas, where most of the deadwood resources were to be found, and loss of habitat for many vertebrates and invertebrates. They decided that deadwood harvesting should be limited to specified areas with concentrations of downed-deadwood, and that the harvest be used to accomplish other management objectives. Also, in 1991, the amount of the permit was cut to one-half cord and the price per permit was increased to $25.00. Since that time the sales of deadwood permits have fallen. Table 2 shows the history of downed-deadwood sales on the Sierra Vista Ranger District from 1976 to 1993. The 1994 deadwood season will take place after the writing of this paper.

Table 1.— Recent History of Green Fuelwood Harvesting on the Sierra Vista Ranger District from 1976 - 1994

Year	Price/ Cord	Species	Cds Offered	Comments
1976	$2.50	Oak	<500	No limit
1977	$5.00	Oak	>3000	2 cord limit/fam./yr
1978	$5.00	Oak	>5100	2 cord limit/fam./yr.
1979	$10.00	Oak	1500	1cd/fam/yr + 500 cd commercial
1980	$10.00	Oak	1000	Commercial cutting eliminated
1981	$10.00	Oak	1000	
1982	$10.00	Oak	1000	
1983	$10.00	Oak	1000	
1984	$10.00	Oak	1000	
1985	$10.00	Oak	1000	
1986	$25.00	Oak	1000	@ 650 cords sold
1987	$25.00	Oak	1000	@ 650 cords sold
1988	$25.00	Oak/Jun.	700	@ 400 cords sold
1989	$25.00	Juniper	700	@ 400 cords sold
1990	$25.00	Juniper	700	346 cords sold
1991	$50.00*	Juniper	650	76 cords sold
1992	$50.00*	Juniper	650	35 cords sold
1993	$50.00*	Juniper	200	28 cords sold
1994	$50.00*	Juniper	200	25 cords sold

* $25.00 per 1/2 cord - Limit one-half cord per family per year

Table 2.—Recent History of Downed-Deadwood Fuelwood Harvesting on the Sierra Vista Ranger District from 1976 - 1993.

Year	Price/ Cord	Area	Cds Offered	Comments
1976	$ 2.50	Dist.Wide	<500	No limit
1977	$ 5.00	Dist.Wide	@ 600	2 cord limit/fam./yr
1978	$ 5.00	Dist.Wide	@ 800	2 cord limit/fam./yr.
1979	$10.00	Dist.Wide	500	1cd/fam/yr
1980	$10.00	Dist.Wide	500	
1981	$10.00	Dist.Wide	500	
1982	$10.00	Dist.Wide	500	
1983	$10.00	Dist.Wide	500	
1984	$10.00	Dist.Wide	500	
1985	$10.00	Dist.Wide	500	
1986	$25.00	Dist.Wide	500	@ 350 cords sold
1987	$25.00	Dist.Wide	500	@ 350 cords sold
1988	$25.00	Dist.Wide	500	@ 380 cords sold
1989	$25.00	Dist.Wide	500	@ 400 cords sold
1990	$25.00	Dist.Wide	500	437 cords sold
1991	$50.00*	Copper Cyn	250	108 cords sold
1992	$50.00*	Copper Cyn	250	69 cords sold
1993	$50.00*	Copper Cyn	200	51 cords sold

* $25.00 per 1/2 cord - Limit one-half cord per family per year.

SUMMARY

Intensive fuelwood harvesting has been a part of the ecosystem in southeastern Arizona for the last 100 years. Only recently have shortages in this resource occurred. The demand for fuelwood predictably has grown along with the population of the local communities, however, it also has been shown to fluctuate as a response to changes in the price of alternative home heating sources. Past harvesting practices, along with new ecologically based constraints, have prompted new restrictions and guidelines for the future; and since very few homes today utilize fuelwood as a sole source of heat and/or cooking, fuelwood harvesting in the next century will be quite different than the fuelwood harvesting which occurred over the last 100 years.

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Preserve Design for Maintaining Biodiversity in the Sky Island Region

Dale S. Turner[1], Susan Brandes[2], Mark Fishbein[3], and Paul W. Hirt[4]

Abstract.—The Sky Island region of Arizona, New Mexico, Chihuahua, and Sonora is distinguished by some of the greatest species diversity in temperate North America, but land management priorities in the region have never reflected that unique value. Jurisdiction is widely dispersed among various federal, state, and private landholders. There has been very little coordination of management efforts, and the closest approximation to a common management philosophy has been the maximization of utilization. We propose an alternate model, involving international and interagency cooperation, and based on conservation of native biological diversity as the priority value to be considered in land-use decisions. Using the principles developed for the North American Wilderness Recovery (Wildlands) Project, we propose a system of core preserves surrounded by buffer areas and linked by movement corridors. We suggest a process for establishing baseline measures of biodiversity, along with associated monitoring, restoration and other management programs.

UNIQUE BIOLOGICAL VALUES

The sky-island bioregion of southeastern Arizona, southwestern New Mexico, and the northern portions of the Mexican states of Sonora and Chihuahua is one of the most ecologically diverse landscapes in North America. It is the meeting place of four major North American biogeographic provinces: the Sonoran and Chihuahuan deserts, and the Rocky Mountain and Sierra Madrean forests. In addition, the great variation in elevation from valleys to mountain peaks creates a vertical layering of habitats that further intensifies species richness (Brown and Lowe 1980, Brown 1982). The "mountain islands" rise to cool and moist forested heights above the surrounding "sea" of desert and grassland — the latter as inhospitable to many mountain inhabitants as the analogous seas are to land dwellers of oceanic islands.

Southeastern Arizona is internationally renowned for its rich variety of plants and animals. For example, Arizona botanists Janice Bowers and Steven McLaughlin (McLaughlin 1992) recently estimated that each mountain range managed by the Coronado supports 800-1200 plant species and that the flora of the entire forest probably exceeds 2000 species. This total is believed to be greater than that for any other U.S. National Forest and exceeds the total number of plant species inhabiting the entire northeastern United States.

The U.S. Fish and Wildlife Service (1978) reported that southeast Arizona harbored the greatest diversity of mammal species of any area north of Mexico. The report proposed protection for "eight unique and nationally significant wildlife ecosystems" in Arizona, and all but one occurred in the southeast part of the state. Two U.S. Forest Service reports (1988, 1990a) identified within the Coronado National Forest 56 species of plants and 128 species of mammals, birds, fish, reptiles, and amphibians listed as endangered, threatened or potentially threatened under state and federal conservation programs. This number far exceeds that of any other forest in the Southwest Region (figs. 1-4).

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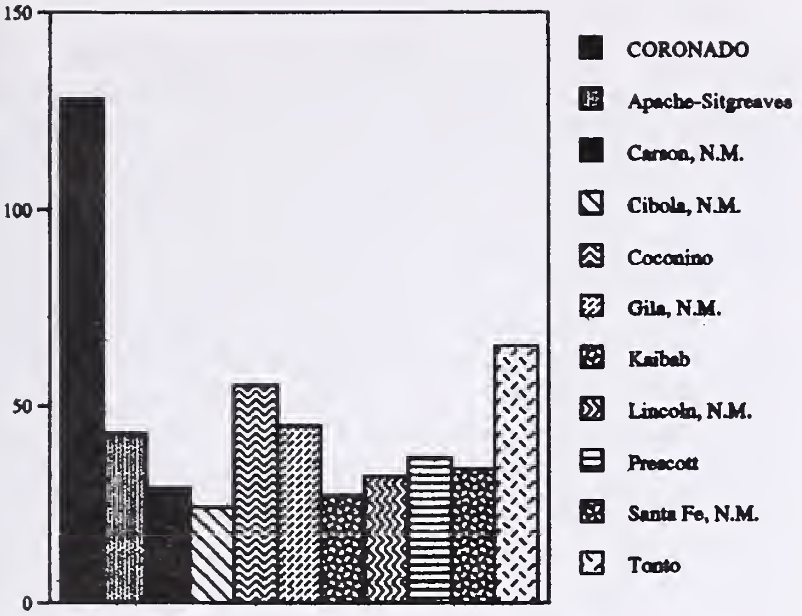
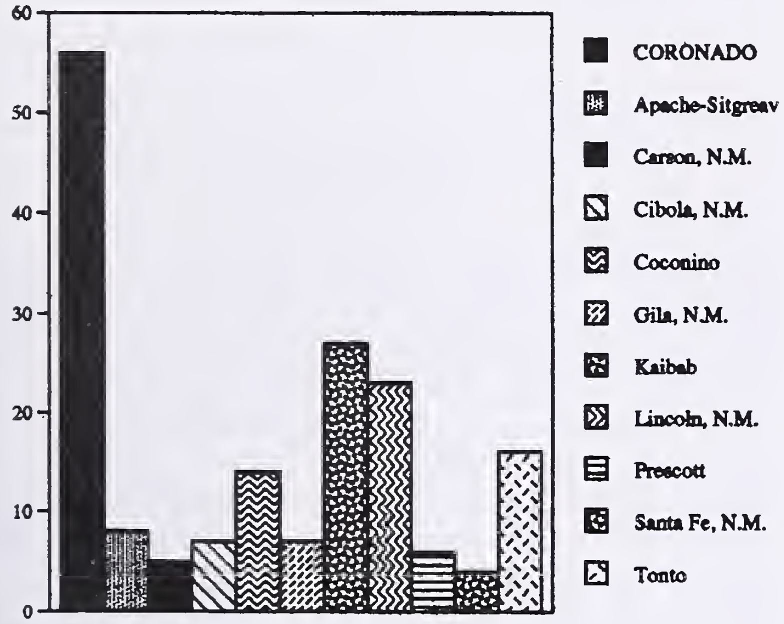


Data from Regional Forester's "Sensitive Species List," August 1988

Figure 1.—Number of threatened, endangered, and sensitive wildlife on Southwestern National Forest.



Data from Regional Forester's "Sensitive Plant List," May 1990.

Figure 2.—Number of threatened, endangered, and sensitive plants on Southwestern National Forest.

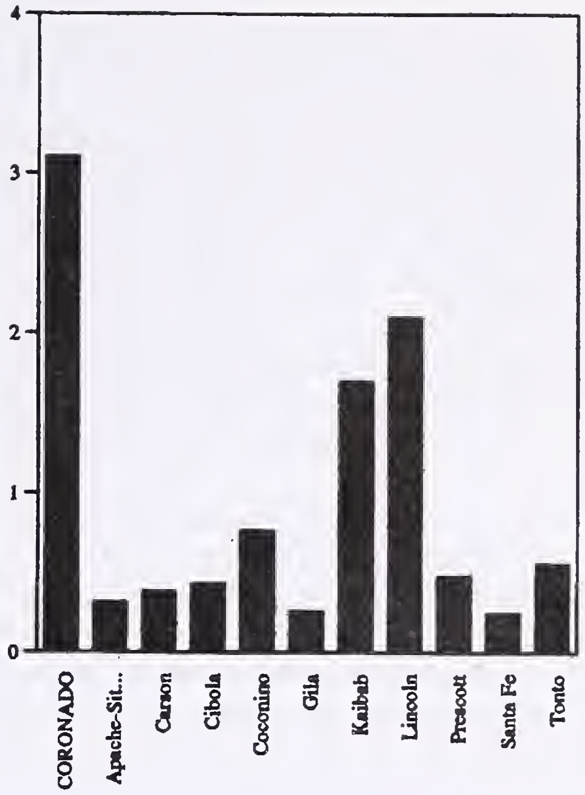


Figure 3.—Number of threatened, endangered, and sensitive PLANT species per 10^5 acres per forest.

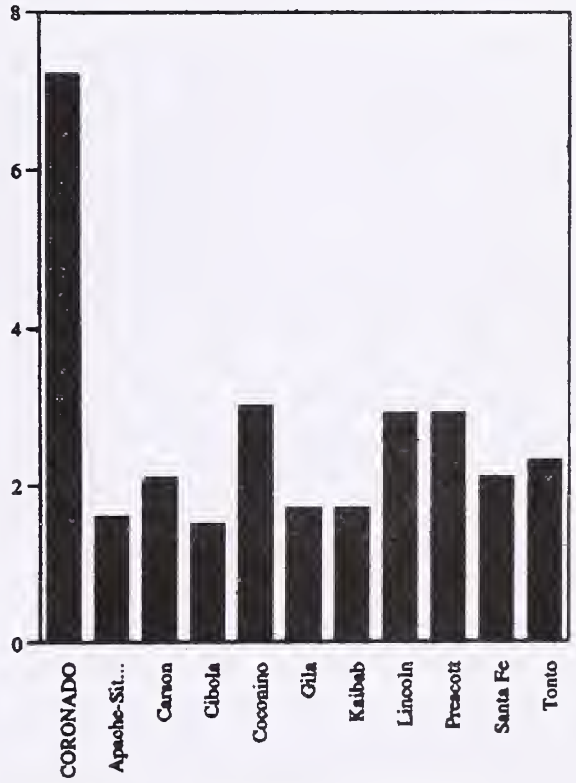


Figure 4.—Number of threatened, endangered, and sensitive WILDLIFE species per 10^5 acres per forest.

MIGRATION CORRIDORS AND BIODIVERSITY

Many animals (e.g. bears, eagles, and wolves) must move great distances to survive, often migrating seasonally over extensive areas in search of suitable foraging or breeding sites. Since each island is relatively small, this migration often results in movements from one mountain range to another, making the protection of habitat in multiple ranges and migration corridors between them especially important. Over time, organisms must also be able to colonize new habitats as climate or vegetation change reduces the suitability of their present habitat. Local extinction rates on sky islands are relatively high. The ability to migrate allows the transfer of genetic information between populations which helps ensure adaptability to environmental change and long-term survival (Schonewald-Cox et al. 1983).

Migration into and out of the sky island region is especially important. As development pressures in northern Sonora and Chihuahua become more severe, protected areas in the sky island region of the United States may serve as refugia for many vertebrate species that migrate across the international boundary. Similarly, if global climate grows warmer, these same species will become even more dependent on the sky islands as cool climate refugia.

Because of the topographic diversity of the region, migration corridors in the sky island region are relatively easily identified. Generally, these corridors are defined by north-south trending mountain chains and their intervening river systems that permit passage between areas of suitable habitat.

BARRIERS TO BIODIVERSITY

Migration corridors have suffered tremendously during the past century, as urbanization and rural development place physical barriers to movement or eliminate important components, such as food or cover, from previously used corridors. The Interstate 10 and 19 highway corridors function like the Berlin Wall, bringing death to essentially all terrestrial animals trying to cross them.

The growing popularity of industrial tourism has brought urban-style habitat loss into the very heart of mountain ranges. Paved forest roads and hardened campsites have brought immediate local habitat destruction, and resulted in long-term degradation for much broader areas.

Astronomical development on mountain tops is having similar effects, with the added quality of year-round use introduced to forests that were previously snowbound every winter.

We must also recognize the extractive focus of most land managing agencies, which has encouraged mining and grazing on all land that will support such activities. Mining has brought a total loss of habitat to localized areas and the construction of large new roads into remote areas. Grazing has brought more subtle losses, such as a decline in plant diversity, invasion by exotic species, disruption of predator/prey balances, and degradation of riparian zones.

The sky-island region comprises a wide variety of land owners, both public and private, and includes both state and international boundaries. This mixed estate makes landscape-level management difficult. Management planning and decisions are rarely coordinated, even between adjacent federal land holdings.

Preservation of biological diversity is perhaps the most important facet in the global effort to maintain a healthy environment and a sustainable resource economy for present and future generations. The Forest Service's most recent national management program, the 1990 RPA Program (U.S. Forest Service 1990b), recognized the value of biological diversity and the need for vigilant protection and restoration of native ecosystems on National Forest lands. But efforts to inventory and protect native species diversity on the national forests have languished while traditional resource extraction activities continue at an intensive and often unsustainable pace.

PRESERVE DESIGN AND THE SKY ISLANDS

Parts of the sky island region are currently managed as wilderness, but they are too small to maintain native biodiversity and natural evolutionary processes. Scientists have argued in recent years that even our largest national parks are inadequate to preserve their full complement of native species or to perpetuate natural landscape processes (Harris 1984, Kushlan 1979, Newmark 1985). The largest established wilderness area in the sky islands, the Rincon/Saguaro National Monument complex with 98,590 acres (Foreman and Wolke 1992), is far too small to hold viable populations of large predators. Even if it were, the land managing agencies do not currently have any mandate to manage for biodiversity in designated wilderness. By law and convention, wilderness areas are set aside for primitive recreation, though they may contain other values. Grazing, mining, and other activities harmful to wilderness and biodiversity can and do take place within many designated wildernesses.

The region's one National Wildlife Refuge has a more appropriate mandate, but again, it is a tiny speck on the broad biotic landscape. In addition, such refuges are not immune to pressure for uses that are incompatible with biodiversity.

BIOCENTRIC PRESERVE DESIGN

A large body of work has grown up in the last decade on the characteristics of preserve design necessary for the protection of biodiversity (Shafer 1990, Soule 1986, see also references in Noss 1992). Some of the key principles were identified by Jack Ward Thomas (Thomas et. al. 1990) and later extended by Reed Noss (1992):

1. Species well distributed across their native range are less susceptible to extinction than species confined to small portions of their range.
2. Large blocks of habitat, containing large populations of a target species, are superior to small blocks of habitat containing small populations.
3. Blocks of habitat close together are better than blocks far apart.
4. Continuous habitat is better than fragmented habitat.
5. Habitat blocks with connecting corridors are better than isolated blocks, and corridors that link habitat blocks function better when the habitat within them resembles that preferred by vulnerable or declining species.
6. Blocks of habitat that are roadless or otherwise inaccessible to humans are better than roaded and accessible habitat.

These principles became an organizing theme for the North American Wilderness Recovery Strategy, better known as the Wildlands Project. We are proud to offer our proposal as a piece of that continental effort.

A SKY ISLAND BIODIVERSITY PRESERVE

In line with these principles, we have formulated a proposal to manage this region in a manner appropriate to its biological values. This proposal deals only with the part of the sky islands that lie within the United States. We look forward to comments from our Mexican counterparts to improve this proposal and hope for the chance to work cooperatively on binational plans for the entire region.

A preserve system designed to restore and maintain the native biodiversity of this region must consist of two major components: specific management guidelines and a regional zoning plan.

Management of the region should have biodiversity preservation as the primary objective, with other uses secondary to that. In practical terms, this requires several steps. First, there must be a thorough inventory to establish baseline measures of biodiversity. Policy makers in Washington, DC, have underscored the importance of such inventories and taken an important first step to secure them by establishing the National Biological Survey. The goal of biodiversity inventories is to characterize the floristic and faunistic composition of a region and to identify and monitor those species that are most rapidly declining or which face the greatest threats.

Biodiversity occurs at several distinct and equally important levels, all of which need to be considered. These levels include:

- species diversity
- genetic diversity within species
- biotic community or habitat diversity
- landscape-level diversity between mountain ranges

At the species level, we need complete floral and faunal inventories of each sky island with particular attention paid to historically neglected taxonomy groups, e.g., invertebrates, fungi, etc.

At the genetic level, efforts should be made to ascertain the genetic structure of populations of rare, endemic, or endangered species.

At the level of biotic communities, we need to define and delineate the habitat types that exist on each sky island. Brown and Lowe's classification system (Brown 1982) makes a good point of departure, but it should be resolved to a finer scale within the sky islands.

At the landscape level, we must bear in mind that mountain ranges are not replicates of each other. Each has a unique assemblage of species and communities. Consequently each should be inventoried to determine what unique contribution it makes to total landscape diversity in the sky island region.

Two important biodiversity management principles are especially applicable to the sky island region—redundancies and linkages. Under the former, multiple examples of each biotic community (redundancies) are maintained rather than single samples. The Forest Service's Research Natural Area (RNA) program is a model of how not to manage for biodiversity, since it seeks only singular (and small-scale) representation of each vegetation type. Preserving biodiversity requires more than the zoo or ark approach to species and habitat preservation. Secondly, linkages between similar habitat types enlarge the available habitat for species experiencing survival difficulties. Animal and plant populations naturally fluctuate, and may die out in localized areas. This process has been amplified by human activities, making migration corridors essential for recolonization of extirpated populations. Linkages connect habitat fragments and thus greatly enhance survival opportunities for species and communities experiencing environmental change.

Restoring species or communities that are declining or extirpated is an essential prerequisite of managing for biodiversity. Studies of species that are likely candidates for listing as Threatened or Endangered need to be accelerated in order to determine where listing is appropriate. Species recommended for T & E status need to be formally listed and have critical habitat designations and recovery programs expedited. Current recovery programs for T & E species need to be *implemented*. And, finally, recovery programs should focus more broadly on all levels of biodiversity—genetic, community, and landscape diversity, in addition to species diversity. The traditional narrow approach to recovering threatened plant species, for example, often emphasizes the number of individual plants without considering the need to sustain pollinator populations that are necessary for natural reproduction of the plant species.

We must emphasize that recovery efforts for T & E species should also protect suitable but currently unoccupied habitat that can be colonized at some future date by that species.

The same efforts expended on behalf of T & E species should be extended to other levels of diversity, such as communities. Wetlands in the sky islands, for example, are both rare and absolutely crucial components of species, community, and landscape diversity. There should be mechanisms for declaring endangered biotic communities, and measures to recover them.

Perhaps even more important than protecting species is the restoration and protection of natural processes. In particular, a natural fire regime should be reestablished through a strong program of controlled and wild fires.

Monitoring environmental change and human impacts is crucial to biodiversity preservation. Monitoring assesses the effectiveness of management actions and the validity of management assumptions, while it illuminates changes over time in the physical and biological environment. It provides essential baseline data to evaluate and reconfigure plans for restoring and protecting native biological diversity. The Coronado National Forest's five-year progress report on its current land management plan recognized the importance of putting "Monitoring on an equal basis with project implementation" (U.S. Forest Service 1993: 1). Monitoring should be most intensive for species and communities experiencing the greatest declines or threats to their survival and for management actions aimed at recovering threatened species or communities.

In setting management policy, federal and state resource agencies should alter their priorities. The traditional approach to land management is to maximize land use while maintaining minimum standards of environmental protection. Under this old regime, commercial use of resources was constrained only by attempts to maintain the productivity of those resources. A small number of products and services became the management focus. Instead, preservation of native biodiversity should become the management focus, with resource uses allowed to the extent that they do not impair this primary objective. Activities that enhance or do not damage biodiversity may be encouraged, while activities that harm biodiversity should be prohibited. Multiple use can remain the *de facto* management context, but rather than driving decision making it would instead be subordinated to the overriding goal of maintaining biodiversity and natural ecological and evolutionary processes.

For zoning, we propose to reverse the matrix of land use patterns in the sky island region. Where the forested heights are now islands of wild habitat surrounded by a sea of human-dominated landscapes, there should instead be small islands of human use within a sea of recovering wilderness.

An ideal preserve system would consist of core areas - those with the highest biotic value - surrounded by buffer zones and connected by broad corridors (Noss 1992). The major towns could persist in some balance with the natural landscape. Low-intensity human use of the landscape could continue in the buffer zones, provided it was kept to a sustainable level.

We foresee the management of core reserves as roadless wilderness. Restoration will be a management emphasis, including encouragement of native species and restoration of those which were extirpated, removal of exotic species (including livestock), returning a natural fire regime, and closing existing roads.

Buffer areas would serve to insulate the core reserves from intensive land uses and insulate developed areas from depredating large mammals when they reach healthy populations in the cores. They would support a variety of low-intensity human uses, including some roads and habitat manipulation for target plant and animal species.

Corridors would be managed to provide suitable habitat for the species that might use them, and to avoid any significant barriers that might interfere with their movement. They should be broad enough to provide a continuous swath of habitat, free from edge effects, connecting the core reserves.

CORRIDORS AND COOPERATION

Of all the organisms that inhabit the sky island region, only humans recognize the existence of political and administrative boundaries These boundaries do, however, affect the organisms that cross them. Management decisions made by an agency on one side of a boundary may conflict with those on the other side. For this reason, we propose much greater interagency and international cooperation in the preservation and management of regional biodiversity and wildlife migration corridors (Noss 1983, 1987).

These corridors can only be effectively managed through cooperative arrangements between U.S. agencies, between U.S. and Mexican agencies, and between governmental and private organizations and landholders. In the U.S., for example, cooperation between the Forest Service, U.S. Bureau of Land Management, U.S. Fish and Wildlife Service, state and local governments, private landholders, and The Nature Conservancy is needed to integrate regional land management and protect the integrity of migration corridors. Other organizations (e.g. Sierra Club, Audubon Society, Arizona Wildlife Federation) and individuals should participate in management planning for the corridors. There is a similar spectrum of Mexican agencies, organizations, and individuals that must be involved in constructing international management agreements.

RESEARCH AND EDUCATION OPPORTUNITIES

The sky islands form a natural laboratory for basic research in ecology and evolution. The region is uniquely configured to provide opportunities for studies of island biogeography, effects of climate change on biotic systems, genetic structures of fragmented populations, and the ecological dynamics of local extirpation and recolonization. The large body of work by scholars who have used the Southwest Research Station provides evidence of the area's potential.

Just as the Coronado National Forest stands unequaled in the National Forest System as a repository for biological richness, so does it possess the potential to serve as an unparalleled outdoor school for environmental education. Whether forest visitors drive to a campground or backpack into a wilderness area, whether they come to hunt and fish, watch birds, or marvel at meadows filled with wildflowers, none can leave the forest without learning something about the incredible diversity of life in this region.

Educational goals for the region can be met by expanding such successful interpretive programs as that at Sabino Canyon Recreational Area, developing new low impact interpretive trails and the signing of access roads, developing educational exhibits and programs for campgrounds, offering internships for students of all ages to learn how land managers are conserving biological diversity, and establishing programs to introduce urban dwellers to the qualities of natural areas.

The development of educational programs for the management agencies offers an excellent opportunity for cooperative ventures with the region's educational and scientific institutions, conservation organizations, users' groups, civic organizations (e.g. chambers of commerce), and local governments. The development of such educational programs has the potential to vitally stimulate local economies, too. It must be emphasized, however, that while the temptation exists to extensively utilize the wealth of resources in the sky islands for education, this and other uses must yield priority to conserving biological diversity at all times. It is only the presentation of this resource that provides this region with its unique educational value.

HOW TO ACCOMPLISH THIS

Parts of this proposal would be impossible within the context of current federal land management policy. To fully implement it will require state and federal legislation, including a special designation for this region. It would further require a substantial international agreement along the lines of a biosphere reserve.

But much of what we propose can be put in place this year by the current land managers.

We recognize that the changes we have proposed are not trivial. But we also recognize that large changes can be made with enough time and with a shared vision of where we want to go. The sky island region has suffered because those who care about the region lack that vision and because there has not even been a shared sense of this region's unique values and potentials. This conference should bring progress toward that second point and sets the stage for the work yet to be done.

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Ecosystem Management Planning in the Forest Service's Southwestern Region

Arthur S. Briggs and Cathy Dahms[1]

Abstract.—This presentation discusses the Forest Service's new ecosystem management policy which is being implemented through the National Forest Management Act Plan and its revision. This approach is a broad scale, inter-regional strategy that is being developed cooperatively by the four Rocky Mountain Forest Service Regions, Rocky Mountain Forest and Range Experiment Station and the Intermountain Research Station. This approach incorporates ecosystem management policies into sub-forest and project planning levels through an integrated resource management process.

In Patricia Aburdene and John Naisbitt's book on Megatrends, they talk about the idea of critical mass. Critical mass is a term that came from physics, referring to the point where there is enough radioactive material to begin a nuclear reaction, after which the process becomes self-sustaining. It can also be likened to an avalanche. Billions of snow crystals pile up without any effect and then BOOM! Suddenly, an avalanche occurs. The same phenomenon occurs with products that people buy. Do you remember when telephone answering machines first came out? What percent of people owned answering machines before suddenly everyone had to have one? Or what percent of businesses owned FAX machines before it became the norm? For FAX machines, we know it was much less than 50%. Sociologists refer to critical mass, too, to see at what point an idea turns into a landslide and eventually becomes a belief held by the majority of people. In a sociological context, it is thought that the threshold for critical mass ranges between 5 and 20 %.

What does this have to do with ecosystem management? In the 1930's and 1940's, there were a handful of ecologists advocating many of the concepts being discussed today in ecosystem management. By the late 1980's, many scientists and land managers were talking about and supporting an ecological approach to land management, and after 1988, there has been a virtual outpouring of papers on the subject. In 1992, the Forest Service committed to ecosystem management, with other land management agencies and regulatory agencies soon following. Entire journals have been devoted to the topic, conferences such as this one have been held either partially or totally about the concepts of ecosystem management, and what is most significant, partnership efforts have sprung up all over the country to look at ecosystems both at broad scales and small scales. I contend that we have reached critical mass for ecosystem management. Ecosystem management is an idea whose time has come. However, it is still an evolving philosophy, so all of us are still struggling with how to transform the philosophy into action.

What is ecosystem management? The Forest Service has defined it as "taking an ecological approach" to achieve the mission of the Forest Service by blending the needs of people and environmental values in such a way as to have diverse, productive, healthy and sustainable ecosystems. You will notice that the Forest Service definition is tied to our mission. Missions are different between agencies and between landowners - this does not impair our ability to implement ecosystem management. Regardless of our mission, ecosystem management seeks to take an ecological approach with a common goal of achieving diverse, healthy, productive, and sustainable ecosystems.

Chief Jack Ward Thomas, in February of 1994, explained what "taking an ecological approach" means. He stated, "Ecosystem management is a holistic approach to natural resource management, moving beyond a compartmentalized

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approach focusing on the individual parts of the forest. It is an approach that steps back from the forest stand and focuses on the forest landscape and its position in the larger environment in order to integrate the human, biological, and physical dimensions of natural resource management. Its purpose its to achieve sustainability of all resources." Looking at the larger landscape has profound implications for management. Landscapes don't stop at our administrative or political boundaries. They don't stop at the edge of our communities. When taking an ecological approach, we have to look at areas that cross ownerships. Instead of working separately, we need to work together to understand the bigger picture. Because people influence ecosystems and are influenced by them as well, to achieve sustainable ecosystems also means sustaining the communities interacting with those ecosystems.

Some people have gotten the impression that ecosystem management means managing the land without regard to people. That is a myth - people are an integral part of ecosystems, and ecosystem management includes people and society's expectations for the land as well as the physical resources. We have altered the landscape in obvious ways, such as road building, timber harvesting, and recreation development, but also in more subtle ways, such as our decades of fire suppression across the country. People are tied to the land both for our livelihoods and for our spiritual needs. In fact, while an ecosystem management approach means utilizing scientific expertise in managing ecosystems, we also need to capitalize on the land wisdom of people who have years of observation and experience to offer, and incorporate that knowledge into our planning. Ecosystem management is an approach to ensure sustainability of the ecosystem by promoting management decisions that are environmentally feasible, economically viable, and socially acceptable.

Since we are seeking to maintain or improve the condition of the land as the context for providing sustainable levels of goods and services (one analogy is keeping the goose that lays the golden eggs healthy so it can continue to lay its golden eggs), restoration of ecosystem health is one of the goals of ecosystem management. It is an emphasis area for the Southwestern Region of the Forest Service, and is getting increasing attention across the western U.S., particularly because of the increased fire activity this past season.

Why is ecosystem management different from what we've been doing in the past? I've already mentioned one aspect - scale. Ecosystems occur at various scales and across our boundaries. Where boundaries cross, it does not mean that the same type of intensity of management is expected or desirable across the entire landscape, but our management is to achieve sustainability across the larger landscape, in such a manner so as not to preclude future options. So, one of our major shifts in thinking is understanding ecosystems at various scales in space and through time, rather than just at the site level. When looking at an ecosystem at one scale, we seek to understand the connection between all levels.

Another change is shifting from individual projects - planning a timber sale, a recreation project, a watershed improvement project - to looking at the whole area at once. Instead of looking at one activity in isolation, which tends to pit one resource against the others, we look at all the things that are needed to move the landscape into a more desirable condition, involving all disciplines in a mutual goal.

A third change in our thinking has been described as a shift from a production model (also called factory model) to a systems approach. A production model focuses primarily on outputs, and in the Forest Service, we spent a tremendous amount of time and dollars into optimizing outputs - board feet, recreation user days, etc. In the systems approach, we are as concerned with what goes into the system as we are with what comes out. For an ecosystem, this translates to an understanding of the composition, structure, and functioning of the ecosystem. We manage not just for outputs, but also to maintain the ecological integrity – the patterns and processes, both socioeconomic and biophysical - of an area. I like the comparison of ecosystems to a tapestry. All the different resources are the threads which make up the tapestry, and all the threads are essential to maintaining the strength of the tapestry.

These shifts in our thinking have also changed the way we approach the planning process. The cornerstone of implementing ecosystem management is in developing desired. Conditions (or desired future conditions as some people refer to them) for an area. In the past, we tended to propose projects for a site, analyze their effects, then implement and monitor the project. Under ecosystem management, we are developing desired conditions for an area first. Instead of then looking at a universe of potential projects, we can focus on those projects that will move us toward our desired conditions for the future. In developing desired conditions, the stakeholders of an area, representing a diversity of interests, meet to discuss the current condition of the land, what the land looked like in the past, and seek common ground in visualizing what that area should look like in the future - a vision that is sustainable through time.

Some people believe that desired conditions must be a return to the past, and that we must return ecosystems to what they looked like at an earlier point in time in order to have healthy ecosystems. Changes to ecosystems, both from nature and from people, are a continual process. We can learn how healthy ecosystems functioned by studying the past, but we must apply this knowledge to the future.

When we're able to develop common desired condition goals, we have a win-win situation for both the participants and the land. Once desired conditions are agreed upon, we can then explore options to move us toward the desired conditions. It helps in prioritizing what we need to do; we can concentrate on those areas where the current condition is furthest from the desired condition rather than those already close to or at desired conditions. And we can use desired conditions and the partnerships we have developed to coordinate our management between land managers.

To develop desired conditions for a broad scale area, we conduct assessments of the area. Assessments are going on all over the country, from areas a couple of tens of thousands of acres in size to multi-state areas like the Columbia River Basin. The dictionary definition of an assessment is an estimate of the importance or value of something. An ecosystem assessment would be looking at the importance of an ecosystem by characterizing different aspects of the ecosystem and then using that information to develop sustainable desired conditions. While assessments may seem complicated (and they can be, due to the complexity of ecosystems), they are really just people looking at the ecosystem in the past, present, and future. Assessments typically contain a history of the area, a description of existing conditions, potentials to determine landscape capability, and what the area will look like in the future given current trends or alternative management scenarios. Sometimes an assessment team will look at monitoring needs and/or research needs, and ways they can jointly meet those needs.

Assessments are done as a partnership effort between all stakeholders. Typically, different land managers will have different expertise and different data to bring to the table. It presents a wonderful opportunity to bring together all this information and to develop a common understanding of the existing situation and future trends.

It is human nature to try to get all the information we feel we need for an area. This can be a trap - we could end up spending all of our time collecting data and never end up doing anything on the ground. So the way we are looking at implementing ecosystem management, whether it's reacting to changes in the environment (like hurricanes, floods, a Mount St. Helen's explosion, or events that are happening more slowly through time), changes in society's values, or changes we need to make in our assessments or our land management plans, is through adaptive management. Adaptive management means going ahead with the information that we do have, taking small steps so as not to preclude future options, monitoring what we've done and evaluating its effectiveness, and then changing our management as needed.

Very few things in life are ever easy, and ecosystem management is no exception. There will be significant challenges to face. I believe we can meet those challenges with the help of all those interested in caring for the National Forests and having National Forest management serve the people.

A Nature Reserve System for the Gila River-Sky Island Region of Arizona and New Mexico: Some Preliminary Suggestions

Tony Povilitis[1]

Abstract.—Bio-regions are becoming a key focus in conservation planning. The Gila River-Sky Island region (GSR) of southern Arizona and New Mexico, situated at the convergence of 4 biogeographic provinces, ranks among the most ecologically diverse in North America. Species diversity is exceptional, with the region supporting the largest number of vertebrate and butterfly species west of the Great Plains. Unfortunately, the region's biodiversity is threatened by rapid human population growth, increased urbanization, and other intensive land uses. Some 156 species native to the GSR are considered at risk of extinction. Still, the GSR is one of the least impacted regions of the U.S., with a human density of less than 5 persons/sq km and with over 75% of its land in public ownership. This paper applies familiar conservation planning principles to the GSR. Seven conservation core areas were selected based on biotic community coverage, endangered species presence, low levels of human use, and a predominance of public lands. Twenty-three conservation corridors linking these areas were also identified, with 5 ranked the most promising using landscape condition, landownership, and other criteria. The overall "reserve system" appears to meet the spatial and habitat requirements of selected indicator species, including jaguar, desert bighorn, and Mexican spotted owl. Conservation of the GSR will depend on regional economic sustainability as well as on reserve planning. To advance the GSR as a foremost rural and natural area of the U.S., a regional coalition for conservation and economic sustainability is suggested.

There is growing interest in the conservation of biological regions (Council on Environmental Quality 1990, California, State of 1991, Mann and Plummer 1993, Greater Yellowstone Coalition 1994). Compared with smaller land units, "bio-regions" have far greater potential to conserve large mammals (Schonewald-Cox 1983), a full range of habitat specialists (e.g. Forest Ecosystem Management Assessment Team 1993), migratory bird species (e.g. Skagen and Knopf 1993), and vertebrate metapopulations (e.g. Bleich et al. 1990). They support far more natural diversity than do smaller areas since diversity is a function of available space and landscape-level geologic, edaphic, and climatic processes (Hunter et al. 1988, Noss 1990, Povilitis 1994).

This paper offers suggestions for conserving the Gila River-Sky Island region (GSR) of southeastern Arizona and southwestern New Mexico as one of America's premier rural and natural regions. The area, covering some 82,000 sq km, was chosen for study because of its landscape heterogeneity, comparatively natural condition, and increasing vulnerability to land development and urbanization.

THE GILA-SKY ISLAND AREA

Biological Setting

The GSR includes a broad band of mountain ranges and valleys situated at the juncture of four major biogeographic provinces (fig. 1). The Rocky

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Mountain province occurs on the north with primary associated vegetation types being spruce-fir (*Picea-Abies*), pine-Douglas fir (*Pinus-Pseudotsuga*), juniper-pinyon (*Juniperus-Pinus*), grama-galleta steppe (*Bouteloua-Hilaria*), and saltbush-greasewood (*Atriplex-Sarcobatus*) (Kuchler 1985).

Madrean evergreen woodland (*Quercus-Juniperus*) of the Mexican Highlands and grama-tobosa shrubsteppe (*Bouteloua-Hilaria-Larrea*) of the Chihuahuan Desert enter the GRS from the south and southeast. Creosote bush-bursage (*Larrea-Franseria*) and palo verde-cactus shrub (*Cercidium-Opuntia*) vegetation types of the Sonoran Desert advance from the southwest.

A remarkable faunal convergence parallels that of vegetation communities for the GSR. For example, geographic range boundaries of nearly half of the GSR's 554 vertebrate species fall within the region (Burt and Grossenheider 1980, Hall 1981, Stebbins 1985, Peterson 1990, Page and Burr 1991).

The GSR supports the largest number of vertebrate and butterfly species of any area of the U.S. west of the Great Plains (fig. 2, Pearson and Cassola 1992) suggesting an exceptional overall species diversity for the region. About 5% of GSR vertebrate species are not found elsewhere in the U.S.

The GSR includes a large percentage of federally listed mammals (100%), reptiles and amphibians (83%), birds (80%), and fishes (64%) for the states of Arizona and New Mexico. Overall, some 156 GSR species are considered to be at risk of extinction (Table 1). Primary factors contributing to species endangerment throughout the American West are excessive or poorly planned urban and agricultural development, livestock grazing, and water impoundments, diversions, and withdrawals (Povilitis 1992).

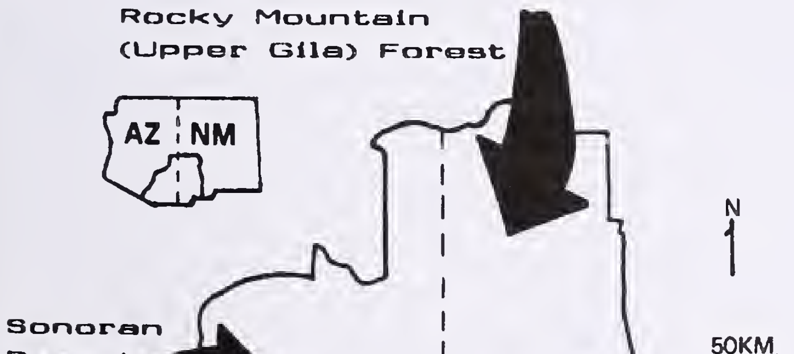

Figure 1.—Convergence of biogeographic provinces, Gila River-Sky Island Area (based on Bailey 1980, Brown and Lowe 1980, Udvardy 1975).

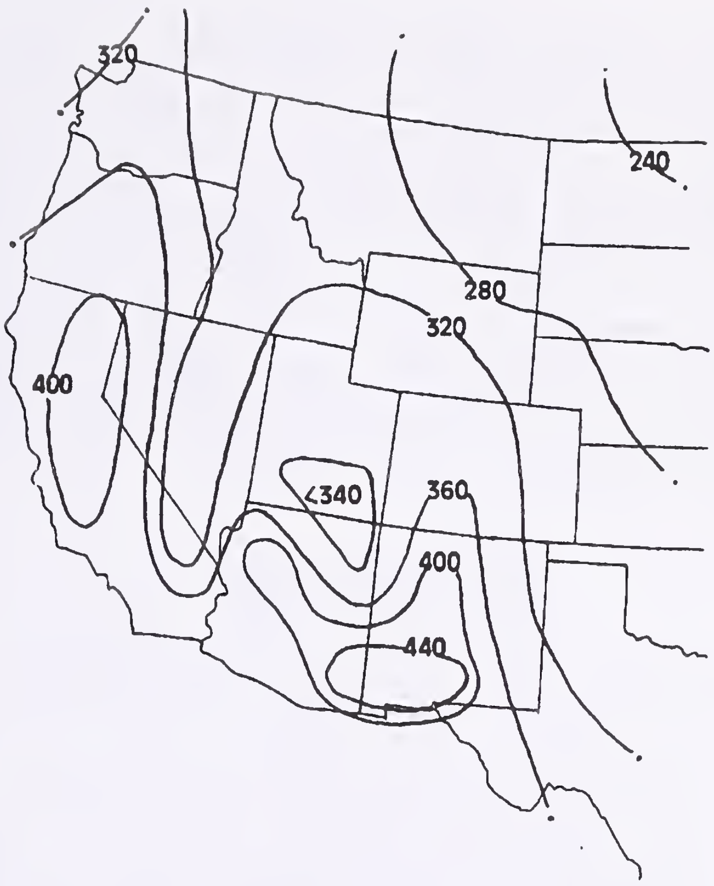

Figure 2.—Isoclines connecting approx. centers of squares with a similar number of vertebrate species for the western U.S.

People and Economy

Biological conservation on a grand scale is still possible for the GSR because of low human population density and because much of the region is publically owned. The GSR includes approx. 400,000 people (4.9 people per sq km), nearly third of which occur in seven population centers (fig. 3, Bureau of Census 1990). The GSR population increased by 19% between 1980-90 (Arizona Yearbook 1992, Southwest New Mexico Council of Governments 1992).

Landownership in the GSR is approx. 76% public and 24% private (based on Bureau of Land Management 1980, 1982). Public lands include national forest (40%), Bureau of Land Management (BLM) administered lands (21%), and state lands (39%). The GSR contains 25 congressionally-designated wilderness areas totalling nearly 1.3 million acres (about 4% of its total area) (BLM 1991, 1992).

Primary economic activities in the GSR include agriculture (fig. 3), livestock production, tourism, trade, sevices, mining, and light manufacturing (Arizona Yearbook 1992, Bureau of Business and Economic Research 1989). Counties located entirely or largely within the GSR had per capita incomes (approx. mean $9,300) well below that for Arizona and New Mexico as a whole (approx. mean $12,400). GSR counties had a higher average unemployment rate (approx. mean 10.7%) than did Arizona (7.2%) and New Mexico (8.0%) statewide (Arizona Yearbook 1992, Bureau of Census 1992).

RESERVE SYSTEM

The following conservation principles are suggested for the GSR:

- Conservation "core areas" where natural cover-type conversion is avoided and where land use practices are fully compatable with the conservation of biological diversity. The importance of protected core areas in conservation planning is widely recognized (Batisse 1986, Noss and Harris 1986, Shafer 1990).
- Conservation corridors or areas of natural or lightly developed habitat that connect core areas. The importance of corridors to a reserve system is also widely acknowledged (Shafer 1990, Hudson 1991, Saunders and Hobbs 1991).
- Sustainable development, namely, economic development that improves the quality of human life while conserving native species, ecosystems, and natural resources (IUCN et al. 1991). Sustainable development requires a shift away from land uses and economic activities that adversely impact ecosystems to those that are compatible with their long term viability.

Table 1.—Number of federally listed and globally threatened species native to the Gila River-Sky Island Region (1).

	Vertebrates	Invertebrates	Plants
Federally listed: endangered, threatened, or candidate one	36	2	14
Additional Global Rank 1-3 (imperiled to vulnerable)	10	20	74

Sources include Arizona Game and Fish Department 1994, New Mexico Natural Heritage Program 1993, U.S. Fish and Wildlife Service 1993a, 1993b, 1993c.

(1) Numbers are approximate given geographic range uncertainties for some taxa.

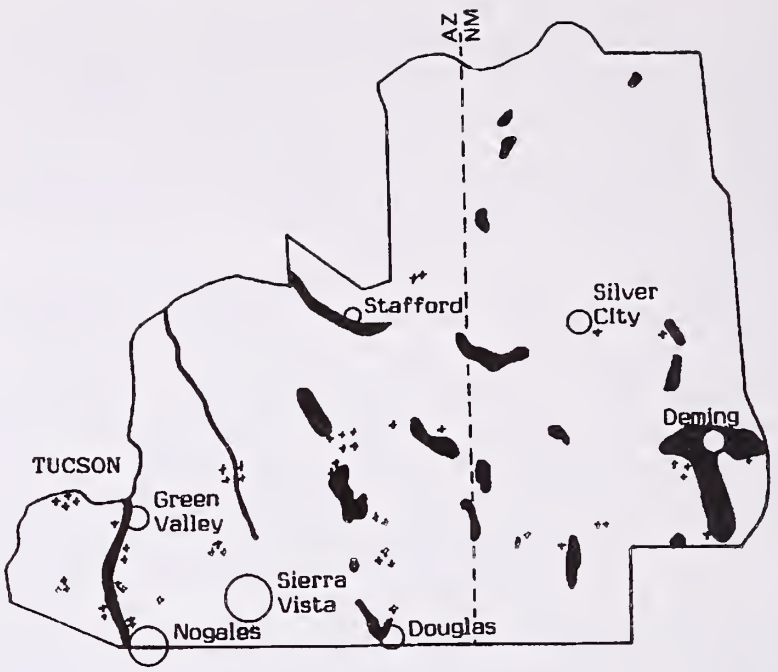

Figure 3.—Primary agricultural areas (black), population centers (circles), and rural land development areas (crosses) in the Gila River-Sky Island Region (Bureau of Census 1990, Hecht and Reeves 1981, Williams 1986).

Core Areas

Seven core areas were identified for the GSR covering nearly 70% of the region (fig. 4). The core areas consist of 54% federal, 30% state, and 16% private lands. They avoid overlap with major population centers and largely exclude primary agricultural and land development areas (fig. 3). Nearly 9% of the core areas are congressionally-designed wilderness.

The core areas include the major biotic community and ecotonal types found in the GRS (Table 2). The Mogollon area contains 5 biotic communities and 9 corresponding ecotones that are absent or marginally represented elsewhere in the core area system. Playas and associated ecotones occur only in the Peloncillo area. The Galiuro area stands out as the most biologically diverse of GSR core areas, based on community number, ecotone number, and ecotone density.

The proposed core areas include nearly all endangered or threatened species presently found in the GSR. Exceptions involve localized species such as Parish's alkali grass (*Puccinellia parishi*) (Grant Co. N.M.).

The Animas (N=46) and Mogollon (N=39) areas contain the largest number of imperiled species (Table 3). However, the smaller Altar (1 species/124 sq km) and Canelo (1 species/158 sq km) areas have 2-4 times the density of imperiled species as these areas.

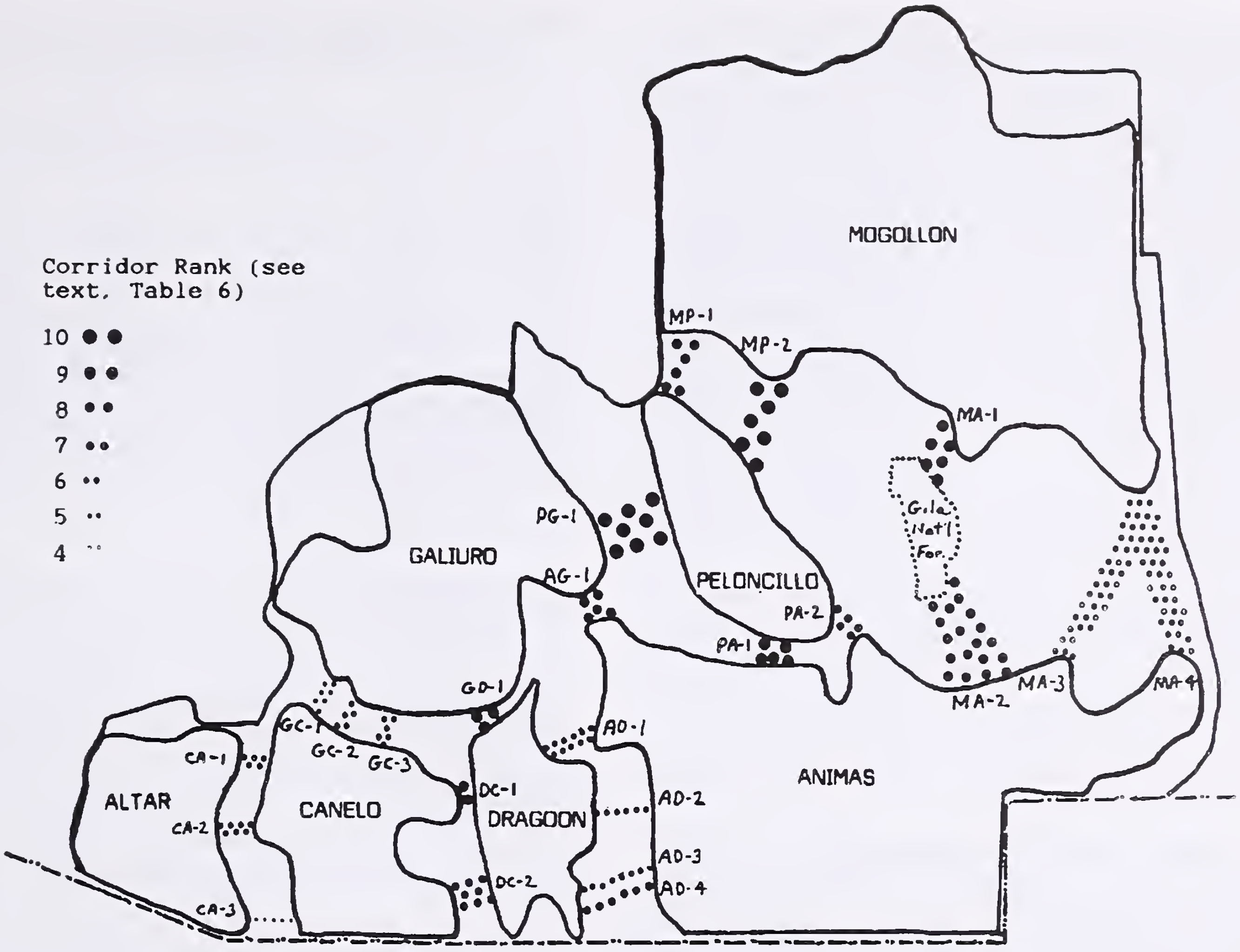

Figure 4.—Nature reserve design for the Gila River-Sky Island area showing biological core areas and corridors.

Table 2.—Major biotic communities (single numbers) and ecotones (double numbers) by Gila River-Sky Island core area (based on Brown and Lowe 1980, Kuchler 1985). Ecotone density (km/sq km, derived from 1:1,000,000-scale map measurement) is given in parenthesis.

Mogollon	1 2 3 4 5 6 11	1-2 1-3 2-3 3-4 3-5 *3-6* 4-5 4-11 5-6 (0.11)
Peloncillo	6 7 8 9 *12*	3-7 6-7 6-8 7-8 7-9 7-12 (0.12)
Animas	*1* 3 4 6 7 8	*3-5* 3-6 4-6 4-7 6-7 6-8 7-8 (0.12)
Galiuro	*1* 3 5 6 7 8 9 10	3-5 3-6 4-6 *5-6* 5-7 *5-9* 6-7 6-10 7-8 7-9 7-10 *8-9* (0.19)
Dragoon	6 7 8	6-7 6-8 7-8 (0.12)
Canello	*3* 4 6 7 9 10	3-6 4-6 4-7 6-7 7-8 (0.11)
Altar	6 7 9 10	6-7 6-10 7-9 7-10 (0.07)

Key: 1. Rocky Mountain subalpine forest; 2. Subalpine grassland; 3. Montane conifer forest; 4. Plains/Great Basin grassland; 5. Great Basin conifer woodland; 6. Madrean evergreen woodland; 7. Semi-desert grassland; 8. Chihuahan desert shrub; 9. Arizona upland desert schrub; 10. Interior chapparal; 11. Saltbush/greasewood; 12. Playas

Italicized biotic communities indicate minimal acreage (<100 sq km); italicized ecotones indicate minimal occurrence (1% of total ecotone distance).

Table 3.—Number of endangered and rare species identified for Gila River-Sky Island core areas (1). Figures in parenthesis are the number of species believed limited to the corresponding core area.

	Vertebrates	Invertebrates	Plants
Mogollon	15 (6)	5 (5)	19 (15)
Pelloncillo	7 (0)	0 (0)	0 (0)
Animas	13 (2)	11 (11)	22 (16)
Galiuro	12 (1)	0 (0)	10 (4)
Dragoons	7 (0)	0 (0)	3 (0)
Canelo	13 (2)	0 (0)	13 (7)
Altar	12 (3)	0 (0)	13 (6)

(1) Includes federally endangered, threatened, and category 1 species, and globally ranked G1-3. Numbers are approximate given distributional uncertainty for some taxa.

Three mammalian carnivores, the desert bighorn (*Ovis canadensis mexicana*), and the Mexican spotted owl (*Strix occidentalis lucida*) were selected as indicator species to test core area suitability for the region's most sensitive native wildlife.

Habitat availability and potential population sizes — Proposed core areas total approx. 57,800 sq km. This acreage falls within the 10,000-100,000 sq km range believed necessary to support large wide-ranging mammals (Schonewald-Cox 1983, Newmark 1987). Available habitat within the core area system appears adequate to support significant populations of indicator species (Table 4).

The Mogollon, Animas, and Galiuro areas provide the bulk of suitable habitat for grizzly bear (*Ursus arctos*) (85%) and wolf (*Canis lupus*) (80%). The Animas, Galiuro, and Dragoon areas are critical for jaguar (*Panthera onca*), providing approx. 70% of suitable core habitat. The Mogollon area is essential to the spotted owl, with 85-90% of GSR spotted owl habitat located there. All core areas would help support the desert bighorn whose viability depends on herd persistance in scattered areas of broken-terrain habitat.

Human population density — Population densities of greater than 2.3-4.6 persons per sq km make large carnivore conservation improbable (based on criteria for the wolf, Henshaw 1979 and Johnson et al. 1992). GSR core areas, with the exception of Altar, fall within or below this range (Table 5).

Road density — Road density should not exceed .58-.62 km/sq km (Mech et al. 1988, for wolf; Povilitis 1993, for grizzly bear). High road densities signficantly increase the rate of human-induced mortality and behavioral displacement of sensitive species. All GSR core area fall below this threshold (Table 5).

Table 4.—Estimated suitable habitat (sq km) and potential population size for selected conservation indicator species for the Gila River-Sky Island Region (1).

Species	Suitable Habitat	Population Size
Jaguar	38,000	429
Grizzly bear	42,200	587
Mexican wolf	42,200	118-274
Desert bighorn	12,200	610-5,002
Mexican spotted owl	4,100-5,800	313-446 adult pairs

(1) Potential population sizes were derived by applying animal density estimates to estimated suitable habitat in the GSR:

Jaguar — 1.4 animals/100 sq km for madrean evergreen woodland and semi-desert grassland (probable primary jaguar habitat, Brown 1983) and 0.5 animals/100 sq km for other habitats. Since density data is unavailable for jaguar in the Southwest, population density figures for mountain lion (*Felis concolor*) were substituted (Donaldson 1975, McBride 1976). The Mogollon area was excluded because of the absence of madrean evergreen woodland and semi-desert grassland.

Grizzly bear — 1.39 animals/100 sq km (Povilitis 1993) for all habitat except desert basins and flats.

Mexican wolf — 0.28-0.65 animals/100 sq km (Bednarz 1988, U.S. Fish and Wildlife Service 1987) for all habitat except desert basins and flats.

Desert bighorn sheep — 5-41 animals/100 sq km (San Andres Mtns., N.M., A. Fisher, N.M. Game & Fish Dept., pers. comm.; Cabeza Prieta NWR, Ariz., R. Schumacher, Refuge Manager, pers. comm.) for broken terrain habitats.

Mexican spotted owl — 8.28 adult animals/100 sq km for national forest land and 6.4 adult animals/100 sq km for other suitable forest habitat (McDonald et al. 1991).

Table 5.—Factors affecting the suitability of Gila River-Sky Island core conservation areas for native large carnivores.

	Size (sq km)	Human Density (people/sq km)	Road Density (km/sq km)	Livestock Density (no./sq km)	
				Cattle	Sheep
Mogollon	19,800	0.3	0.21	2.8	0.35
Peloncillo	2,800	1.5	0.32	3.5	0.13
Animas	16,700	0.5	0.23	5.0	0.32
Galiuro	8,700	0.5	0.25	5.6	0.40
Dragoon	2,500	2.7	0.50	4.9	0.80
Canelo	4,100	1.6	0.46	5.0	0.19
Altar	3,100	6.7	0.35	3.4	0.02

Sources include Burdett et al. 1990; Bureau of Census 1990; N.M. Agricultural Statistics Service 1991; National Forest Travel Maps for Coronado (1991), Apache-Stigraves, and Gila (1990) National Forests; Southwest New Mexico Council of Governments (1992); M. Snyder, pers. comm., University of Arizona Extension.

Livestock — Estimated livestock densities in GSR core areas range from 2.8-5.6 cattle/sq km and .02-.80 sheep/sq km (Table 5). Livestock densisites are generally lower than for the Yellowstone wolf reintroduction area (5.5 cattle/sq km and 4.1 sheep/sq km, peak values) (U.S. Fish and Wildlife Service 1994).

Corridors

Twenty-three areas were identified as having highest potential as biological corridors for the GSR. These areas were ranked for natural cover/condition, presence of an interstate highway, and type of land ownership (Table 6).

The Galiuro, Mogollon, and Animas areas are connected through the Peloncillo area by three "class 9 or 10" (highest ranked) corridors (PG-1, MP-2, PA-1) (fig. 4), consisting mostly of public lands. Corridors directly connecting the Animas area to other core areas ranked lower primarily because of private land development along Interstate highway 10 (I-10) and in Sulfur Springs Valley (between the Dragoon and Animas core areas). Valley agricultural and housing development threaten to sever biological connectivity between the Animas area and other core areas to the west.

A "class 9" corridor (GD-1) of mostly public land connects the Dragoon and Galiuro areas across I-10. Other corridors interlinking the Dragoon, Galiuro, Canelo, and Altar areas ranked lower largely because of private land development. For example, because of development spreading east and south of Tuscon (fig. 3) along Interstates I-10 and I-19, all corridors connecting the Canelo area with the Galiuro and Altar areas were ranked "class 6" or less (lowest ranks).

Inter-regional Linkage

Linkage between the GSR and other regions is also important. For many species, it is unlikely the GRS alone could support population sizes (i.e. in the thousands, Soule 1987) required for their long-term viability. Nor can the GSR alone support migratory species which also depend on adajacent bio-regions, or provide sufficent land area for biotic communities to shift and rearrange in response to future climate change resulting naturally or from the effects of anthropogenic "greenhouse" gases (Neilson et al. 1989).

Table 6.—Evaluation of biological corridors for the Greater Gila-Sky Island Region.

Corridor(1)	Natural Cover and Condition (2)	Roads(3)	Ownership(4)
MP-1	6	1	1
MP-2	6	1	3
MA-1	6	1	2
MA-2	6	0	2
MA-3	4	0	2
MA-4	4	0	2
PG-1	6	1	3
PA-1	6	0	3
PA-2	5	0	2
AG-1	5	0	3
AD-1	4	1	1
AD-2	4	1	1
AD-3	4	1	1
AD-4	4	1	2
GD-1	6	0	3
GC-1	3	0	2
GC-2	4	0	2
GC-3	4	0	2
DC-1	6	1	1
DC-2	5	1	1
CA-1	5	0	1
CA-2	4	0	2
CA-3	3	0	1

(1) MP=Mogollon/Pelloncillo; MA=Mogollon/Animas; PG=Pellincillo/Galiuro; PA=Peloncillo/Animas; AG= Animas/Galiuro; AD=Animas/Dragoon; GD=Galiuro/Dragoon; GC=Galiuro/Canelo; DC=Dragoon/Canelo; CA=Canelo/Altar

(2) combined rank for natural cover (i.e. land not converted for agriculture or other uses), where 3=90%, 2=50-90%, 1=2%; and land development, where 3=little or no housing development, 2=scattered development, and 1=moderate development.

(3) 1=no interstate highway; 0=interstate highway

(4) private land 3=%, 2=10-50%, 1=50%;

The Altar area connects the GSR with the El Pinacate bio-region to the west, which includes the Tohono O'Odham tribal lands, Organ Pipe National Monument, Cabeza Prieta National Wildlife Refuge, and two Mexican biosphere reserves (Williams 1994). The Dragoon and Canelo areas link the biologically diverse Galiuro area directly with northern Mexico. The Animas area links the GSR with Mexico's northern Chihuahuan desert and the proposed Casas Grandes reserve (B. Miller, Univ. Nac. Autonoma de Mexico, pers. comm.). The Peloncillo Mountains, which extend nearly 200 km north to south through the Peloncillo and Animas areas, provide a highland bridge to Mexico's Sierra Madre. Finally, the Mogollon and Galiuro areas connect the GSR northward with the Colorado Plateau region and central New Mexico and Arizona.

Sustainable Development

Biological conservation depends as much on economic sustainability as on the adoption of a nature reserve design. Sustainability requires human population and economic activity levels that are consistent with the carrying capacity of supporting ecosystems (IUCN et al. 1991). Efforts to promote regional sustainability and conservation are already underway for other areas of the U.S. such as Yellowstone (Greater Yellowstone Coalition 1994), the Southern Appalachian Mountains (Council on Environmental Quality 1990), and the San Juan Mountains (Greater San Juan Partnership 1994).

Under sustainable development, GSR economic activities would shift from those tending to have adverse environmental and cultural impacts to those that do not. Business activities consistent with this goal include sustainable ranching and farming practices (Soule and Piper 1991), cooperative regional industries (e.g. involving the network marketing of indigenous products, arts, and crafts), wildlife-based tourism (Whelan 1991), recycling of solid waste such as paper and wood products, and the accelerated use of solar and wind power (Bennett 1991) as the region's primary energy source. A diversified sustainable economy for the GRS could be expected to ease regional unemployment and poverty conditions, particularly under a program to stabilize the region's population.

CONCLUSIONS

Conservation of the GSR will require bold new land development policies that afford protection to primary natural areas and connecting habitat corridors. Biological fragmentation of the region by current land development patterns, particularly along interstate highways I-10 and I-19, in the Sulfur Springs Valley, and in the lower San Pedro Valley (with the proposed expansion of Fort Huachuca, U.S. Army 1992), is of major concern.

In order to conserve the GRS, a regional coalition of community leaders, landowners, businesses, government, and concerned citizens for conservation and sustainability is needed. The fact that a broad range of land-based traditions, lifestyles, and interests as well as environmental values are at stake should help unite citizens. Such a coalition will have to pressure state and federal governments for population policies that can help bring regional population growth under control.

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Ecosystem Planning in the Upper Watersheds of the San Pedro and Santa Cruz Rivers of the Coronado National Forest

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Abstract.—Ecosystem management is a philosophy for considering all elements as a whole when planning for the future of an area. In a demonstration project on the Coronado National Forest portion of the upper Santa Cruz and San Pedro Rivers, these physical, biological, and social factors are being used to match people demands with land capability. Progress of the project, cooperative efforts, and results of research in the area are presented.

INTRODUCTION

The Sierra Vista Ranger District of the Coronado National Forest has initiated an ecosystem management demonstration project for an area of 59,490 hectares (ha), stretching from crest of the Huachuca Mountains on the north to the border of Mexico, and from Montezuma Pass on the east to the Patagonia Mountains on the west. This area encompasses several unique vegetation communities, including madrean oak woodland and plains grassland. There are a number of rare plant and animal species that inhabit the area. The headwaters of two important rivers, the San Pedro and the Santa Cruz, are within the management area boundaries. In addition, the area surrounds one of the largest parcels of privately owned land in Arizona, along with a number of smaller private inholdings. The rural lifestyle of the residents on these lands, defined mainly by cattle production, has been a major contributing factor to the maintenance of open space and the undeveloped appearance of the landscape.

The feeling of open space is cherished by residents and visitors alike. The large expanse of undeveloped land provides continuity of habitat for many species of wildlife. Diversity of habitats, with oak woodland adjoining grassland, bisected by riparian areas, supports a diversity of species. The land is productive for cattle grazing, fuelwood, and game habitat. The most commonly hunted game is white tail deer. The area also represents a major portion of the habitat for Mearn's Quail, a unique species that attracts hunters and adds to birdwatching value. Recreational visitors enjoy sight-seeing, hiking, birdwatching, hunting, fishing, camping, local history, and spiritual renewal. For the most part, visitors to the area concentrate in the Parker Canyon Lake developed recreation sites and on main roads. Hunting activities account for the highest concentrations of dispersed camping. Growing populations in the nearby city of Sierra Vista (30 minutes away), as well as metropolitan Tucson (two hour drive), will mean increased numbers of visitors in the future.

DEFINING ECOSYSTEM MANAGEMENT

Ecosystem management planning is the logical continuation of National Forest Planning, which was implemented as a result of the National Forest and Rangeland Resources Planning Act of 1974 as amended by the National Forest Management Act of 1976. The Coronado National Forest Plan (Forest Plan) was completed in 1986, and has been amended several times. This plan covers the 1.7 million acres within the Forest and is broad in scope. Project or site level plans are carried out under Forest Plan direction for various management actions. Examples of site level plans are fuelwood sales, prescribed burns, allotment management plans, or campground development. Planning at the ecosystem level will allow the Forest Service to look at areas broader than sites,

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while focusing on an area that exhibits some commonality in the natural processes that define it. This will lead to more efficient and meaningful use of information, and better understanding of the cumulative effects of management.

Information needed to carry out ecosystem management will come from many sources. Emphasis will be placed on public involvement of the community and other interested people, conservation partnerships with other agencies and organizations, and partnerships between the Forest land managers and the scientific community.

The key to successful ecosystem management is the concept of a desired future condition. Desired future conditions are descriptions of what people want to see on the land in the future. These descriptions will lead to specific goals and objectives for an ecosystem management area, which can then be incorporated into the Forest Plan. They are based on the best knowledge about the dynamic natural systems; the soils, plants, water, and wildlife. Within the context of the health, sustainability and potential of the natural ecosystem, and with consideration of social, cultural and economic needs, the desired future condition will guide land management decisions.

The Forest Service mandate is to make available desired resource values, uses, products and services in ways that also sustain the diversity and productivity of the ecosystem over time. By taking an ecological approach to the management of this ecosystem we are recognizing that it is complex and dynamic, and that people depend on it's values and uses.

SETTING THE BASELINE

The goal for the Lone Mountain/San Rafael Valley Ecosystem Management Project for 1993 through 1994 was to lay the groundwork for the continuing process of ecosystem management. A four member core team was established and started work on the project in March of 1993. There were three major activities that were the focus of this effort. Although these activities were often interrelated it is useful to identify them separately: 1) Definition and delineation of ecosystem units, 2) gathering existing information and identifying information needs, and 3) public participation. What follows is a description of progress to date in each of these categories.

DEFINITION AND DELINEATION OF ECOSYSTEM UNITS

Ecosystem boundary delineation is the subject of extensive debate, and any definition of an ecosystem for management purposes should recognize that the system is open at many levels. The boundary for the Lone Mountain/San Rafael Valley Ecosystem is defined primarily by upper watershed boundaries. The headwaters of two major river systems, the Santa Cruz and the San Pedro, are within the area. Also included is the Redrock Canyon sub-watershed, which is hydrologically linked to the San Rafael Valley, and has been the site of intensive ecosystem restoration activities over the past four years. Parts of the boundary are defined by land ownership. There are private lands which are not included. Also, the international border with Mexico defines the southern boundary. Although these areas are not included, the process of ecosystem management will facilitate cooperation across ownership boundaries through partnerships and participation of the local community.

Beyond the hydrological linkages, the bases for delineation of the area are the open, undeveloped landscape, the shared species across vegetation types, the riparian corridors, the common social environment, the interconnected management activities and potential for partners.

LANDSCAPE UNITS

The ecosystem, as defined, encompasses 59,490 ha. It is further divided into three major landscape divisions; Lone Mountain (30,350 ha), San Rafael Valley (22,260 ha) and Redrock Canyon (6,880 ha). Lone Mountain is dominated by an extensive Madrean oak woodland. The upper watershed of this unit includes the high peaks of the Huachuca Mountains. Vegetation communities such as mixed coniferous forest and deciduous oak woodlands are common at these higher elevations. This landscape unit is a major water contributor to the San Pedro River of northern Sonora and southeastern Arizona. Elevations range from 1372 meters (m) at the Mexican border to just under 2865 m at Miller Peak. Major activities include camping and fishing at Parker Canyon Lake, hunting for whitetail deer and javelina, hiking in the Miller Peak Wilderness, livestock grazing, and caving. Twenty five of the Forest's sensitive plant and animal species, including several spotted owl pairs, also occur here.

The major feature of the 22,250 ha San Rafael Valley is gently rolling plains grassland. This grassland along with the adjoining mixed encinal, chaparral, and Mexican pine oak woodlands represent the headwaters of the Santa Cruz, a major drainage of the Gila River. Elevations range from near 2,133 m in the Canelo Hills to 1,524 m at the valley floor. Livestock grazing, birdwatching, quail hunting, and sight-seeing are important activities in this landscape. Several grassland and cienega sensitive species are found in the area. The Bog Hole Wildlife Area, a 120 ha Arizona Game and Fish Department management area, is located in the middle of this unit.

Redrock Canyon is the third major landscape unit of the ecosystem area. This 6,900 ha watershed drains to the northwest into Sonoita Creek and eventually the Santa Cruz River. It is also linked hydrologically to the adjacent San Rafael Valley. The canyon bottom is wet and contains a mixture of riparian communities. Dispersed recreation, livestock grazing, Mearn's quail and whitetail deer hunting, and bird and butterfly watching are important uses in the canyon. Redrock contains several cultural resource sites such as petroglyphs, archaic habitation locations, and a turn-of-the-century ore mill. The endangered Gila topminnow occurs in Redrock. The ecosystem management activities that are ongoing in this area emphasize riparian recovery, livestock grazing, sensitive animals and plants, dispersed recreation, and watershed conditions.

ECOSYSTEM UNITS

More specific ecosystem units within the landscapes were identified based primarily on soil, topography and vegetation associations. These units may occur within all three landscapes, for example riparian areas, or be restricted to one landscape. Delineation at this level proved to be a challenge using existing information. The Regional terrestrial ecosystem mapping survey has not been completed for the area. The most continuous data set available was the Region 3 General Ecosystem Survey (Forest Service, 1991). This data was supplemented with data from the Rangeland and Woodland Ecological Site Guides (Soil Conservation Service, 1988), the Soil Survey of Santa Cruz and Parts of Cochise Counties, 1979) and the Coronado National Forest Plan (Forest Service, 1986) and various allotment management plans.

Six different ecosystem units were delineated within the management area, ranging in size from ten to hundreds of hectares in size. They are plains grassland, oak woodland, riparian areas, shrub (steep slopes), mesquite/oak savannah, and coniferous forest. Existing conditions for these units was described, as well as potential. Desired future conditions will be developed for the land units at this level, as well as at the landscape level and for the entire ecosystem management area.

GATHERING EXISTING INFORMATION AND IDENTIFYING INFORMATION NEEDS

An ecosystem approach to management requires information about ecosystem components that is continuous across the management area, and relevant to several different scales. This means looking at biotic organization, geographic patterns, and changes over time at various appropriate levels. For example, information about rare species is collected at the stand or individual level, while descriptions of a plant community are a different biotic level at a broader geographic scale. Time scales are incorporated by historical or paleo-ecological studies.

Another component of the time scale which addresses the future as well as the past, is monitoring. In order to provide continuity in rangeland vegetation measurements, the Core Team revisited established monitoring sites. These sites were established in 1958 and had been re-evaluated in 1966. In 1993 the transects were re-evaluated using the same measurement technique used in previous years (Parker Three-Step) as well as plant community composition measurements based on dry weight estimates. Participants in the monitoring included District and Forest personnel, the permittee, and members of the Audobon Society. Interpretation of the data will help determine where the plant community is in relation to the desired future condition.

A monitoring plan has been completed for the Redrock Canyon projects. Implementation of this plan began in 1993, with emphasis on riparian vegetation response, erosion, and upland conditions. Monitoring for sensitive plants is being accomplished through a Challenge Cost Share Agreement with the Nature Conservancy. Surveys will be conducted for five plants in the ecosystem planning area. Management recommendations for these sensitive plants will be made to contribute to the management plan.

In addition to the biological and physical data, information about past ecological conditions, disturbance regimes (natural and anthropogenic), and cultural and economic values needs to be considered in ecosystem management. Literature searches using the Forest Service WESTFORNET system were started to identify sources of information and to begin building a research database for the area. In order to add to the ecosystem management database, a number of studies were initiated with cooperators from the University of Arizona. Following is a brief description of these studies, the deliverable products, and principal investigators:

Three Issues in the Human Dimension of National Forest Ecosystem Management. I. Economic Impacts of Cattle Grazing in the Lone Mountain/San Rafael Ecosystem Management Area. II. Monitoring Plan for Economic Evaluation of Recreation. III. Data Organization for Efficient Information Access and Analysis. 1) An estimate of the total output of cattle ranching in the Lone Mountain/San Rafael Ecosystem Management Area. 2) An explanation of the assumptions used to estimate total output, including information summarized on the number of cattle and value per cow. 3) An estimate of total economic impacts (i.e., direct, indirect and induced effects) of cattle raised in the management area on the economies of Cochise and Santa Cruz counties. 4) An explanation of the other economic sectors most likely to be affected by changes in total output in cattle ranching in the Santa Cruz and Cochise county economies. 5) Recreation use and value monitoring plan suggestions. 6) Discussion paper on Hyper-Text links as a basis for an information system.

Principal Investigators: Dr. Russell Gum, Dr. Dennis Cory, and Dr. Julie Leones, Dept. of Agricultural Economics, University of Arizona.

A Land Use History of the San Rafael/Lone Mountain Study Area. Includes an annotated bibliography of significant literature related to the management area, with an emphasis on human impacts and human induced environmental change. Also, an inventory of significant historic photographs, with focus on photos which can be used to determine the extent of ecological change. Listings will include location (may be approximate), subject matter, date (may be approximate), photographer (if known), condition of photograph and the name of the repository which holds the photograph. Approximately ten photographs will be selected for reproduction and included in the project report. **Principal Investigators:** Diana Hadley, Ecological Historian and Dr. Thomas Sheridan, Anthropologist, Arizona State Museum, University of Arizona.

Summary of the Natural History of the Southern Huachuca Mountains and the San Rafael Valley: Tempos and Modes of Vegetation Change Over the Past 20,000 years. A summary of existing literature concerning the natural history, over the past 20,000 years, of the Lone Mountain/San Rafael Valley Ecosystem Project area. The review of existing literature will be supplemented by personal observation and communication with other researchers working in similar areas. Recommendations for future study will be made. This work will complement the cultural history study underway for the same area. **Principal Investigator:** Dr. Tony Burgess, The Desert Laboratory, Department of Geosciences, University of Arizona.

Fire History of a Watershed in the Huachuca Mountains, Arizona. 1) A report resulting from analysis from at least 20 fire scarred trees within the watershed on the south side of the Huachuca Mountains (the Lone Mountain Ecosystem Management pilot project area). The final report will include a complete description of all analysis, results, and interpretations. The report will also include a discussion of the Huachuca fire history in comparison with fire histories in other southern Arizona mountain ranges, and suggestions for future fire history studies that may be conducted in the area. 2) At least one fire scar cross section with a polished surface that may be used by the Coronado National Forest for public display. 3) A presentation to the Coronado National Forest employees on results and implications of the study. **Principal Investigator:** Dr. Thomas Swetnam, Assistant Professor of Dendrochronology and Watershed Management, Laboratory of Tree-Ring Research, University of Arizona.

Gap Analysis Data for Wildlife Habitat in Arizona: Electronic Vegetation /Wildlife Habitat Map of Arizona. Upon completion and release to the statewide Gap Project, this data will be incorporated into the district GIS. **Principal Investigator:** Dr. Lee Graham, School of Renewable Natural Resources, University of Arizona.

Processing and analysis of ecosystem information will require the use of a Geographic Information System (GIS). One of the major goals of the Sierra Vista District is to have a functioning GIS in place in 1994. The University of Arizona Advanced Resource Technology Laboratory has entered into a Challenge Cost Share Agreement with Rocky Mountain Forest and Range Experiment Station to assist in building a GIS database for the management area. This database will have a minimum of thirty-nine layers operational by the end of FY 94. Training opportunities for Forest Service personnel are included in the agreement. **Project Coordinators:** Dr. Leonard DeBano, Rocky Mountain Forest and Range Experiment Station and Dr. Phillip Guertin, School of Renewable Natural Resources, University of Arizona.

PUBLIC PARTICIPATION

Public involvement for the project to this point has been directed toward research organizations that can provide information about the area, organized groups that have an interest in the area, and the local community that is most directly affected by management decisions.

Research Partnerships

A partnership with the University of Arizona has been established, the basis of which is understanding and implementing ecosystem management on Forest Service lands. This partnership was facilitated and enhanced by the presence on the Coronado National Forest of a research liaison from Rocky Mountain Forest and Range Experiment Station, Dr. Leonard DeBano. A major participant is the School of Renewable Natural Resources (SRNR) which in 1993 co-sponsored, with the Coronado National Forest, a graduate level seminar on ecosystem management. The seminar was led by Dr. George Ball of SRNR. Employees of the Coronado represented about half of the enrollment, resulting in a good mix of students, faculty and land managers.

The SRNR has also participated, through a Cooperative Agreement, by developing a video and viewer's guide for use as information and education about what ecosystem management is, with the Lone Mountain/San Rafael Valley area as a specific example. The primary purpose of the video and is to introduce the concept of ecosystem management to the people in the communities involved. The viewer's guide will function as a handout to people who watch the video, and as a stand alone mailer to reach a larger audience. This project was coordinated by Dr. George Ruyle of SRNR.

In addition, the Advanced Resource Technology Laboratory (part of SRNR) has a cooperative agreement with the Rocky Mountain Forest and Range Experiment Station to help build the Geographic Information System database for the ecosystem management project. They will be training Coronado National Forest employees in the use of the GIS, with example exercises featuring the project area. The SRNR coordinator for this project is Dr. Phil Guertin.

Other participants in the project from the U of A are the Arizona State Museum (cultural history of the project area), the Department of Geosciences Desert Laboratory (report on area paleo-ecology), the Tree-Ring Laboratory (fire history of the Huachuca Mountains), and the Department of Agricultural Economics (economic impacts of cattle grazing, and a monitoring plan for economic evaluation of recreation).

Under a Challenge Cost Share Agreement, The Nature Conservancy will be assisting with the planning effort for the Lone Mountain/San Rafael Valley ecosystem project. The focus of the Conservancy's efforts will be to document and contribute information on the large number of sensitive plant and animal species that occur in the project area. The Conservancy will review plans and contribute to the development of specific management guidelines. In addition, the Conservancy will coordinate participation of a planner from the Centro Ecologico de Sonora to be part of the Forest ecosystem planning team.

The participation of the Rocky Mountain Station will continue to be important to the project. There are a number of opportunities for initiating research in the area that will provide insight into ecosystem processes, and may lead to management options for reaching a desired future condition. The Station has contributed to developing a research database for use by the District.

International Partnerships

The Coronado has been designated as a Sister Forest with the Sierra de los Ajos Forest Reserve in Sonora, Mexico. The purpose of the Sister Forests program is to promote technical exchange for mutual benefit. The program is also designed to respond to the growing demand that Forest Service personnel apply their skills to internationally recognized problems.

The Sierra de las Maraquitas Natural Area is one of fourteen designated Natural Areas in Mexico. It is located immediately adjacent to the Lone Mountain/San Rafael Valley management area. The organization that is developing plans for this Natural Area is the Centro Ecologico de Sonora. A planner from the Centro, Cristina Melendez, has been interacting with the Lone Mountain/San Rafael Valley Core Team by attending meetings and participating in field activities. Coordination between the Centro Ecologico and the Coronado National Forest is being facilitated by The Nature Conservancy, who have a working partnership with the Centro, as well as with the Forest Service. The participation of a Mexican collaborator in the planning effort will contribute to achieving ecosystem management goals by addressing numerous management issues of concern in the planning area that transcend the international boundary. Examples are fire management, watershed management, and habitat management for rare species.

Other Partnerships and Contacts

A wide variety of local agencies and organizations have been contacted regarding the ecosystem management project. The general nature of the contacts has been to share information, and to begin to identify those who are interested. Groups, organizations and individuals have participated at varying levels up to this point. The critical period for public involvement is just beginning, with the development of descriptions for desired future conditions.

SUMMARY AND CONCLUSION

The Lone Mountain/San Rafael Valley Ecosystem Managment Project progresses as our information comes together. Desired future condition statements have been developed for the Redrock Canyon landscape, and projects have been intiated to improve ecosystem conditions. Data input into the GIS has been prioritized for the Lone Mountain landscape, which is the oak woodland, San Pedro watershed. There is currently a planning group working on developing desired future condition statements for this landscape. We will then move on to the San Rafael Valley. Although the process of ecosystem management is ongoing and continually adapting, we will call this demonstration project complete when we amend the Forest Plan with the management standards and guidelines that are specific to the Lone Mountain/San Rafael Valley Ecosystem, and a monitoring program is in place to measure our progress toward the desired future condition.

Conservation Opportunities in Borderlands: The Arizona-Sonora Perspective

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Abstract.—The Arizona-Sonora borderland contains species from the Chihuahuan, Madrean, Sinaloan, and Sonoran biogeographic provinces, which provides a great opportunity for management and research of shared natural resources. This area is characterized by 11 protected areas including wildlife refuges and biosphere reserves. Approximately 75% of species listed as threatened, endangered, and candidate in Arizona, also occur in Sonora. Portions of the Colorado, Sonoyta, Concepción, Santa Cruz, San Pedro, and Yaqui rivers - containing many of these species - are also shared between these two border states. Proposed economic developments along the borderland will represent a challenge to protect and manage the flora and fauna found in this area. The Arizona Game and Fish Department maintains joint efforts with several private and public groups and agencies on both sides of the border to ensure long-term existence of threatened and endangered species and their habitats. Conservation and management programs for the Sonoran pronghorn (*Antilocapra americana sonoriensis*), bighorn sheep (*Ovis canadensis mexicana*), Gould turkey (*Meleagris gallopavo mexicana*), masked bobwhite (*Colinus virginianus ridgwayi*), desert tortoise (*Gopherus agassizii*), native fishes (*Cyprinodon macularius, Poeciliopsis occidentalis, Ictalurus pricei, Gila ditaenia, Gila intermedia*), Mexican spotted owl (*Strix occidentalis lucida*), Mexican wolf (*Canis lupus baileyi*), thick-billed parrot (*Rhynchopsitta pachyrhyncha*), maroon-fronted parrot (*Rhynchopsitta terrisi*), and breeding birds in Sonora are already underway. These efforts include surveys and monitoring activities and reintroductions within their historic range. A key element of several projects has been development of management plans addressing conservation needs for these species.

INTRODUCTION

For many people, the 358-mile Arizona-Sonora border only represents part of the political limits between two nations. This is too simplistic. This borderland comprises an impressive array of cultural and biological diversity. The area, in fact, should more properly be referred to as the junction of three nations: the United States of America, the Tohono O'odham Nation, and the Republic of Mexico.

The diversity of the borderland region is well represented in 11 special management areas including the Cabeza Prieta, Buenos Aires, and San Bernardino national wildlife refuges; Organ Pipe Cactus National Monument; Coronado National Forest; San Pedro Riparian National Conservation Area, Arizona; Upper Gulf of California, and Pinacate and Gran Desierto de Altar Biosphere reserves; Sierra de los Ajos; Sierra Mariquita; and Sierra San Luis, Sonora (fig. 1). If we consider an arbitrary limit of 60 miles north and south of the border, then we have a more complex mosaic of public, private, and ejido (common property) lands, as well as other protected areas.

Approximately 75% of the species listed as threatened, endangered, or candidate in Arizona, also occur in Sonora. Portions of the Colorado, Sonoyta, Concepción, Santa Cruz, San Pedro, and Yaqui rivers - containing many of these species - are also shared between these two states (Table 1).

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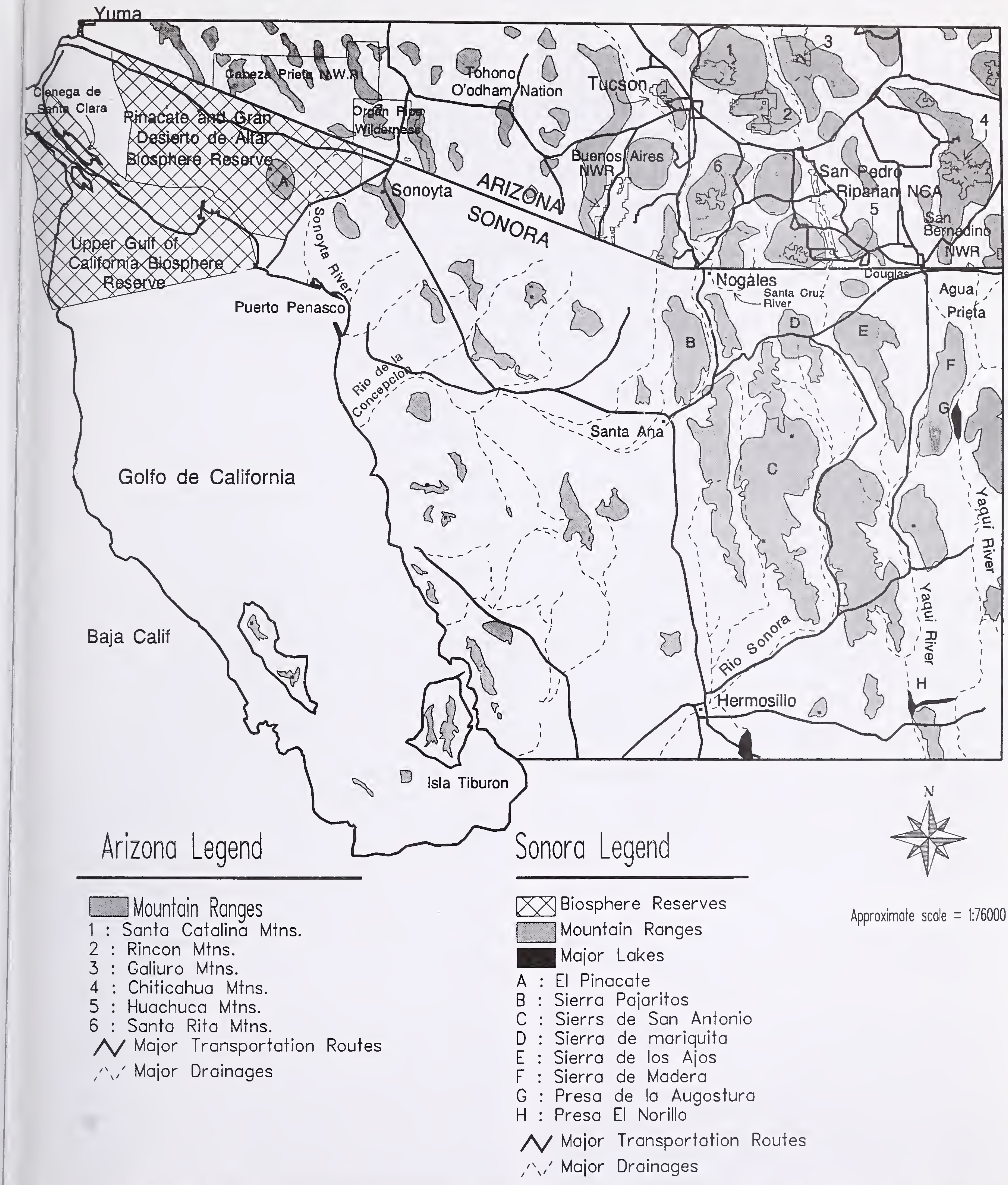

Figure 1.—Borderland region in 11 special management areas including the Cabeza Prieta, Buenos Aires, and San Bernardino national wildlife refuges; Organ Pipe Cactus National Monument; Coronado National Forest; San Pedro Riparian National Conservation Area, Arizona; Upper Gulf of California, and Pinacate and Gran Desierto de Altar Biosphere reserves; Sierra de los Ajos; Sierra Mariquita; and Sierra San Luis, Sonora.

Table 1.—Species common to Arizona and Sonora listed as threatened (T), endangered (E), rare (R), or of special concern (SP) under the Endangered Species Act (ESA) of 1973, as amended, and the Norma Oficial Mexicana (NOM) NOM-059-ECOL-1994. No listed amphibians, invertebrates, or plants are common to Arizona and Sonora.

Scientific name	Common name	ESA	NOM
	FISHES		
Cyprinella formosa	beautiful (Yaqui) shiner/carpa yaqui	T	T
Cyprinodon macularius	desert pupfish / cachorro del desierto	E	E
Gila ditaenia	Sonoran chub / carpita sonorense	T	T
Gila elegans	bonytail chub / carpita elegante	E	E
Gila purpurea	Yaqui chub / carpita Yaqui	E	E
Ictalurus pricei	Yaqui catfish / bagre del Yaqui	T	R
Poeciliopsis occidentalis	Sonoran topminnow / guatopote de Sonora	E	T
Ptychocheilus lucius	Colorado River squawfish / charalote	E	E
Tiaroga cobitis	loach minnow / carpita locha	T	E
Xyrauchen texanus	razorback sucker / matalote jorobado	E	E
	REPTILES		
Crotalus willardi	ridge-nosed rattlesnake / víbora de cascabel	T	SP
	BIRDS		
Colinus virginianus ridgwayi	masked bobwhite / codorniz mascarita	E	E
Falco femoralis septentrionalis	northern aplomado falcon / halcón fajado	E	E
Falco peregrinus	peregrine falcon / halcón peregrino	E	T
Grus americana	whooping crane / grulla blanca	E	E
Gymnogyps californianus	California condor / condor de California	E	E
Haliaetus leucocephalus	bald eagle / águila calva	E	E
Mycteria americana	wood stork / cigüeña americana	E	T
Rallus longirostris yumanensis	Yuma clapper rail / ralón barrado grisáceo	E	E
Strix occidentalis lucida	Mexican spotted owl / búho manchado	T	T
Vireo atricapillus	black-capped vireo / vireo gorrinegro	E	T
	MAMMALS		
Antilocapra americana sonoriensis	Sonoran pronghorn / berrendo sonorense	E	E
Canis lupus baileyi	Mexican grey wolf / lobo mexicano	E	E
Felis onca	jaguar / jaguar	E	E
Felis pardalis	ocelot / ocelote	E	E
Felis yagouaroundi	jaguarundi / jaguarundi	E	T
Leptonycteris curasoae yerbabuenae	lesser long-nose bat / murciélago lengüilarga	E	T

The Arizona-Sonora borderland has a long history of farming, ranching, and mining activities. As populations grow in the Southwest, the borderlands will continue to be the focus of development. Proposed economic developments resulting from passage of the North American Free Trade Agreement (NAFTA) will increase the challenge to protect and manage the flora and fauna found in this area.

A diversity of species from the Chihuahuan, Madrean, Sinaloan, and Sonoran biogeographic provinces are represented here (Lowe and Brown 1982). In much of the western portion of the borderlands the predominant physiographic characteristics are arid lands. On the eastern side, we find Great Basin and semidesert grasslands in lower elevations, and Rocky Mountain coniferous forests and pine-oak woodlands at higher elevations. Many of the sub-basins shared between Arizona and Sonora have permanent streams and important riparian habitats (Lowe and Brown 1982).

The Arizona Game and Fish Department (AGFD) has long maintained a working relationship with organizations and agencies on both sides of the border to ensure long-term existence of threatened and endangered species and their habitats. AGFD's relationship with Mexico was initiated nearly 15 years ago. To facilitate these management activities, AGFD drafted a cooperative agreement signed by the governors of Arizona and Sonora in 1989. Under this master agreement, AGFD formalized a strong partnership with the Centro Ecológico de Sonora (CES) with consummation of a Cooperative Agreement in 1993.

CES, a conservation group located in Hermosillo, Sonora, was created in 1984 under the authority of Dr. Samuel Ocaña as the Governor of Sonora (1979-1985). Now serving as the Director of CES, Dr. Ocaña has been the major force behind their unprecedented growth during the last few years. CES, although partially supported by the State of Sonora, is not considered a State agency. Its mission is to implement conservation, management, research, and environmental education programs of the flora and fauna of Sonora.

Collaborations with CES include joint field work, training, technical assistance, and financing for several projects. In Mexico, modern wildlife management and conservation practices have just started, and only in selected cases. It is crucial to the success of the projects to maintain training and continuous technical assistance. A measure of success will be realized when conservation programs are self-sufficient and have a long-term existence on both sides of the border.

In addition to biological training, AGFD has conducted several Hunter Education seminars in Mexico and is initiating Project WILD (an educational program to teach students about wildlife and habitat) into CES' educational program. We strongly believe wildlife conservation programs must include both the wise use of natural resources, and the environmental education and awareness of future generations.

Over the last few years, our partnership with CES has been recognized as the most successful one in obtaining financial aid from the U.S.-Mexico Joint Committee for the Conservation of Flora and Fauna. These resources represent a complement to CES' fundraising efforts for their various programs. Support has also been provided by local government authorities, as well as groups like The Nature Conservancy (TNC); U.S. Fish and Wildlife Service (USFWS); Packard, Ford, and Tinker foundations; Sonoran Institute; the Cabeza Prieta, Buenos Aires, and San Bernardino national wildlife refuges; Centro de Estudios del Desierto y Oceanos (CEDO); Arizona-Sonora Desert Museum; Arizona Desert Bighorn Sheep Society (ADBSS); Foundation for North American Wild Sheep (FNAWS); and National Fish and Wildlife Foundation (NFWF), for the CES's, and borderlands, conservation programs.

Joint field activities, from conducting fish surveys to Gould turkey trapping in the Sierra Madre Occidental, to aerial reconnaissances in the Ciénega de Santa Clara, and telemetry studies of Sonoran pronghorn and desert bighorn sheep in the Pinacate Biosphere Reserve, have been rewarding to all groups. More importantly, many of these efforts have resulted in management plans that enhance conservation of these shared resources.

JOINT WILDLIFE COLLABORATIONS

Native Fishes

In 1986, joint surveys and natural history studies of native fish communities found in shared watersheds were initiated, and continue as one of the strongest cooperative efforts between the AGFD and CES. This multi-species project continues to gather important information on the biology, status, and distribution of many sensitive species of fishes. Significantly, some of these surveys have generated published reports with Mexican and Arizona biologists as co-authors. In addition, biologists from AGFD and CES have contributed to the development of recovery plans for the Sonoran chub (*Gila ditaenia*), desert pupfish (*Cyprinidon macularius*), and Sonoran topminnow (*Poeciliopsis occidentalis*).

Natural distribution for the threatened Sonoran chub occurs within the Río de la Concepción Basin (Fig. 1). In the United States, the species is restricted to Sycamore Creek near Nogales. In 1986, biologists from the AGFD and CES sampled 25 localities in Sonora and found the species to be widely distributed, highly abundant, and relatively secure (Hendrickson and Juárez 1990). The Arizona population, however, seems to have been geographically isolated from the others in the basin for a long time (Carpenter and Maughan 1993) and there is the possibility that a single catastrophic event could eliminate the United States population. Therefore, it is important to study the results of this probable isolation and to continue with periodic monitorings on both sides of the border.

Over the past several years, fish biologists have periodically visited 20 localities in Arizona and sampled nearly 30 sites in Sonora, as part of the long-term monitoring for the Colorado River form of the desert pupfish (*C. m. macularius*). The Quitobaquito pupfish (*C. m. eremus*) remains relatively secure in Arizona thanks to the efforts of the Organ Pipe Cactus National Monument. In the 1950s, the desert pupfish was extirpated from Arizona and only seven reintroduced populations remain. Natural populations in Sonora are found in the delta of the Colorado River and the Sonoyta River. Hendrickson and Varela-Romero (1989) and Abarca et al. (1993) reported the species present only at 12 localities. The range of the desert pupfish has been drastically reduced over the last century by habitat destruction and/or modification and introductions of exotic fishes. Natural pupfish populations in the Ciénega de Santa Clara are clearly threatened by the presence of a dozen of different exotic competitive and predatory species (Abarca et al. 1993). Notoriously abundant in the Ciénega are sailfin mollies (*Poecilia latipinna*) and mosquitofish (*Gambusia affinis*). The former is widely distributed in Arizona's waters, thus precluding recovery of the pupfish and the Sonoran topminnow in many areas.

In the southeastern corner of Arizona, a portion of the headwaters of the Yaqui River is believed to have been the habitat for eight fishes: the Yaqui topminnow (*Poeciliopsis occidentalis sonoriensis*), Yaqui chub (*Gila purpurea*), Mexican stoneroller (*Campostoma ornatum*), beautiful or Yaqui shiner (*Cyprinella formosa*), Yaqui catfish (*Ictalurus pricei*), roundtail chub (*Gila robusta*), longfin dace (*Agosia chrysogaster*), and Yaqui sucker (*Catostomus bernardini*). Today, only the Yaqui topminnow, Yaqui chub, beautiful shiner, Mexican stoneroller, and longfin dace are present in the San Bernardino/Leslie Creek National Wildlife Refuge, an area being administrated by the USFWS. Thanks to binational cooperation, beautiful shiner and Yaqui catfish broodstocks were brought to the United States in 1989 and 1987/1990, respectively, from waters of the Yaqui River in Mexico. Yaqui catfish broodstocks are being held at Dexter National Fish Hatchery and Technology Center, Dexter, New Mexico, pending specific plans for their reintroduction into the refuge.

Plans for future watershed evaluations and management are being considered in a more integrated approach and will likely include water quality, aquatic invertebrates, and riparian vegetation and herpetofauna.

Considering the trends of Arizona's aquatic ecosystems, the probability exists that all Arizona's native fishes will soon be listed as either threatened or endangered. As a result of the potential economic development resulting from NAFTA, watersheds could become the most threatened ecosystems. This means that long-term monitoring and conservation practices of shared watersheds will become more important than ever.

Desert Bighorn Sheep

AGFD and CES have aggressively pursued a desert bighorn sheep (*Ovis canadensis mexicana*) cooperative project. Various attempts had been made to estimate the number of bighorn sheep in Sonora. Mendoza (1976) stated that "very little has been published with respect to this desert species in Mexico." In his report on the status of bighorn sheep in Sonora, Mendoza gave a "conservative" population estimate of 935 animals. Recent work concentrated on the mountain ranges in west central Sonora (Castillo-Sánchez 1992). Surveys done in 1989 and 1991 resulted in population estimates which appeared consistent with the work done by Mendoza. The consensus was that the population in Sonora probably did not exceed 1,000 animals, but the actual status was unknown.

In 1992 and 1993, 37 hours of helicopter surveys were flown in Sonora to determine the present distribution of bighorn sheep, as well as a population estimate. In addition, the classification of the animals would allow for an analysis of population status as well as to provide information needed for the proper management of this species. Observers were from the Dirección General de Ecología, Subdelegación Forestal y Fauna, CES, and AGFD.

A total of 42 separate mountain areas were flown. Most of these areas were flown concentrating on the more rugged inaccessible portions. While this allowed for observation of the majority of the sheep, observations during ferry flights between ranges showed numerous sheep also occurred in areas not surveyed. A total of 287 groups were seen, resulting in 970 individual classifications. Of the 17 areas flown in 1993, 14 were different from those flown in 1992. A total of 365 of the 1993 observations were from areas not covered during 1992. This results in a 2 year total of 893 discrete observations; with desert bighorn sheep seen in 32 of the 42 ranges surveyed. The ram:ewe:lamb:yearling ratio was 46:100:25:22. Observation rates were 11.3 sheep per hour in the northern ranges and this rate increased to 39.9 sheep per hour in the ranges west and south of Caborca. By comparison, the average rate of observation in 1992 in Arizona, was 11.5 sheep per hour.

Recent survey work done in Arizona indicates that a relatively small portion of the population is seen during a helicopter bighorn sheep survey (Miller et al. 1989). Using a conservative observation rate of 40 per cent, the estimated population in the surveyed area would be 2,233 bighorn sheep. Since only portions of each mountain range were flown and, additionally, some sheep areas in Sonora were not flown, therefore, the total population of bighorn sheep in Sonora undoubtedly exceeds 2,000 animals (Lee and López-Saavedra 1993).

The results of this work produced the following observations. While the United States has been involved in a massive water development program for the last 30 years, Mexico's sheep population seems to be doing exceedingly well without such a program. The ranges in Sonora would be an excellent place to determine whether additional water sources serve to help increase and distribute sheep through a mountain mass.

Several areas in Sonora have very dense sheep populations which could serve as source stock for transplants into previously occupied habitat. Habitat analyses and studies of historical accounts would help ensure the success of these sheep transplant efforts on all the historic ranges in the state. Proper management of this unique resource can only be achieved through development and implementation of a technically sound management plan.

Sonoran Pronghorn

The Sonoran pronghorn (*Antilocapra americana sonoriensis*) is a subspecies of concern in Mexico and the United States. In Mexico, Villa-Ramírez (1978) reported that Sonoran pronghorn were in critical danger of extinction. The Arizona population was listed as endangered in 1967.

The causes for population declines are speculative for several reasons. The primary reason for this is that Sonoran pronghorn were first afforded separate taxonomic status in 1947 (Goldman 1945); after widespread population declines had occurred. Possible causes for decline include: competition with domestic livestock, illegal harvest, drying of rivers, and others (AGFD 1981).

Recovery of Sonoran pronghorn populations requires knowledge of population status and trends throughout its range. As a result, AGFD developed a cooperative research program with CES. The first step in this program was an aerial population survey in December 1989. The survey focused on the area of the Pinacate region; an area thought to harbor the last individuals of this subspecies in Mexico (Castillo-Sánchez, pers. comm.). During this effort, 18 Sonoran pronghorn were classified. This approximated what was thought to be the total population in Mexico (Castillo-Sánchez, pers. comm.).

Collaborative research continued in 1990 when a second aerial survey was conducted. During these surveys, 33 Sonoran pronghorn were classified. Importantly, several pronghorn groups were observed in stable sand dunes east of Puerto Peñasco; an area where recent documented observations were large absent.

One of the goals of the work in Mexico was to develop sufficient information to develop a management plan outlining needed actions to maintain or enhance Sonoran pronghorn. To obtain these data, a radio telemetry study was initiated in 1991. A subsequent capture expanded the number and distribution of collared Sonoran pronghorn.

There have been several important benefits from this research program. Most important is the development of a management plan that outlines actions needed to recover Sonoran pronghorn in Mexico (Castillo-Sánchez 1992). Another important contribution of this project has been technology transfer. This was one of the first research efforts where radio telemetry studies were led by a biologist from Mexico. Other data accomplishments included improved information on disease status, movement and habitat use patterns, distribution, and population status.

Although much has been accomplished, additional information is needed to optimize recovery efforts. Areas occupied by Sonoran pronghorn are roadless, harsh environments where access is very difficult. Future plans include use of satellite telemetry units that will allow collection of additional information to base management actions. Other remote sensing tools will be used to collect information on Sonoran pronghorn habitat. Management of animals that share binational distributions require shared research and management programs. Understanding population and habitat characteristics is important to range-wide recovery.

Other Important Areas of Collaboration

There are a variety of research and management cooperative projects on which AGFD has worked with CES, both in the past, and those currently being implemented. Description of each project is beyond the scope of this paper, however, we would like to outline some of the important aspects of these projects.

The **Gould turkey** (*Meleagris gallopavo mexicana*) a species of great interest in Arizona. This is the wild turkey that occupied most mountain ranges in southeastern Arizona prior to settlement. Subsequently, populations have been eliminated from Arizona, but appear to be thriving in parts of northern Mexico. Working closely with governmental and academic organizations in the states of Sonora and Chihuahua, AGFD has conducted training seminars in both states in the past few years. Additionally, AGFD has supported, both monetarily and with personnel, field surveys for this subspecies in these two states. As a result of these efforts AGFD was able to capture and translocate Gould turkeys into Arizona early in 1994. It is likely that an additional capture can be conducted in 1995.

A species of particular concern throughout its range is the **desert tortoise** (*Gopherus agassizii*). The species is listed as threatened in Mexico. Both the USFWS and AGFD have provided funding and training for this project in Sonora. In the United States, population declines, increased incidence of diseases, and loss of habitat are all threats to the desert tortoise. Although we are just beginning to understand some biological aspects of this species in Sonora, preliminary results indicate both a low incidence of disease and different habitat preferences than those of the Mohave and Sonoran desert populations. In Sonora, the desert tortoise is exploited for its commercial value and for human consumption. An intensive educational program to protect this desert dweller is underway and a management plan is being developed by Mexican biologists.

The **masked bobwhite** (*Colinus virginianus ridgwayi*) was extirpated from Arizona by 1900 because of livestock overgrazing. However, small populations remained in north-central Sonora where a broodstock was taken and shipped to a USFWS laboratory which initiated captive rearing activities. Years later, it was thought the species had disappeared from Sonora, but recent surveys discovered additional populations in the wild. Thanks to this international cooperation, bobwhite populations were established on the Buenos Aires National Wildlife Refuge. Today, an intensive monitoring program of the masked bobwhite and habitat restoration of grasslands in Sonora are being implemented for the conservation and recovery of this species.

The **Mexican spotted owl** (*Strix occidentalis lucida*) is another species of special interest for Mexico and the United States. Various cooperators in the United States and CES are conducting field surveys to determine seasonal abundance, distribution, potential threats, and management needs of this owl in northern and eastern Sonora.

The **Mexican wolf** (*Canis lupus baileyi*) was eradicated from the wild in the United States through persistent control efforts to eliminate depredation of livestock by wolves with the last known wolf taken in 1970. Occasional sightings of "wolves" in Arizona are reported but to date, none have been confirmed. It is believed that a few wolves may remain in the wild in Mexico, however, their presence has not been confirmed recently. An intensive captive breeding program was initiated in 1977 in the United States and Mexico with six wolves taken from the wild in Mexico. This program has already produced offspring that increased the captive population to 89 as of August 1994. Despite this success, it is imperative to determine the status of Mexican wolves in the wild. Thanks to a strong collaborative effort among agencies and several groups in both countries, financial and technical assistance is being provided for field surveys in Mexico.

Once widely distributed in the forested mountains of northern Mexico and southeastern Arizona, the **thick-billed parrot** (*Rhynchopsitta pachyrhyncha*) had disappeared from most of its northerly range by the 1930s. The species now probably only occupies the rugged Sierra Madre Occidental of Chihuahua and eastern Sonora, Mexico. Deforestation, subsistence hunting, and poachers capturing parrots for sale in the black-market pet trade are serious threats for this species. Beginning in 1986, a multi-agency effort to return thick-bills previously confiscated from illegal pet traders and owners was launched. Thick-bills were able to establish a consistent pattern of movements and activities and even wintered along the Chiricahua's 8000 ft conifer-clad crest. During the summer, parrots inhabited pine forests in the Mogollon Rim. However, it is believed that predation, drought, and fire caused the demise of the reintroduced population. The last reintroduction in 1992 was unsuccessful. AGFD is now supporting thick-billed parrot surveys in the Sierra Madre Occidental and **maroon-fronted parrot** (*Rhynchopsitta terrisi*) surveys in the Sierra Madre Oriental. If thick-billed parrot populations are stable in Mexico, AGFD may begin to explore the possibility of translocating a population to the Chiricahua Mountains.

The Yaqui, Bavispe, and Aros basins contain five breeding areas for the endangered **bald eagle** (*Haliaetus leucocephalus*). Discovered in 1986, this population is one of the two bald eagle populations that breeds in a desert environment and nests in the relative abundance of cliffs. Since 1988, the USFWS has been the lead for a monitoring program for the nesting sites located in the area. Biologists from TNC, CES, and AGFD have participated in field work to gather important information about the biology of the species. Future investigations will determine if the Bavispe River bald eagle population is linked to the Arizona population.

There are more than 3000 **Breeding Bird Survey** (BBS) routes across the United States and Canada. In an effort to establish monitoring on a truly continental basis, the BBS is looking into the feasibility of establishing routes in Mexico. In 1993, AGFD joined forces with CES and the International Association of Fish and Wildlife Agencies (IAFWA) to initiate a pilot project on BBS with 17 proposed routes to be surveyed throughout Sonora. The routes will be established to develop a long-term database on the status and trends of Mexico's breeding birds that is comparable to the existing BBS database.

Another important component of today's management and conservation programs is the electronic storage of information, or databases. These modern tools allow us to share data of wildlife distribution, abundance, and other important biological aspects. This cooperation will enhance the exchange of data and directly result in better management of shared natural resources.

Wetlands are an important habitat for many species that breed north of Mexico. This is a habitat that is under increased pressure due to resort development in coastal wetlands and conversion for agricultural purposes in the interior. AGFD is providing funding and technical expertise to scientific and management groups in Mexico to develop a GIS database of the major wetlands in northwestern Mexico.

CONCLUSIONS AND RECOMMENDATIONS

The preservation of biodiversity seems to be an overwhelming challenge, and success will only be possible through the concerted efforts of numerous individuals and organizations (Prescott and Hutchins 1991). This partnering process is particularly true for sensitive species and habitats and to successfully protect and manage natural areas and watersheds needed to sustain key species as well as the integrity of entire ecological systems. Additionally, the multiple partnership concept is a necessity in today's national and international conservation programs, due to the complexity of natural resource issues being resolved, and the increasing cost and logistic obstacles to implement those programs. In particular, binational wildlife collaborations should consider three key elements for their success: a) identify common goals on research and management actions; b) overcome language barriers; and c) recognize and understand the cultural/political realities and environmental regulations within each country, state or agency/group.

Once largely ignored by the United States and Mexico, the borderland is now the focus of attention by both countries. With the implementation of NAFTA, opportunities for trade and economic cooperation between the two countries are better than ever. Traditionally, the economies of border cities in Mexico are largely based in the "maquiladora" industry. Likely, NAFTA will result in the growth of these cities, an increase in the movement of goods through the region, and the expansion of industrial and commercial areas away from the border. If unplanned, this economic growth could threaten important areas of biodiversity. An effective and cooperative network of public officials, academics, and industry must be established to meet the challenges of environmental protection and recovery of endangered species.

Other recommendations include:

- Increase the network of special management and protected areas.
- Protect habitats from detrimental land use practices.
- Protect aquatic communities and riparian areas along shared rivers and evaluate potential impacts by the proposed industrial developments.
- Conduct periodic population and genetic monitoring.
- Promote scientific investigations on natural resources in the borderland.
- Conduct general biological surveys in those areas where little is known about natural resources.
- Re-establish populations within their historic range of distribution, regardless of the political boundary.
- Avoid the introduction of and encourage the elimination of nonnative species.
- Encourage participation of the local communities in biological studies, as well as in conservation and management programs.

- Determine the rate of human exploitation of economically important species. For those overexploited species, implement viable alternatives that are socially, economically and ecologically acceptable.
- Establish mechanisms to exchange information from various database systems containing information of the natural resources of the area.
- Identify Arizona and Sonora institutions to be depositories of data and museum collections.
- Develop a binational directory of researchers and managers working in the Arizona-Sonora borderland.
- Implement environmental education programs.
- Set up climatic and gauging stations along the border to document information on various environmental parameters.

Finally, wildlife conservation and management programs have received significant attention in Sonora. A regional system of natural protected areas has been established and other areas have already been identified for protection. Hunting opportunities are being actively pursued by selected groups and local authorities. The possibility of utilizing trophy species, such as bighorn sheep, in addition to mule and white-tailed deer, means that important revenues for Sonora could be generated over the next decades. Similarly, sport fisheries opportunities, both marine and freshwater, have a tremendous potential to provide significant income. To prevent unplanned utilization of wildlife resources, a comprehensive and strategic wildlife management program must be developed in this border state in order to meet the challenges of the 21st century.

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Wolves and Grass: A Watershed Perspective On the Mexican Wolf Recovery Plan

Jim Tolisano[1]

INTRODUCTION

In 1976 the U.S. Fish and Wildlife Service (USFWS) listed the Mexican wolf (*Canis lupus baileyi*) as a federally protected endangered species under the U.S. Endangered Species Act and began a process that could lead to the howl of wild wolves in the American southwest once again. As part of its listing of the wolf, the USFWS accepted the responsibility to identify opportunities to restore viable wolf populations to their former range. Round River Conservation Studies has joined in the efforts to bring back the wolf by carrying out field research programs designed to provide the quantitative and qualitative measurements needed to identify feasible recovery sites for existing captive or remnant wild wolves.

Since the fall of 1993 Round River field research crews have been assembling a variety of data within the preferred recovery site for the Mexican wolf in southeastern Arizona designed to assist the planning and implementation of the proposed recovery effort. The majority of Round River's research has emphasized an assessment of trends in watershed conditions within the Blue Range study area of the USFWS's Mexican Wolf Recovery Plan. Studies have measured plant composition and cover, erosion patterns, changes in water quality, and riparian community recovery within this proposed recovery site.

The assumption is that there will be a direct correlation between the health of these watersheds and the recovery of the wolf. With healthy watersheds will come the food base to support the deer, elk, rabbit and other prey on which the wolf depends. Healthy watersheds, particularly those which include intact, diverse riparian communities, will include the movement and disperal corridors which this prey base and the wolves require to sustain genetically viable populations. In this way, there is a life thread connecting wolves and grass. Round River field researchers are following that thread in the hopes that it can lead back to the wolf as the representative of the wildness and diversity that once characterized the rich biotic communities of the American southwest.

Following the Round River

Round River Conservation Studies is a nonprofit research and education organization operating in conjunction with the College of Santa Fe's Center for Environmental Studies. Round River's purpose is two-fold: to extend field-based technical support services for proposed or ongoing conservation projects; and to provide practical research and educational opportunities for undergraduate and graduate students enrolled in environmental conservation degree programs. All Round River projects include a Project Coordinator, a Research Director, and at least one Research Associate. These professionals provide training and guidance to field research assistants in carrying out data collection and compilation tasks.

Research is carried out during 12-week intensive field sessions, with staff and assistants working in the field for virtually this entire period. Results from each 12-week field season are compiled and subjected to extensive peer review. Following peer review, results are published and made available to interested government agencies, non-governmental organizations, and individuals.

The Mexican Wolf Recovery Plan

Very little scientific data exist to describe the life histories of the Mexican wolf, and in fact there was extensive dispute among scientists as to the number of subspecies which occurred. Most proponents suggest that three subspecies of *Canis lupus* were known to exist in ranges extending from portions of eastern and central Arizona, the Mogollon plateau, southern New Mexico, western and central Texas, and the Sierra Madre Occidental area of western Mexico (Bednarz, 1988, 1989;).

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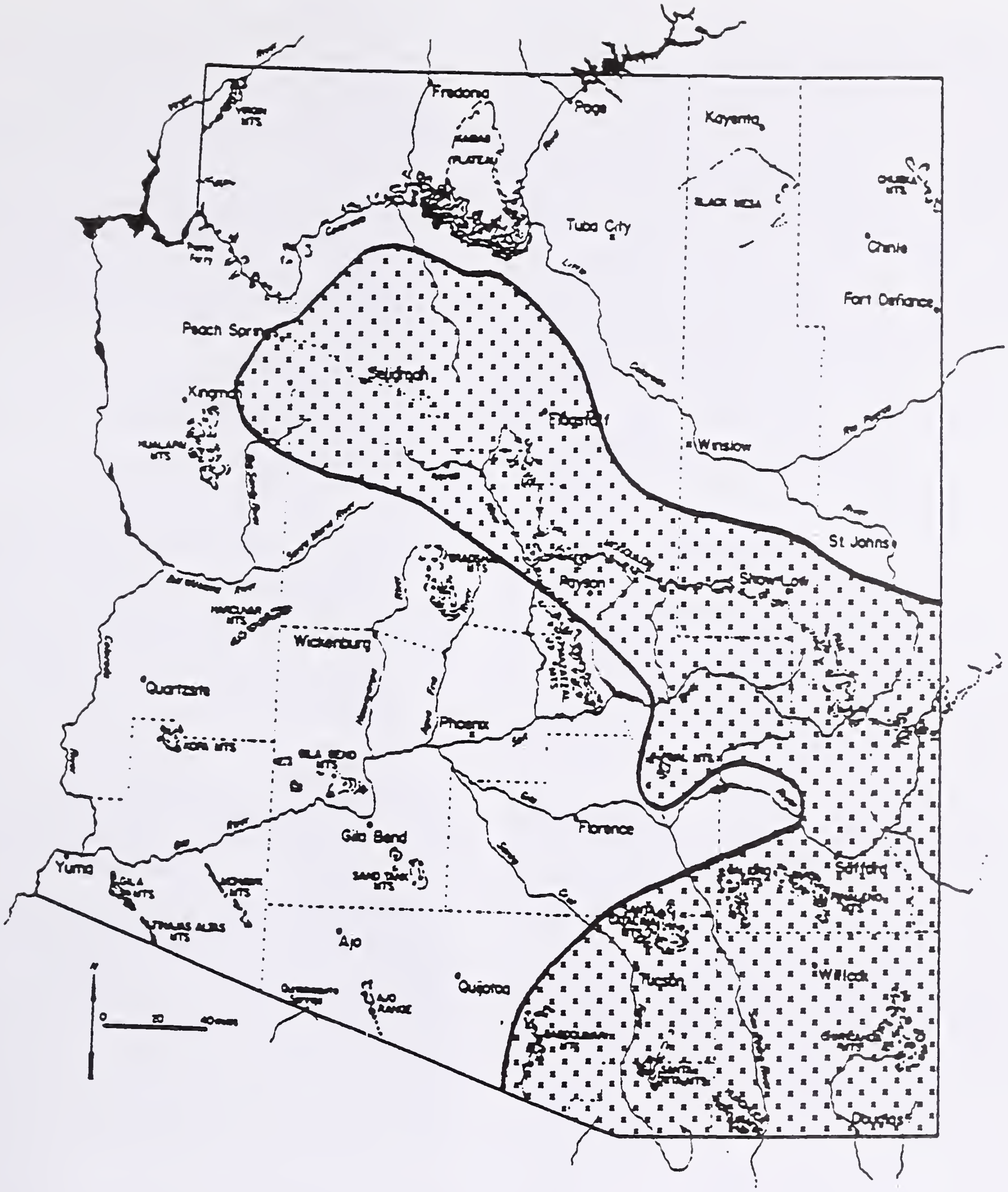

Figure 1.—Historical distribution of *Canis lupus baileyi*, *C.l. mogollonensis* and *C.l. monstrabilis* in Arizona (after Brown 1983).

Brown (1983) reports historic locations of *C. l. baileyi, C. l. mogollonensis* and *C. l. monstrabilis* in Arizona from the stateline southeast of St. Johns south the border with Mexico, west to the Baboquivari Mountains, north to the south rim of the Grand Canyon (fig. 1). The Mexican wolf was found in a variety of habitats throughout this range. In Arizona the wolves appear to have been most commonly associated with Madrean evergreen forests and woodlands (Brown, 1983). This vegetation type is indicative of a predominance of pine *(Pinus ponderosa, p. edulis, p. cembroides*), juniper (*Juniperus osteosperma, J. deppeana, J. monosperma*), and a wide variety of oak species (*Quercus spp.*). Grassland vegetation typically dominates the understory. Within this vegetation type riparian corridors appear to have served as important travel corridors for wolves within and between preferred habitat (Brown, 1983).

In 1976 the Mexican Wolf (*Canis lupus baileyi*) was listed by the USFWS as an endangered species, thus providing the wolf full protection under the Endangered Species Act of 1973 (ESA). At this time there were unconfirmed reports of remnant wolf populations inhabiting remote areas of northern Mexico, with occasional individuals pre-

No resident populations of wolves were believed to remain in the wild in the U.S. The last confirmed wolf recorded in the U.S. was struck by an automobile in southwestern New Mexico in 1970 (Brown, 1983).

The listing of the wolf under the ESA also mandated USFWS to assess the feasibility of re-establishing a viable population of Mexican wolves in the wild within their historic range in the southwestern U.S. As a result, the Mexican Wolf Recovery Team was established by USFWS in 1979, and a **Mexican Wolf Recovery Plan** was drafted in 1982. With slight modifications, this document has served as the principal guide for all subsequent wolf recovery efforts. The prime objective of the Recovery Plan as stated in the document is as follows:

> *"To conserve and ensure the survival of Canis lupus baileyi by maintaining a captive breeding program and re-establishing a viable, self-sustaining population of at least 100 Mexican wolves in the middle to high elevations of a 5,000 square mile area within the Mexican wolf's historic range."*

After extensive review and public input a total of six potential release sites were selected for more detailed analysis. These sites included the following:

a) Big Bend National Park, Texas
b) White Sands Missile Range, New Mexico
c) Atascosa/Patagonia Mountains, Arizona
d) Blue Range Primitive Area, Arizona
e) Chiricahua Mountains, Arizona
f) Galiuro/Pinaleno Mountains, Arizona

Subsequent analysis has concentrated on determining the degree of desirable habitat components in each of these sites, as well as the social and economic feasibility of reintroduction in these areas. The Mexican Wolf Recovery Plan (1982) and the Recommendations Pertinent to Releases of Mexican Wolves (1984) identified a range of desirable habitat requirements (Table 1).

In addition, the following factors are also suggested as desirable:

1. Significant portion of the area in oak woodland or pine-oak forests with adjacent grasslands.
2. Human population density of less than six per square mile, with no permanent residences.
3. Little or no livestock use.
4. Habitat capable of sustaining populations of ungulates adequate to support wolves in addition to a moderate hunter harvest in areas where hunting seasons are currently open on the wild ungulates on which wolves would prey.
5. Deer population density of twelve or more per square mile.
6. Currently managed by a public agency or by an organization strongly committed to wildlife management and willing to emphasize wolf management in the area.

Table 1.—Desired Habitat Requirements for Recoveryof the Mexican Wolf.

1.Within the historic range of *Canis lupus baileyi, C. l. mogollonensis* or *C. l. monstrabilis*.
2.Elevation of at least 4,000 feet above sea level.
3.Human population density of less than twelve per square mile.
4.Habitat capable of sustaining populations of wild ungulates adequate in numbers to support the number of wolves to be released and the anticipated first generation progeny.
5.No proposals or anticipated proposals for intensive development or other habitat alteration that could significantly affect the area's capacity to support wolves and their prey.
6.No endangered or threatened prey species populations present that would be detrimentally affected as a species by the presence of wolves.
7.Free water available in secluded areas of habitat.
8.Mostly broken, mountainous terrain.

Data to support estimated prey requirements to maintain a Mexican wolf population is unfortunately nonexistent (AZFS, 1992). The **Recommendations Pertinent to Releases of Mexican Wolves** (1984) is thus understandably vague in its minimum prey requirements. Current conjectures suggest that the desired level of 12 or more deer per square mile of area does not appear to be associated with any confirmed data about wolves in general, or the Mexican wolf specifically (AZFS, 1992; Bednarz, 1989). A review of several researchers work assessing the biomass needs of the northern timber wolf suggests that suggests that somewhere between 1.9-16.3 mule deer and 2.6-22.8 white-tailed deer may be required to sustain a population of wolves (AZFS, 1992). Clearly, additional research will be required to refine these estimates to a more meaningful management goal.

Several of the potential release sites have subsequently been eliminated from consideration or demoted in priority due to political, legal or other social constraints. At present, the four potential sites in Arizona are receiving the greatest deal of attention, with the Blue Range Primitive Area representing perhaps one of the more promising areas. Within the Blue Range Primitive Area much attention has been given to the Sandrock Range Allotment as a possible initial release site. As a result, the Round River Conservation Studies Habitat Suitability Study to Support the Mexican Wolf Recovery Plan has chosen to devote its initial work to assessing habitat suitability within the Blue Range Primitive Area, and to particularly concentrate on habitat assessments within the Sandrock Allotment and immediately adjacent potential release areas.

Geographic Study Area

The RRCS Habitat Suitability Study to Support the Mexican Wolf Recovery Plan will primarily emphasize field investigations within the Blue Range Study Area. Within this study area field research assistants led by professional staff will work principally within the Sandrock Allotment and adjacent lands within the Blue Range Primitive Area.

The Blue Range Study Area

The Blue Range Study Area is 1575.8 square miles of land bordered by the Fort Apache and San Carlos Apache Indian Reservation on the west, and the Arizona/New Mexico state line on the east. It extends north to the Apache National Forest boundary and south to within twelve miles of the Apache National Forest southern border.(AZGF, 1992) The Blue Range Study Area is fully contained within the Apache National Forest, and in close proximity to the Gila National Forest. Contained within the study area are both the Blue Range Primitive Area and the Sandrock grazing allotment.

Approximately 95 percent of the study area is public land comprised of U.S. Forest Service (USFS) and state land. State land represents only 1.5 percent of this total. In 1992 the population within the study area consisted of 8,874 people with an average of 2.8 persons per square mile. (AZGF, 1992).

The average temperature over the area is 47.3 F with an extreme high of 100 F and an extreme low of -32 F in Springerville and Alpine respectively. (AZGF, 1992). Precipitation varies over the study area with an average of 20.78 inches occurring annually. Extremes of 36.9 inches and 6.63 inches have been recorded. Over the course of an average year most precipitation is recorded during summer monsoons occurring from July to mid-October. A winter precipitation period can also occur between January and March, with rain more common than snow in lower elevations.

Twenty perennial watercourses occur in the study area, along with two reservoirs. Approximately 730 developed water sources exist, with an annual capacity of 543.12 acre-feet, and an annual livestock and wildlife use of 321.07 acre-feet (AZGF, 1992).

Vegetation types range from Semidesert Grassland to Petran Subalpine Conifer, and include seven vegetation types based on Brown and Lowe's classification regime. (Brown and Lowe, 1982). Approximately 7.2 percent, or 72,547 acres of the total study area is classified as Madrean Evergreen Woodland (Table 2).

The main land use in the area is livestock grazing, with 9,054 head of cattle grazed in 1992 (ADGF, 1992). This represents an approximate stocking density of 5.7 cattle per square mile. Livestock are prevalent on the higher plateaus during summer and fall months, with ranchers moving cattle to the lower canyons and riparian bottoms during winter months. Logging and mining are also prevalent in the area, although both are declining in economic importance. Recreational use, including hunting and horseback riding, is increasing (ADGF, 1992) The area as a whole is fairly inaccessible, with a road density of only 0.8 miles of road per square mile of land, including residential and city streets. (ADGF, 1992).

No known threatened or endangered species (TES) which could be adversely affected by the presence of Mexican wolves are known to occur in the Blue Range Study Area. However, a number of competitor and other predator species do occur in the area. Wolves have been known to be killed by black bears, and will occasionally return the favor

Table 2.—Vegetation of the Blue Range Study Area (from ADGF, 1992).

Vegetation Type	Acreage	Square Miles	Percent of Total Vegetation
Petran Subalpine Conifer	26,204	40.9	2.6
Petran Montane Conifer	577,001	901.2	57.2
Great Basin Conifer	250,601	391.4	24.8
Madrean Evergreen	72,547	113.3	7.2
Interior Chaparral	638	1.0	0.1
Subalpine Grassland	27,356	42.7	2.7
Plains & Great Basin Grassland	52,693	82.3	5.2
Semidesert Grassland	1,446	2.3	0.1
Total Vegetation	1,008,486	1,575.1	100

(Brown, 1983). Conversely, wolves are known to represent a threat or nuisance to several other predators, including coyote, gray and kit fox, mountain lion, bobcat, and long-tailed weasels, all of which are known to occur in the study area. Unfortunately, the full impact of wolf presence on most of these species is poorly understood. More detailed understanding of these inter-species dynamics will be warranted if wolves reinhabit these areas.

Preliminary estimates based on extrapolations from district Wildlife Managers' annual reports suggest that approximately 5.4 deer, and 6.9 ungulates occur per square mile in the Blue Range study area. The elk population represents 17 percent of the ungulates found on this site, with deer representing another 79 percent (AZFS, 1992).

The Blue Range Primitive Area is contained within the Blue Range Study Area. It consists of 281.2 square miles of protected land (Foreman and Wolkes, 1992). A primitive area is an area managed to preserve wilderness values, yet including fewer restrictions than Congressionally designated wilderness areas.

The Sandrock Allotment

The Blue Range Area includes the Sand Rock livestock allotment, which is currently without an active grazing program. Through an agreement with the adjacent land owner, control of the allotment was returned to the USFS when the private land was sold. The USFS deferred the allotment from grazing and removed the livestock in 1983. The intent of the deferment was to improve the condition of the watershed, especially the riparian areas, and to emphasize the management of the loach minnow (*Tiaroga cobitus*) and black hawk (*Buteogallus anthracinus*), two T&E species occurring in the allotment. The results of the deferment is presently being reevaluated by analyzing the condition of the range, riparian areas, the watershed in general and future uses (Frank Hayes pers. com. 1992; USDA Forest Service 1987).

The SandRock allotment consists of 95.9 square miles of land, of which 55.2 square miles are within the boundaries of the Blue Range Primitive Area. The vegetation consists of Madrean Evergreen Woodland and Great Basin Conifer Woodland in the south, transitioning to Petran Montane Conifer Forest in the north. The allotment is very secluded, with road access only available to the border of the allotment from the north or south, requiring non-motorized travel to the interior portions (Frank Hayes pers. com. 1992; USDA Forest Service 1987).

The Message from the Land: Research Results 1993-1994

Round River's initial research on range conditions, habitat suitability and riparian system characteristics was designed to assess trends in ecosystem dynamics in the Blue Range study area. Essentially, Round River's approach uses measurements of watershed values that can enable us to determine if the existing habitat will support the diverse prey base on which the Mexican wolf depends. If the grass, forbs, shrubs and trees are present which can sustain elk, deer, rabbit and other species enticing to the wolf, then the study area can truly become home to the lobo once again.

The field work completed by Round River in 1993-94 largely replicates earlier research studies carried out during periods of intensive cattle grazing. Between 1962 and 1968 the U.S. Forest Service had field crews measure range and riparian conditions within the Sandrock allotment. Using a variety of traditional techniques, these measurements indicated that both the range and riparian areas within the allotment were in a state of declining ecological health. Results from range studies conducted by the Forest Service showed vastly reduced plant litter and a decline in plant species diversity and cover, particularly among the native grasses. This reduced ground cover was resulting in more rapid runoff, accelerating erosion, and degradation of aquatic communities. The rich plant and animal diversity in the riparian areas was disappearing due to the combination of damaging floods from the degraded watersheds, and overgrazing by cattle.

In 1983 the Forest Service decided to close the allotment to grazing and provide a period of rest for the watershed. Round River's field measurements of current range and riparian conditions represents the first attempt to quantify and qualify the impacts from this rest period. During a 12-week period in the fall of 1993, and subsequent 12-week field seasons in the spring and fall of 1994, Round River research assistants replicated 17 pace transects, 13 permanent cluster transects, and 14 range condition photo points in an effort to assess trends in range conditions in the Sandrock allotment. These transects involved measurements of overstory and understory plant cover, frequency of species occurrence, dominant grass and forb species, and soil erosion conditions.

Research assistants also replicated 14 riparian condition transects along the mainstem Blue River and several tributary drainages, and carried out new baseline riparian surveys every 0.5 mile within a 30 mile reach of the Blue River. Riparian surveys provide measurements and qualitative information on overstory and understory plant species diversity and development, streamflow characteristics, and total area in the riparian community. Overall watershed conditions were qualified using a survey procedure to measure soil, hydrologic, and biological parameters on 0.25 acre plots replicated in more than 30 sites within the Sandrock allotment. Additional field work used tracking surveys and randomized walking cruises to document the presence and habits of federally and state-listed threatened, endangered, and sensitive (TES) species, and develop annotated species lists for mammals, birds, reptiles and amphibians, and native plants.

Range Condition Analyses

The results from these field studies indicate that the biological communities within the Blue Range study area are experiencing a mix of ecological impacts. Data collected on range conditions within the Sandrock allotment indicate a trend towards recovery of some grass species, increased ground cover from grass and forb litter, and increased grass and forb species diversity. The *Aristida* and some other cool season grasses show signs of being on the increase, after virtually disappearing during the earlier Forest Service studies. Similar to other reseach recently conducted in semidesert grassland and woodland communities in southeastern Arizona, the tallest bunchgrasses appear to have responded most positively to release from grazing (Bock and Bock, 1992). Approximately 33 percent of all study plots showed an increase in plant cover, and the vigor of plant growth observed was also showing an increase from the earlier data. Plant litter formed from dead or decaying plants was up in all study plots, and represents an important form of ground cover to promote watershed conservation. This increased plant litter also provides important habitat for many small mammals, birds, and invertebrate species.

Not all study sites showed such improving trends, however. Approximately 33 percent of the study plots showed the same plant cover and frequency as the original data from the 1960's, and 33 percent showed some declines in cover and frequency. This may be due to the fact that soil and microclimatic conditions in parts of the Sandrock allotment are still not conducive to seed germination and seedling survival. Surprisingly, many of the opportunistic species which are typically considered undesirable on these rangelands (catclaw acacia, snakeweed, etc.) are also on the increase.

There is also an obvious expansion of pinyon pine and juniper woodlands occurring within the study area. The original Forest Service surveys done in the 1960's suggest that less than 20 percent of the allotment was then in pinyon-juniper woodland, while the recent survey work indicates that these woodlands may now cover more than 40 percent of the area. This trend may be the result of fire suppression, degraded soil conditions more conducive to woodland cover, or a decline in the seed dispersal and germination rates for the semidesert grassland and Madrean Evergreen woodland communities which were formerly more evident. What is important is that this change is influencing the matrix of birds and mammals inhabiting the study area. There has been an apparent conversion from white-tailed deer to mule deer dominant herds in the study area, and this may be the result of a more homogenous woodland replacing a formerly more diverse woodland/grassland mixture.

Some of the conflicting messages from Round River's recent data collection can be traced to a variety of factors. The original data assembled by the Forest Service was collected more than 15 years before cattle were removed from the allotment. Thus, conditions could have deteriorated significantly before the rest period was begun, and the current measurements merely reflect some of that unaccounted deterioration. Also, there is some uncertainty about procedures followed by the original data collection teams, and a possibility exists that the interpretations of plant cover and frequency applied by Round River researchers in the field vary from those of the former Forest Service teams.

However, it does appear that the damage that has occurred to these rangelands from a century of intensive grazing, the elimination of fire, and natural variations in weather is deep and recovery will be slow. The signs from a decade of rest may represent merely the beginning of a patient recovery this watershed requires. In fact, it may take centuries before the thin soil layers, soil microorganisms, seed plants, and small wildlife return to reclaim their former home.

Trends in Riparian Community Recovery

A more promising story is found in the riparian areas within the Blue Range study area. Surveys of riparian communities within the Sandrock allotment indicate a significant increase in the tree, shrub, and forb diversity within these communities, as well as the areal coverage of riparian vegetation. Greater than four species of tree and shrub were found in each replicated 0.25 acre field plot measured within the allotment. This represents an increase in overstory diversity on more than 50 percent of the plot sites from original 1982 data. The dominant woody plants continue to be alder (*Alnus oblongifolia*) and various species of *Baccharis*. Cottonwoods (*Populus fremontii*) and sycamores (*Platanus wrightii*) are now becoming a more representative portion of the overstory in these communities, occupying as much as 10 percent or more of several plot sites. This does represent a change from the 1982 data, and a trend towards maturity in the successional development of the riparian communities. Recruitment of woody plants is abundant within all plot sites, and species diversity again exceeds four species per plot. All size classes were represented in the plots measured, using a methodology which separates overstory vegetation into four diameter and three height classes.

These trends suggest that riparian habitat conditions are improving for the small mammals and ungulate populations on which the Mexican wolf would be expected to prey. In fact, surveys of small mammals, birds, and reptiles and amphibians within the riparian communities show a high level of diversity. Equally important is the fact that the vast majority of the bird, mammal, and reptile and amphibian species documented by Round River field assistants have occurred within 0.25 miles of a riparian area. Included in these data are four endangered reptile and amphibian species recorded to date.[1] More than 70 species of birds were identified in the riparian area during a two week census period in April of 1994, including four endangered species.[2]

Round River field researchers are presently mapping the approximate boundaries of the riparian communities along the Blue River and several principal tributaries. Mapped delineations will include estimates of the area of riparian vegetation in place, with indications of the dominant overstory species. Comprehensive species lists for birds and small mammals are also being developed for these riparian communities.

The expansion of these riparian areas also represents an recovery of former movement and dispersal corridors for wildlife in the region. Many mammals, birds, and invertebrates within the biotic communities in the study area depend upon the cover, water and food supplies within the riparian communities to sustain them as they move within their home area, or disperse to new areas. These movement corridors are essential to sustain genetically viable populations for both the wolf and their prey base.

Conversely, surveys conducted outside of the Sandrock allotment where cattle grazing continues show that overstory riparian species regeneration is rare to nonexistent. Almost everywhere off the allotment the living overstory consists of cottonwood and sycamore trees with a diameter of 24 inches or greater. There is few trees below this size class in the study plots, and very little or no regeneration occurring beneath these old giants. These particular species represent a mature stage of the riparian community, and are typically not long-lived. Without some dramatic regeneration these older trees will soon die, and the riparian ecosystem will follow suit.

A Trend Towards Watershed Recovery

The message being discerned within these range and riparian surveys is that watershed recovery is occurring within the Sandrock allotment, and has the potential to spread into adjacent lands within the Blue Range study area. This recovery is most evident in the diverse, multi-storied plant and animal communities returning to the riparian areas along the Blue River and its principal tributaries. Considering that more than 80 percent of the wildlife within this region spends part or all of its life cycle within the riparian areas, this recovery represents a profound source of hope for the Mexican wolf and the full assemblage of original residents in the Blue Range. The recovery appears to be strongly correlated with the removal of cattle, particularly from within the riparian communities. It is also suspected that a return of natural fires would further stimulate restoration of the formerly diverse grassland and woodland communities in the region. The slow pace of rangeland recovery is evident, nonetheless, and warrants careful ongoing monitoring and rest to ensure that the watershed in its full context can provide the habitat needed to restore and sustain the original rich biological diversity of this region.

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[1] *These include the Arizona toad (Bufo microscaphus microscaphus), the lowlands leopard frog (Rana yavapaiensis), the Chiricahua leopard frog (Rana chiricahuensis), and the Mexican garter snake (Thamnophis eques)*

[2] *These include the Zone-Tailed Hawk (Buteo albonotatus), the Black Hawk (Buteofallus anthracinus), the Bald Eagle (Haliaeetus levcocephalus), and Peregrine Falcon (Falco peregrinus).*

Following the Trail of the Wolf: Research Plans 1994-95

Round River Conservation Studies is continuing its baseline and long-term biological and ecological research and monitoring in southeastern Arizona to provide qualitative and quantitative assessments of habitat suitability for the Mexican wolf. Round River's research is working with procedures to estimate the distribution and abundance of deer, elk, and other possible prey populations in the Blue Range Study area, and overall habitat suitability for these populations in the same area.

Data is being collected to estimate the distribution and habitat suitability for mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), elk (*Cervus elpahis*), and other possible prey species within one proposed release area for the captive population of the Mexican Wolf in portions of the Blue Range Primitive Area and adjacent lands of southeastern Arizona. A pilot pellet count study is using stratified random surveys along transect lines to carry out pellet counts. The purpose of these measures is to estimate the abundance of deer and elk populations, and general habitat suitability within demarcated geographic sub-unit areas. Walking cruise censuses are also being carried out to document visual observations of deer species and elk in the study area sub-units. During the course of the pellet transects and walking cruises, field researchers are recording information on habitat characteristics in the area, including qualitative descriptions of access to water, vegetation composition and availability, aspect and topography; and soil characteristics. The purpose of these measures will be to present a qualitative assessment of the habitat suitability for deer in the Blue Range study area. These data can then be correlated with results from aerial surveys and other agency inventory procedures to present a more comprehensive estimate of deer populations in the study area.

Research efforts are also being carried out to estimate the distribution of other predators in the study area, specifically to include mountain lion (*Felis concolor*), bobcat (*Lynx rufus*) coyote (*Canis latrans*), Gray fox (*Uracyon cinereoargenteus*), Kit Fox (*Vulpes macrotis*) and bear (*Ursos americanus*). Predator surveys employ stratified scent posts located along transect lines. The purpose of these measures is to estimate the abundance of each species in the study area, and to infer potential impacts of released wolf populations on population characteristics of other resident predators. Surveys rely on track counts and any records of visual sightings from walking surveys. The purpose of these measures will be to enhance the interpretation of results from the scent post surveys. These data will complement existing estimates of predator populations.

Additionally, Round River field researchers are conducting howling surveys designed to indicate the possible presence of remnant wild wolf populations in the geographic study area. The data from these surveys can identify potential areas for more intensive aerial or foot investigations to document sign or sightings of remnant individuals or groups.

Monitoring of Wolf Populations in Mexico

In 1995 Round River field researchers will initiate efforts to assess and monitor the distribution and dynamics of remnant Mexican wolf populations in the Mexican states of Chihuahua and Sonora. Reports of wolves continue to occur in this region, and Round River efforts will enhance work currently being carried out by the organization, Proteccion de la Fauna Mexicana and the Texas A&M University. Specifically, Round River researchers will work with Mexican counterparts to:

- Mobilize participation by all stakeholders in the decisions made by local, regional, and national governments and their agencies affecting the recovery of the endangered Mexican wolf in both Mexico and the southwestern U.S.
- Use howling and tracking surveys, and local community interviews to document the extent and apparent distribution of remnant wolf populations in Mexico as far south as Durango and ranging to the U.S. border.
- Use existing Round River data on prey distributions and relative abundance to model wolf dispersal and movement corridors both from the released captive population in Arizona and remnant wild populations in Mexico, using a proven mathematical model developed through the University of Utah.
- In collaboration with Mexican and U.S. agencies, develop a short and long-term management strategy to facilitate the movement, protection and restoration of a viable population of Mexican wolves in both Mexico and the southwestern U.S.

The Recovery of the Mexican Wolf

The intent of this intensive research effort by Round River is to provide the technical information from which viable decisions can be made as to how, when and where the Mexican wolf can return to the American southwest. The information on watershed conditions, including range and riparian trends, will be essential to determine the capacity of these wildland habitats to support an abundant prey base for wolves and other predators. We need to know if the proposed release and recovery area provides adequate food and water supplies, cover, and movement corridors to sustain abundant deer, elk and other prey base populations. This information will be complemented by estimates of the abundance and distribution of these prey base populations in the Blue Range study area. Estimates of the abundance and distribution of other predators in the region will enable us to speculate on the impact the wolf may have in an ever-changing regional ecosystem dynamic.

The results being produced through the ongoing Round River field investigations are being distributed to the U.S. and state agencies, and local groups working to restore the Mexican wolf to its former home. The data and analysis are being employed by U.S. Fish and Wildlife Service and Arizona Department of Game and Fish personnel to assess the feasibility of possible release sites for captive wolves, and to infer the probable biological impacts from wolf recovery. The data and analysis are also being employed by the U.S. Forest Service to guide their changing land use strategies in the region.

However, in the end the wolf becomes just one more litmus for us to measure the health of these southwestern ecosystems. As with our measurements of water quality, riparian communities, range vegetation, and deer populations, the presence of a restored wolf population in the American southwest will provide an important "blood test" by which we can define whole, healthy ecological communities. And in determining and establishing the conditions necessary to restore the wolf, we also restore our own integrity as a responsible member of that community.

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Ecosystem Management for Lands in Northern Mexico: A Research - Management Partnership

Celedonio Aguirre-Bravo and David R. Betters

Abstract.—This study focuses on the development of ecosystem management practices in Mexico. The project uses a step-by-step approach and combines management and research expertise in both the United States and Mexico. A case study, the Ejido El Largo Madera, is used as an example of the application of ecosystem management principles and supporting decision making tools. It is the first truly cooperative effort involving all key organizations within Mexico and the United States in an applied ecosystem management project setting.

INTRODUCTION

Through time, forests have commonly been viewed as valuable only in terms of an end product such as logs, firewood, turpentine, rubber, or other wood products. Often forests were considered simply as an obstruction to agriculture. As the earth experiences an increasing loss of forest cover, however, it has become clear that the living forest occupies a critical place in hydrological and atmospheric cycles, cultural preservation, wildlife habitat, recreation, pharmaceutical research, etc. Decisions which are made at the local level are found to have regional, and even global, consequences. It is of increasing interest to managers, landowners, governments, and interest groups alike to turn away from traditional, timber-oriented forest management in an effort to incorporate the value of the living forest in the decision making process.

An example of this evolution in thought can be found in Mexico. Due to the extreme variability of the terrain, the country's forests encompass temperate, sub-tropical, and tropical ecosystems. They are characterized by an enormous diversity of plant and animal communities as well as by a variety of cultures which have historically depended on the forest resource for economic survival. Recent surges in population growth and industrialization have greatly increased the rate of forest utilization with a corresponding increase in pressure on these ecosystems. At the same time, chronic economic underdevelopment has driven many rural residents to leave and seek work in major cities already overwhelmed with people, or to join the stream of illegal immigrants headed for the United States. Among those who remain, some have shifted the pattern of land use to the cultivation of drugs to make a living, or simply cleared the land for agricultural crops or cattle.

The traditional timber oriented forest management methods currently used in Mexico cannot begin to address the complicated ecological and socio-economic problems faced in the country (Toledo and Barrera-Bassols 1984). This type of management ignores traditional uses of the forest, such as the gathering of edible mushrooms, wild fruits and nuts, decorative moss, and so on, of which many could be quite lucrative (Moncayo Ruíz 1979). It ignores the possibility of non-timber sources of income such as recreation, hunting, fishing, eco-tourism, developed tourism, debt swaps for nature, or the management and harvest of wildlife for sale in place of the widespread poaching which currently exists. It also ignores regional effects such as downstream water quality and yield, and air quality. In recognition of this, the Mexican government recently passed a set of sweeping natural resource management and environmental protection laws which call, among other things, for integrated, multiple use management of the nation's forests (SARH 1988, SEDUE 1988). Managers are now required by law to include multiple use and multiple resource criteria

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[1] *Rocky Mountain Forest and Range Experiment Station (USDA Forest Service) and Forest Sciences Department (Colorado State University), Fort Collins, CO, USA.*

in their forest management plans. Their task is complicated due principally to two factors; first, to a lack of appropriate information and information management technology, and second, to natural distrust on the part of landowners of the bewildering complexity added to forest management by the inclusion of multiple resources. The concerns of the landowners are valid; timber is their only palpable (legal) source of income. Given this, they are risk adverse; as with many developing economies their economic resilience is low and they prefer to stick with known methods that guarantee some income rather than risk the unknown and untried, even that which promises higher returns (Blair and Olpadwala 1988). Eroding their economic resilience further is foreign competition. The North America Free Trade Agreement has forced Mexico's largely outdated and labor intensive method of production to compete with a flood of improved, high quality, relatively inexpensive wood products from the U.S. and Canada. Though this trade promises to have many benefits in the long run, in the short term, the economic stress will be great.

Further complicating the forest manager's job is the unique system of dual forestland ownership in Mexico. In this system, forest landowners usually do not have complete management and planning responsibility for their land. A group of tenants ("landowners") is allowed to utilize in perpetuity a block of forest (an "ejido" or "comunidad") to provide income. In February 1992, Article 27 of the Constitution was amended in order to allow Ejidos to become owners of their land and transfer property rights freely. The national government, meanwhile, sets policy by which management is regulated. In between the landowners and the government are quasi-public/quasi-private forest management organizations which are charged with complying with government regulations while fulfilling the goals of the landowners (who also provide their operating budgets). The forest manager is therefore often caught between the landowners and the government. Complications arise because management goals and objectives are often radically different between the two ownership groups (Winter and Aguirre Bravo 1990).

OBJECTIVES

In keeping with Mexico's current policy on sustainable development (Zedillo-Ponce de Leon, 1995), and given the need for an ecosystem management approach that provides for both commodity production and preservation of biological diversity, this project is designed to accomplish the following:

- to provide decision makers in Mexico with an information base to support ecosystem management decisions,
- to provide inexpensive ecosystem management technologies for use by forest managers in Mexico, and
- to demonstrate to Mexican landowners, by means of a case study in northern Mexico, that management of non-timber resources can be accomplished jointly with a profitable timber program.

The success of this joint research/management effort will be measured by testing the following hypothesis:

- It is possible to maintain a viable timber economy while initiating an ecosystem management approach.

METHODS

The complete study is divided into five parts:[2] 1) Project Organization, Issues and Goals Identification, Organization of Available Data, Preliminary Training in Geographic Information Systems, 2) Database Development, 3) Feasibility Analysis of Multiple Resource Alternatives, 4) Response/Successional Function and Decision Support Systems Development, 5) Human Dimensions. It should be noted that certain parts of the project may be taking place concurrently and each includes an element of training and education.

Part 1: Project Organization, Issues and Goals Identification, Organization of Available Data and Preliminary Training in Geographic Information.

This phase was completed during the August 1993-June 1994 time period. Meetings were held to identify constituencies in the United States and Mexico and define extent of involvement. The constituents at this point are: USDA Forest Service Rocky Mountain Forest and Range Experiment Station (RMS), USDA Forest Service Region 3,

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[2] *It should be noted that each part has several components. The detailed methodology to complete each component will be outlined in study plans developed by participants having expertise in the particular area.*

Colorado State University (CSU), Secretaria de Medio Ambiente, Recursos Naturales y Pesca (SEMARENAP), Secretaria de Agricultura, Ganaderia y Desarrollo Rural (SAGDR), UCODEFO No. 2 Ejido El Largo-Madera, State Government of Chihuahua, INIFAP and the Autonomous University of Chihuahua. All have been active in the project during the past year.

Issues, values, beliefs, concerns, and goals for the landowners of the Ejido El Largo-Madera were defined in a report jointly prepared by two sociologists, one from El Largo and one from USDA Forest Service. This document outlines the issues, vision, wants and needs and provides direction for the future project phases (Garcia et al. 1994). The issues values and concerns of the landowners will continue to be evaluated throughout the project.

Data and maps concerning the land base for the Ejido El Largo-Madera were collected and transferred to Colorado State University. Three individuals, one from El Largo-Madera's Unit 2, one from SAGDR-INIFAP and one from the Autonomous University of Chihuahua received four weeks of training in GIS at CSU and at Region 3. They began the process of digitizing the available maps. Altogether this critical phase was extremely successful. All parties are enthusiastic of continuing to work together in the future.

Part 2: Database Development

During this phase the capability for database management and GIS analysis will be developed for El Largo-Madera. Appropriate software and hardware will be purchased for on-site analysis. This hardware will match that used in the National Institute of Geography's (INEGI) and the National Commission for Biodiversity (CONABIO) GIS/database initiative in Mexico and the hardware available for education and training at USDA Forest Service and CSU.

Further education and training will be conducted at Forest Service facilities and CSU. This training will focus on database management and more advanced GIS analysis techniques. Systems used by the U.S. Forest Service will be given special emphasis (eg Rocky Mountain Resource Information System and Terrestrial Ecosystem Survey) and the study will be linked with Project 615 (USDA Forest Service 1985, 1989). As in the first part of the study the training will include participants from all key organizations involved in the project. It is anticipated that after this phase the capability for database management and GIS analysis will be entirely "in-house".

The remaining maps will be digitized with the assistance of Region 3. Existing data will be entered into the data base. This data will include that available from Unit 2 (which is primarily timber-oriented) and other data sources (ie Starker 1982) such as Ducks Unlimited, World Wildlife Fund and the World Bank. Sources identified by Gingrich (1991) will also be useful. Data from INIFAP, CONABIO, and Cartografía Forestal will be used where applicable (INIFAP, 1994). Technicians from the Ejido El Largo-Madera and SAGDR-INIFAP will be responsible for completing this task.

Part 3: Feasibility Analysis of Multiple Resource Alternatives

In the first part of this project the landowners were asked to define what they felt were viable land management options and important issues for the Ejido El Largo-Madera. Essentially this sets the stage for determining initial questions that must be answered in the ecosystem management program. In this part of the project these alternatives are analyzed to determine their technological, ecological and economic feasibility. This type assessment early-on in the project is critical to maintain the landowner support for an ecosystem management program.

The key areas to be researched include: recreation potential, increasing wildlife and biodiversity, increasing water yields and quality, raising livestock, and value-added wood projects. These items were consistently mentioned by the ejidatarios as alternatives they would like to see as part of the Ejido's future management. Obviously, they go beyond the traditional timber emphasis that now dominates the Ejido's employment base and economy. They are important in order to reduce the current dependency on timber and the vulnerability of the Ejido to wood product market forces. The purpose of Part 3 is to examine options and determine their feasibility and associated risks within the framework of ecosystem management.

The area has significant potential for tourism (Lowerre, 1990). The Ejido has several archeological sites, particularly involving the Anasazi. It also is close to Paquime, La Cueva de la Olla, and 40 casas, three of the most important archeological sites in northern Mexico. The region is the ancestrial home of the Tarahumara and Tepehuany Indians and is the location of the famous

Copper Canyon. The archeology of the area is not that well known by the ecotourist community and there is a possibility of significant number of visitors, particularly since its within driving distance of the U.S -Mexico border. Visitors from Europe and Japan are also beginning to visit the area (Gingrich 1993). An Archeology Center is a possibility. The U.S. Forest Park Service can aid in the analysis of this alternative (Bright 1990, EPA 1992). Further the area has major lakes, such as Laguna Babicora and Laguna del Tres and rivers, such as Rio Papigocas and Rio Tutuaca, along with their tributaries that can support large populations of trout. A fish hatchery and expanding fishing opportunities are also a possibility.

The forest area now is virtually devoid of wildlife. The region has several endangered and threatened species including the Mexican Gray Wolf, Imperial Woodpecker and others. Several additional species survive in limited numbers (Lowerre 1990). At El Largo-Madera limited wildlife populations are largely due to the even-aged pine emphasis (on 4 commercial species known as the "Ponderosa" group) in the timber management program. Options to improve habitat and biodiversity need to be researched including means of developing and protecting riparian and aquatic areas. Restoring representative habitats with appropriate spatial and temporal arrangements is important. In the forest areas alternatives may include irregular forest systems coupled with agroforestry and possibly with plantations that increase productivity and decrease the area in the timber program (However, plantation feasibility needs long-term experimental study first.) Further, education and law enforcement programs must be initiated to deal with poaching problems.

The forest is a key source of water for the local population as well as for larger population centers and agricultural activities in the States of Chihuahua, Sinaloa and Sonora. Water yields and quality are key to the health of the people and to the economic development of the region. Water is significant to maintaining viable populations of fisheries and wildlife. The lakes and rivers of the area are extremely important to migrating waterfowl. Means to improve yields and quality are important to the Ejido and the region. Binkley and Brown (1993) have compiled information regarding effects of management practices on water quality in the U.S. Their study will be a good starting point to address options here.

Since the Ejido has concentrated in timber management little attention has been given to multiple use including livestock grazing. Certain areas may have potential of this option but only while considering carry capacity and ecological impacts. The San Bernadino-Animas ecosystem management project with the Coronado National Forest should provide useful information for analyzing this alternative as well as others (USDA Forest Service 1994).

Finally value-added wood products may make the timber program more profitable and allow more flexibility in the ecosystem management programs. Currently only rough cut timber is produced or logs sold for pulp. The Ejido could produce finished, precision-cut lumber, furniture or crates for the region's vegetable producers. Under NAFTA, precision-cut lumber can also involve timber shipped to Mexico, finished and shipped back to the U.S. However it must conform to U.S. grading practices (WWPA 1992). The examination of new markets is very important at this time given NAFTA and the competition that Mexico will likely receive from the Canadian and U.S.wood products industry (Mikesell et al. 1991). The recent study by SRI International (1993) will provide useful information to begin this study. The World Bank's Forestry Development project assessments for wood products should also prove useful (World Book 1991). Finally, a major Canadian research effort with INIFAP in Chihuahua Mexico may have components that could apply here. Canada has established a Model Forest Program to develop working models of sustainable forest management (Canadian Model Forest Program, 1994). Within this program there is an international component. Mexico has two sites participating in a joint effort to provide working models of sustainable forestry. One site is located in the State of Chihuahua. Certainly, the proposed study at El Largo-Madera will need to be coordinated with the Canadian program.

In this part of the study each of these options (as well as others that may be developed eg extractive reserves for medicinal and other useful plants) will be assessed in terms of costs and benefits, markets, ecological impacts, management options and training and education needs. An interdisciplinary team of researchers and managers will be organized to complete the work. The team will be divided into subgroups with expertise necessary to address each alternative. Each subgroup will be responsible for writing a detailed study plan for their work. The team will match cooperator expertise in Mexico with those in the U.S. Participants will be identified from universities and government research and management agencies in both countries.

Each subgroup will prepare a report and results of these studies will be published in both English and Spanish. Each possibility will be discussed, in detail, with the landowners and strategies for implementation will be defined, as appropriate. The scheduling of activities related to the alternatives and their resource interactions will be examined in the next part of the study.

Part 4: Response/Successional Functions and Decision Support System Development

In this part of the study the information management and GIS systems of Part 2 of the study will be integrated with additional decision support tools to create a decision support framework for developing and monitoring an ecosystem management program for the Ejido.

The work here will involve several segments including: land classification, suitability analysis, identification of additional data needs, response/successional functions, ecological monitoring and assessment, and decision support system to construct an ecosystem management plan.

4a: Land Classification

Land classification will rely heavily on GIS map coverages to create classification schemes useful for decision making. The ecosystem classification will be hierarchical and be applicable to response/successional function and suitability analysis information needs (Urban et al. 1993). The classification will define analysis areas which contain reasonably homogeneous abiotic and biotic conditions which will respond to a management option in a consistent manner. The classification will facilitate the manipulation and presentation of relevant information and ecosystem management options on maps. The classification developed will closely follow the USDA Forest Service's Ecosystem Classification System and include ecological, geo-physical and socio-political criteria. The classification will use habitat typing (plant association) methods used in the southwestern region of the U.S. (eg Larson and Moir 1986; Larson et al. 1987).

4b: Suitability Analysis

A suitability analysis will be applied to determine the potential of classified areas for different types of uses and for meeting ecosystem management needs. The approach begins by outlining uses and the criteria for determining suitability of those uses. Some sites may be found to be single use oriented whereas others multiple use.

Suitability will not be defined purely in bio-physical terms but will also include socio-economic criteria. For example, an area which, from all other standpoints, seems a perfect location for timber production but is expensive to access due to distance or poor roads, may be classified as most suitable for another type of use(s). Another example of integration of bio-physical and socio-economic factors is the typical pattern of land use around settlements in the Ejido. Often these areas are used for growing crops or livestock regardless of land suitability. However their existence is extremely important from a traditional and cultural standpoint.

4c: Identification of Additional Data Needs

During the course of the defining alternatives, database development, classification and suitability analysis data needed but unavailable, outdated, or questionable will be identified. Statistical procedures for collecting this information will be developed and, where necessary, field sites will be established to gather data. It's anticipated that this will be a long-term effort. This work will be cooperatively accomplished by Mexico and U.S. participants.

The Ejido El Largo-Madera has been designed as an experimental forest linked to a similar experimental forest in the U.S. This joint USDA Forest Service-Mexico effort provides an excellent opportunity to augment the database with information currently not available. Remote Sensing and Land-Sat imagery from the Southern Forest Experiment Station's Forest Distribution Maps of Central America and Mexico from AVHRR data should also prove useful here. Finally, the indigenous people are directly connected with the ecology and are intimately more familiar with environmental diversity. They can be important to helping locate and identify unique plant associations.

4d: Response/Successional Functions

The creation of accurate response/successional functions is extremely important to forecasting ecological and social impacts of management options and determining if desired future conditions are attainable. Parallel to this task will be the development of a plan for implementing ecological monitoring and assessment actions. Past efforts in Northern Mexico to develop such functions have largely focused on the timber resource; very few predictive models for other resources exist.

The team of scientists and managers organized to complete Part 3 of the study will also be involved in helping construct these response functions. This team will be augmented with individuals having expertise in developing ecological/economic process models. In Mexico the participants will come from universities and INIFAP. In the U.S. they will be from EMAP-EPA, RMS, and universities. Models already available (Schuster et al. 1993) will be used where applicable. The team will work closely with the Ecosystem Management Study Teams of U.S. Forest Service and other federal agencies. Information sharing and collaboration with U.S. Forest Service National Forests having similar environmental conditions will be important to completing this work. It is anticipated that this will also be a long-term study. As new information becomes available the models will be refined.

4e: Decision Support System

The decision support system integrates the analytical tools and information base developed in all parts of this study. The key components of the system here include GIS, the database system and the response/successional functions. Planning tools such as INFORMS may also be included (Schuster et al. 1993). It should be noted it is not the purpose of this study to develop a unique support system. Several "systems" have been or are in the process of being developed in the U.S. that may have applications here. In as much as possible existing analytical tools will be applied in a modular fashion. The support system will be used to analyze and evaluate the feasible management alternatives based on the classification and suitability systems developed previously. The system provides a tool for analyzing the interactions between the resources and social and economic needs. The ultimate purpose of the support system is to provide an aid to developing a long-term implementation strategy for ecosystem management that meets of goals of the Ejido. In order to construct such a strategy several constraints and requirements will need to be considered including: applicable laws and regulations; costs, returns and economic requirements; ecological impacts both spatially and temporally; and sustainability of the socio-economic and ecological systems.

The decision support system will be used to schedule the timber harvesting and reforestation program. This schedule will be developed under the constraints and requirements mentioned above. The timber harvest program will be analyzed at different hierarchial spatial levels. The system will also be used to schedule appropriate activities dealing with wildlife, recreation, livestock and water yields and quality. The system will help in understanding the interrelationships between resource activities both spatially and temporally. Ultimately the system will provide the analysis necessary to prepare an ecosystem management plan. The construction of this system will require expertise from USDA Forest Service as well as universities. The new SPECTRUM effort may be important to helping design the analytical approach. There will need to be education and training as well as means for technology transfer.

Part 5: Human Dimensions

The human dimensions portion of this study is extremely important. In order for the landowners to endorse any ecosystem management strategy they must be involved at every stage of the effort. Not surprisingly the ejidatarios are risk averse. Timber has been their only palpable source of income. Their economic resilience is low and they prefer to stick with known methods that guarantee some income rather than risk the unknown and untried. This is why the feasibility analysis of Part 3 of this study is so significant. Further, it is important to institute public education programs in ecosystem management both for schools and for adults. Videos, in Spanish, will be developed for the overall project as well as for each individual part, so all are kept informed. An El Largo Ecosystem Management Learning Center including "hands on" type experiences will be established to facilitate public awareness and education. Radio and television programs concerning the project will also be part of this effort. Approaches to public education such as Project Learning Tree in the U.S. should provide useful information for constructing a similar program here. As stakeholders, the landowners input will be solicited on a regular basis and Ejido's leadership will be involved in all project meetings. The basis for the decisions must be understandable and credible to the Ejido, they must feel shared ownership in the plan. The sociologists who worked on the first part of the study will also be involved here to complete specific tasks.

In the first part of this study (already completed) the sociologists asked what things within the Ejido the people would like to see changed in order to improve the situation. Overwhelming the respondents wanted the Ejidos management organization structure to be changed. Currently the management decisions are made by a committee of ejidatarios [5 individuals] and a president elected to 3 year terms. The forest technicians of UCODEFO No. 2 serve as advisors to this group and do not have decision making authority for instituting alternatives such as those concerning ecosystem management.

The problems ejidatarios have with this organization largely deal with a lack of communication and a underlying distrust concerning how finances are handled. These problems are likely to be compounded by the complexity added with the inclusion of ecosystem management. As part of this study new means of communicating and management decision making need to be explored. The expectations of the ejidatarios must be balanced in this process. Decision making must be done in an equitable manner. Better financial management is necessary including basic bookkeeping skills. The accounting and auditing system needs to be examined and modified to meet concerns and deal with the broader issues and alternatives suggested in this study. In order to accomplish the improvement of business practices, appropriate U.S.-Mexico university business schools will participate in a management organization review. Representatives from the state and federal governments will also participate.

While the Ejido management organization is somewhat outside the realm of "ecosystem management" it is important to insuring implementation of the strategies developed in this study. The establishment of an organization that is trusted, accountable and communicates is more likely to result in implementable ecosystem management in Mexico's ejido system.

EXPECTED OUTCOMES

This project is mutually beneficial to both countries for several reasons:

- It provides an opportunity to exchange useful information relative to ecosystem management.
- It provides for training and education in many areas for parties in both countries.
- It promotes landscape-level ecosystem management for regions along the U.S.-Mexico border.
- It strengthens the management and research partnership between organizations in the two countries.
- It serves as a prototype model for developing sustainable rural development on lands where the population is highly dependent on the resource base (ejido and tribal lands)
- It provides managers in other areas with a model for development of similar approaches.
- It develops improved dialogue and networks between researchers and forest managers involved in ecosystem management planning.
- It provides the opportunity to develop new data and improve our state of knowledge concerning forest ecosystems in northern Mexico.
- It provides an opportunity through publications and conferences to show how an ecosystem management approach can be applied to similar areas of the World where the local populations are highly dependent on the land base.

The project is innovative in that:

- It is the first joint U.S.-Mexico effort to focus on an area for ecosystem management in Mexico.
- It is the first time an ejido has pledged full support for an ecosystem management program.
- It is the first truly cooperative effort involving all key organizations within Mexico and U.S. federal agencies and U.S. universities.
- It links research and managers together in an applied project setting.

The project will enhance research capacity in that:

- Researchers from both countries will work together as a team to solve specific research problems.
- All researchers will become more aware of what has been accomplished in both countries.
- Researchers will have the opportunities to develop future interaction and collaboration.

SHORT AND LONG TERM DELIVERABLES

Short Term (first year)

- Publish results of the Sociology Study as a RMS bulletin (Part I)
- Complete digitizing of remaining maps and complete advanced training of Mexican participants in data base management and GIS (Part 2)
- Provide technical assistance in establishing GIS system software and hardware at El Largo - Madera (Part 2)

- Provide preliminary economic and technical feasibility reports for value-added wood products, developed recreation and ecotourism and livestock grazing (Part 3)
- Prepare a video and display, in Spanish, describing the overall project for a lay public audience (Part 5)
- Complete a report suggesting changes in the administrative system to support ecosystem management initiatives (Part 5)

Long Term

- Provide an information base and land classification system via GIS to support ecosystem management initiatives (Part 4)
- Establish long-term research sites to provide information not currently available and necessary for ecosystem management (Part 4)
- Complete remaining economic and technical feasibility reports for wildlife and biodiversity, and water yield and quality (Part 3)
- Provide response functions to simulate ecosystem response to management alternatives (Part 4)
- Complete a multiple use or ecosystem management plan for El Largo -Madera (Part 4)
- Establish a long-term public education and involvement system and a reliable and accurate administrative system for El Largo - Madera (Part 5)
- Design and implement a system of ecological monitoring and assessment.

TASK FORCES: DESCRIPTION OF ACTIVITIES

MANAGEMENT SCIENCE RESEARCH

This task force, in cooperation with others, will be responsible for investigating the use of management science and operations research for sustainable ecosystem management and planning. Starting from static, nonspatial models for optimizing viability tradeoffs in multispecies habitat allocation, methods have been developed for dynamic, spatially explicit location and scheduling of forest practices to best accommodate multispecies habitat needs for sustained viability. Although habitat connectivity/fragmentation and wildlife population growth, dispersal and viability functions are the fundamental cornerstones of these methods, problems such as edge effects and habitat size thresholds have also been addressed. This task force will also investigate life-history attributes and regional patterns of animal distribution and abundance within the study area.

WILDLIFE HABITAT RELATIONSHIPS

This task force will study the effects of land management practices on fish and wildlife. Aspects of interest to be investigated include: distribution, abundance, and habitat associations of migrating and breeding neotropical migrants and resident birds; habitat associations of amphibians and reptiles in riparian ecosystems; nocturnal small mammals preyed on by owls; and big game distribution, habitat relationships and management.

MULTIRESOURCE MANAGEMENT

This task force will investigate several aspects of the distribution, structure, and dynamics of the plant biodiversity of the study area. That is, vegetation growth, mortality, regeneration response to even and uneven-aged management in relation to natural disturbance patterns (fire history) and species ecological requirements; mathematical modelling of vegetation dynamics; classification of old-growth forest communities; and vegetation-wildlife management relationships. This group will also study and propose alternative regeneration and stand management techniques to improve and restore habitats for wildlife.

MULTIRESOURCE INVENTORY TECHNOLOGIES

This task force will investigate advanced methodologies to develop a fully integrated multiresource inventory and monitoring system for the study area. Parameters of interest are: point and change estimation (hectares of commercial timber land, volume by principal species, wildlife habitat conditions, forest health conditions, opportunities for recreation); identify explanations for change observed; assist in the development of growth and mortality models for key species; training in multiresource inventory methods.

FOREST ECOSYSTEM HEALTH MONITORING

This task force will investigate the current status, extent, changes, and trends in the conditions of the forests; monitor indicators (insects, diseases, etc.) of forest tree and ecosystem condition and identify associations between natural and human-caused stresses and ecological condition. Scientists of this team are expected to strongly interact with the scientists of the Multiresource Inventory Technologies team. Scientists will also participate in training and education programs.

FOREST PRODUCTS AND MARKETS

Scientists will conduct research and technology exchange activities to support the forest ecosystem utilization community. These activities will involve the total spectrum of wood (e.g., logs, lumber, veneer, etc.) and non-wood (e.g. medicinal plants, extractable chemicals, etc.) products available from the forest ecosystems. Scientists, those with backgrounds in economics and marketing, will study and develop options for making the forest ecosystem utilization community more able to produce high-quality products capable of competing in domestic and global markets.

COMMUNICATION AND OUTREACH

The exchange and dissemination of information and understanding the variability of traditions, perceptions, and attitudes among peoples and the roles of social institutions are fundamental conditions for making ecosystem management operational. Ecosystem management issues, whatever its geographic and social scale, cannot be properly addressed under an environment of imperfect knowledge and information. Scientists within this group will study ways to understand the complexities of the human dimension and will devise means to converge the integration of the human potential into the ecosystem management framework.

PROJECT MANAGEMENT

Due to its complex nature, this project is multi-disciplinary and requires of the collaboration of a large group of people and institutions. This project, therefore, is organized into a two-tier structure consisting of an Ecosystem Management Advisory Board (EMAB) and a Coordination Committee for Ecosystem Management (CCEM). The EMAB will provide advise and suggest priorities to for the Coordination Committee, serve as a liaison to Chief Executives of other institutions, and assist in coordinating with other efforts. Initially, EMAB membership includes the following institutions:

United States Members: USDA Forest Service, Environmental Protection Agency, DOI (National Park Service, National Biological Survey, Bureau of Indian Affairs, Fish and Wildlife Service) and Colorado State University, College of Natural Resources. .

United States of Mexico: Secretariat of Environment, Natural Resources, and Fisheries (SEMARENAP), Instituto Nacional de Investigaciones Forestales y Agropecuarias, State Government of Chihuahua, Universidad Autonoma de Chihuahua, Secretariat of Agriculture and Rural Development (SAGRUDE), and Ejido El Largo y Anexos (Chairman, Board of Directors).

The CCEM will consist of scientist/managers (Principals) appointed by the Executives of the institutions involved in this effort. These Principals will coordinate the participation of scientists and technicians working within the Interdisciplinary Joint Working Groups (Task Forces). Principals and scientists of the different Task Forces will coordinate their activities to assure across collaboration and avoid duplication of efforts.

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Mexican Legislation for Productive Projects in Sky Islands

Laura Pimentel-González [1], **Alfredo Ortega-Rubio,** [2] **and Heidi Romero-Schmidt** [2]

Abstract.—From the Federal Government point of view, the ecological verification is one of the principal factors in order to accomplish an adequate management of the natural resources of any zone. In the case of the Sky Islands, the interinstitutional collaboration between the Governmental Agencies and the Research Centers is essential. In this work we analyze the required factors for to, through interinstitutional works, develop an adequate ecological verification. Also, we offer specific examples os such collaborative efforts on sky islands of Northwestern México.

INTRODUCTION

From the Mexican Federal Government point of view, the ecological verification and legislation is one of the principal factors in order to accomplish an adequate management of the natural resources of any zone. Environmental regulatory framework in México is founded in the Constitution of the Country. Articles 25, 27, 73 and 115. In these Articles there are established the jurisdiction on use of the natural resources andenvironmental protection.

During 1988 the Federal Government of México implemented the General Law of Ecological Equilibrium and Environmental Protection (Diario Oficial, 1988). A comprehensive law covering the total spectrum of environmental aspects.

Environmental Mexican legislation have four main mechanisms, for protection and preservation of the natural resources:

a. Territorial ecological ordinance.
b. Environmental impact assessment studies.
c. Natural system of protected areas.
d. Elaboration of specific ecological rules.

For any new productive project, public or private, it is necessary to present an Preventive Report (EPR), developed by the Companies for the corresponding authorities: Federal (SEDESOL), or State or Municipal authorities.

According with the corresponding authoritie's analysis to the EPR, there are two options:

1. There is no need of more studies or information, or
2. The promoters of the project must contract a Registered Advisor in order to develop an Environmental Impact Assessment (EIA).

EIA could be required in one of the three levels, differing among them by the degree of specificity of information needed: General, Intermediate or Specific. Every one must contain precise information of the proposed project, the description of the physical, biological and socioeconomic environment surrounding the project, the general and specific regulations applied at thezone, the Impacts foresee and the precise measures to avoid or to mitigate them. The final product of the EIA is the Environmental Impact Assessment Report (EIAR) (Bójorquez y Ortega, 1988; 1989), which is presented by the promoters of the project to Federal (SEDESOL), State or Municipal authorities .

Environmental Impact Studies, in the case of the Skyislands, the Federal authorities are the only one with legal competence for to analyze and judge this studies.

Usually there are required more detailed studies and these are reviewed even more carefully. The reasons for such accuracy are related to the importance of the skyislands: in general terms they contained more endemic and endangered species than other zones.

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At Baja California Sur, there exits two biosphere reserves. One of them, La Sierra de La Laguna is a typical case of an Skyisland.

At the influence zone of La Sierra de La Laguna, the developed environmental studies, and their analysis are, even more, accurate and specific.

From 1988 to 1994, there have been proposed 9 productive projects to be developed at the influence zone of La Sierra de La Laguna. Three of these projects were approved to be developed with the presentation of a Environmental Preventive Report. The three projects are only mining exploration activities.

Three projects must to develop an Environmental Impact Assessment General Report. Two of them were small agricultural development and the other one of ecotourism.

The other three projects were rejected for their development.

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Research and Conservation Literature and Database for the Borderlands Region

Leonard F. DeBano[1], Silvia Manzanilla-Naim[2], Roy R. Pollisco[3], and Peter F. Ffolliott[3]

Abstract.—The Borderlands Region in the United States and Mexico is an area of exceptional biodiversity and is of interest to scientists worldwide as an outdoor laboratory. Because of its uniqueness, this region has attracted large numbers of research studies and conservation related activities over the past century. Concurrent with this interest has been the designation of special areas for research and conservation. This multitude of research and conservation activity is not well documented. The paper outlines an initial step in amassing the large amount of published and unpublished information about the Borderlands Region into a common database that could be used internationally to enhance the exchange of resource information and the management of this unique region.

BACKGROUND

The Borderlands Region of the southwestern United States and northwestern Mexico includes the Madrean Archipelago and other "Sky Islands" not biogeographically part of the Madrean Archipelago. This area of exceptional biodiversity and great biogeographic interest contains the Basin and Range Physiographic Province south of the Rocky Mountains and north of the Sierra Madre Occidental in southeastern Arizona, southwestern New Mexico, northeastern Sonora, and northwestern Chihuahua. The flora of this region consists of a diverse mixture of endemic, Rocky Mountain, and Madrean species, and is one of the most floristically diverse areas in North America. Lowlands throughout much of the center of the region support desert vegetation. Depending on elevation, isolated mountain ranges within this region support oak and pine-oak woodlands, pine forests, and on the highest ranges, mixed conifer and spruce-fir forests. Individual mountain ranges may have up to 1000 different native species.

The high biodiversity and uniqueness of the Borderlands Region, and associated geological and floristic setting, is of considerable interest to scientists worldwide. As a result, large numbers of local, national, and international scientists are attracted to this area to conduct basic and applied research. The intense research interest has resulted in the establishment of several long-term research facilities and conservation areas, both in southwestern United States and northwestern Mexico. This research setting has lead to literally thousands of studies in the past and hundreds of studies that are active at the present time. As a result, there is an immense amount of information that has been collected, published, and/or presented in unpublished reports concerning various dimensions of the Borderlands Region. An initial step in bringing this information together resulted in this first conference on the Madrean Archipelago, held in Tucson on September 19-23, 1994 (DeBano et al., 1995). However, although this conference indicated a great deal is known about individual sites throughout the Borderlands Region, much of the published and unpublished information remains widely fragmented within numerous literature sources.

It is the intent of this paper to discuss the need for starting to bring together the literature and other relevant information on the location and general description of research and conservation activities being implemented on designated sites in the Borderlands Region of the United States and Mexico. The results of this effort would greatly enhance both national and international collaboration in the Borderlands Region.

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DATABASE FOR RESEARCH AND CONSERVATION ACTIVITIES

An effort is currently underway to begin consolidating the immense volume of both published and other information on the Borderlands into a common database. A major objective of this database development is to catalog not only published literature, but information about ongoing research studies throughout the Borderlands Region. A brief description of areas been specifically designated as research or conservation areas would be included in this database.

Literature

Literature, including published bulletins and articles, unpublished reports, and theses and dissertations, is considered the first important component of developing the above database. However, much of this literature is scattered throughout several bibliographic databases in the United States and Mexico, or exists as fugitive literature. An initial attempt was made to bring this widely scattered literature together by preparing an annotated bibliography that was distributed to all participants attending this conference (Ffolliott et al. 1994). This bibliography represents only an initial compilation of literature on the Madrean Archipelago region. Bibliographic databases interrogated to compile this bibliography included FS INFO, CAB Abstracts, AGRICOLA, BIO SIF Previews, and Life Science collections. Annotations of the literature cited in this publication are, unfortunately, still incomplete. It is planned to expand this bibliography in the near future to include the papers presented at the conference on the "Biodiversity and Management of the Madrean Archipelago: The Sky Islands of the Southwestern United States and Northern Mexico", and other literature not listed in the initial version of the bibliography. We are therefore asking people with knowledge of literature that should be included in a more-complete update bibliography to send the appropriate citations and a short annotation of each to: Dr. Peter F. Ffolliott, School of Renewable Natural Resources, University of Arizona, Tucson, Arizona 85721.

Research and Conservation Areas

Information on research and conservation areas in the United States and Mexico will be more difficult to develop because there are only a few information sources on such activity. However, information on several well known research areas is listed in Table 1 to illustrate the type of information needed for this type of database.

We are again seeking people's assistance in obtaining data on research and conservation areas by providing information on areas that you are aware of that should be listed. This information base would specifically catalog information on: name of research site; geographical location of the area, including latitude and longitude; ecosystem description (in terms of vegetation); person to contact who is in charge of facility, including their address, FAX, and phone numbers; type of facilities, including laboratory and field opportunities; emphasis and nature of research; institution involved; status of the research area (both active and inactive areas would be appropriate); protection status; date of establishment; and any other comments pertinent to describing the research or conservation effort. We intend to start soliciting this information from participants that attended the conference on the Madrean Archipelago and other interested scientists. Also, ideas on additional information that should be included this database on research and conservation areas is appreciated.

We are asking people that have the above information on research and conservation areas in United States to send this information to: Dr. Leonard F. DeBano, School of Renewable Natural Resources, University of Arizona, Tucson, AZ 85721. Information on research and conservation areas in Mexico should be sent to: Silvia Manzanilla-Naim, Centro de Ecologia, UNAM, AP. Postal 70-275, Mexico, D.F. 04510

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Table 1.—Example of Information Complied for Designated Experimental Areas in Mexico and the United States.

UNITED STATES

Name of Area	Ecosystems	Types of Studies	Institutions Involved	Contact Person
Walnut Gulch Experimental Watershed	Desert grass/shrublands	Agricultural research, global change research, environmental science, natural resource modeling, decision support systems	USDA-ARS	Leonard Lane Research Leader USDA-ARS Southwest Watershed Research Center, 2000 E. Allen Rd., Tucson, AZ 85719 (602) 670-6381
Appleton-Whittell Research Ranch Sanctuary	Upland grassland, oak savannah, oak woodland, sacaton flats, riparian	Ranch research, air quality sampling, aquatic analyses, predator-prey relationships, seed production/utilization, vegetation changes, effects of wildfires	National Audubon Society	Michael Morrison Research Director SRNR, Univ. of AZ Tucson, AZ 85721 Bill Branan Sanctuary Manager Box 44, Elgin, AZ 85611 (602) 455-5522
Buenos Aires National Wildlife Refuge	Desert grassland, live oak, riparian	Biodiversity	U.S. Fish and Wildlife Service	Thea Ulen Outdoor Recreation Planner P.O. Box 109 Sasabe, AZ 85633 (602) 823-4251

MEXICO

Name of Area	Ecosystems	Types of Studies	Institutions Involved	Contact Person
La Bioreserva de Casas Grandes	Altiplanos	Inicacion de una bioreserva ecologia de aves, perritos de las praderas, carnivoros, plantas	Centro de Ecologia, UNAM	Apartado Postal 70-275 Mexico, D.F. 04510 (5) 622-9004
Municipio de Janos, Chihuahua	Pastizal mediano abierto		Centro de Ecologia, UNAM	Circuito Exterior S/N Anexo Al Jardin Botanico Exterior Cd. Universitaria CP. 04510 Mexico, D.F. (5) 622-9004
San Pedro, el Alto y el Cuervo, Municipio de Janos, Chihuahua, Mexico	Pastizal mediano abierto (*Bouteloua* y *Aristida*)	Effecto del perrito de la pradera en la biodiversidad vegetal en el Norte de Mexico	Centro de Ecologia, UNAM	Circuito Exterior S/N Anexo Al Jardin Botanico Exterior Cd. Universitaria CP. 04510 Mexico, D.F. (5) 622-9004

Soil-Climate-Vegetation Relationships in the Sierra de La Laguna, Component of the Sierra Madrean Woodland Element

Yolanda Maya[1]

INTRODUCTION

Soils are the product of many natural factors acting on geologic material across time in a dynamic and continuous process. Some of these factors are physical, such as topography and those which define the climate: temperature, humidity, rainfall, etc. Other factors are biological, such as the effect of vegetation acting on the soil (contribution of organic matter by the dominant species of a vegetal community, for example). Plants, on the other hand, have specific nutrient, drainage and humidity requirements, thus substrate is a determinant of their setting up (Buckman and Brady, 1977).

The Sierra de La Laguna, located at the meridional portion of the Baja California peninsula, is a component of the Sierra Madrean Woodland Element (Axelrod, 1950). It can be described as an island in the middle of the desert. Due to its origin as a granitic batholith arising from the Sierra Madre Occidental on the mainland, it had never been submerged in the sea (Padilla *et al.*, 1988). Consequently, the batholith acted as a type of Noah's Ark, transporting many species from the mainland, some belonging to the Madro Terciarian Flora. In contrast, the entire plains area surrounding the range had a different geologic origin and remained for some time on the bottom of the sea.

The granitic mountain mass is formed by the union of several transversal, smaller ranges (Hammond, 1954), with elevations ranging from 61 ft o.s.l. up to the highest peak (624 ft in altitude). The climate in the Sierra varies from warm semiarid to subhumid temperate, in a gradation corresponding to altitude (Coria, 1988). Several vegetal communities are distributed from base to top as a result of this climatic gradation. They are: xerophilous scrub (from the lowest plains to 91 ft), tropical dry forest (from 91 to 230 ft), oak forest (to 365 ft), oak-pine forest (to 430 ft) and pine-oak forest up to the top, in addition to a small grassland area (Morelos, 1988).

The topography is uniformly craggy throughout the landscape, except for a rough high plateau at the summit, formed by the union of some of the smaller ranges. The almost homogeneous geology of the Sierra de La Laguna, makes this range suitable for observing the role that climate and vegetation have played during soil development.

OBJECTIVE

The principal aim of the present study is to identify the effect of climate and vegetation on the development of the soil in the Sierra de La Laguna.

METHOD

Eleven soil profiles were described in sites representing the different conditions present in the area. To describe the profiles, sampling holes were opened to a maximum depth of 4 ft when possible. Each layer was separated and its morphological characteristics were registered: depth, color and texture, among others parameters. Also, the kind of vegetation, slope, physiography and nature of parental material were recorded. Samples were obtained and analyzed in the laboratory and this information was compared and correlated with already known physical and chemical edaphic processes.

RESULTS

Tables 1 and 2 show the physical and chemical characteristics of four profiles representative of the different conditions present in the Sierra de La Laguna. The selection of these profiles was based

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on the fact that soils of any given landscape present similar characteristics.

It can be observed in the tables that the soils sustaining xerophilous scrub, in the plates and plains surrounding the Sierra are deep, light colored and have a very high base saturation percentage. The main differences between these soils and those of mountain slopes, sustaining tropical dry forest are in depth and content of organic matter. Soils sustaining pine-oak forests at higher elevations, were thin and very dark colored, with a high content of organic matter. The most different kind of soil was that of the grassland, which showed a very high content of organic matter in addition to a low base saturation percentage, reflected by the acid condition of the soil.

CONCLUSIONS

The influence of vegetal communities with very different characteristics, as well as climatological effects are responsible for the development of important differences in soil characteristics. These differences mainly involve organic matter content. As a result, soils in dry and warm climates with xerophilous scrub and tropical dry forest are rather poor in organic matter content, which is reflected in their light coloring.

On the other hand, the pH of these soils is neutral, due to high-percentage ion saturation. This is the result of an extremely low lixiviation of ions from the soil particles.

As for topography, its influence on the development of soils can be observed mainly in depth and maturity. Soils of sheer areas are removed in a continuous and dynamic process almost as soon as they are formed, due to the action of gravity or water. This process is retarded mainly by the direct action of plants, which retain soil particles with their roots and decrease the mechanical action of wind and rainfall on the upper layers. Conversely, areas with little slope receive a constant contribution of material falling from the upper areas; this soil remains, contributing to the course of edaphic processes such as lixiviation and horizonation.

In contrast, soils which have developed in the highest region of the range and which support oak and pine forests under very humid conditions, have a very high content of organic matter. This is reflected in dark coloration, but due to the humid condition prevalent in the area during much of the year, most of these soils present a

Table 1.—General landscape characteristics of sites where the selected representative profiles were described.

Profile No.	1	2	3	4
Physiography	Plains and plates around the Sierra	Slope of La Zorra Canyon	Slope of a mountain	La Laguna Valley (high plateau)
Kind of Vegetation	Xerophilous scrub	Tropical dry forest	Pine-oak forest	Grassland
Climate	Dry arid	Warm semiarid	Subhumid temperate	Subhumid temperate
Parental material	Alluvion	Granite	Granite	Granite
Limitant	None	Rock	Rock	Rock

Table 2.—Results of physical/chemical analyses of described horizons.

Soil horizon A

Profile No.	1	2	3	4
Depth (in)	0-9.5	0-15.7	0-14	0-8.6
Texture	Loamy sand	Sandy loam	Loam	Sandy loam
Color (moist)	Light brownish gray	Brown	Grayish brown	Brown
Color (humid)	Dark brown	Dark grayish brown	Very dark grayish brown	Very dark grayish brown
pH	6.8	6.6	5.6	5.0
Organic matter content (%)	0.8	2.1	4.0	10.0
Base saturation percentage	Very high	Very high	Very high	Low

Soil Horizon B

Profile No.	1	2	3	4
Depth (in)				8.5-13.8
Texture				Silt loam
Color (dry)				Light yellowish brown
Color (moist)				Grayish brown
pH				5.5
Organic matter content (%)				0.6
Base saturation percentage				Moderate

Soil Horizon C

Profile No.	1	2	3	4
Depth (in)	9.5-40			13.8-35
Texture	Sandy loam			Loamy sand
Color (dry)	Light yellowish brown			Pale yellow
Color (moist)	Dark grayish brown			Light yellowish brown
pH	7.0			5.8
Organic matter content (%)	0.3			0.2
Base saturation percentage	Very high			High

very low saturation of bases; consequently, the pH of the soil solution is acid.

Because of the fragility of the soils, due to conditions such as sandy texture and extreme slope, both preservation of the vegetal covering and reforestation are recommended in order to restore the small, but increasingly eroded areas.

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Emergence of Aquatic Insects During March-April 1993 from Streams in the Chiricahua National Monument

E.C. Masteller[1]

Abstract.—Two emergence traps covering approximately four square meters of water surface were placed over Bonita Creek and East Whitetail Creek in the Chiricahua National Monument during the time when surface flow of water was present. Twenty collections were made periodically between 9 March and 15 April, 1993. From these samples 28 taxa have been identified from 800 specimens collected.

The most abundant groups were midges (Chironomidae, Diptera) and stoneflies (Capniidae, Plecoptera). Over seventy-five stoneflies emerged consisting of two species; *Mesocapnia arizonensis* and *Capnia californica*. Twenty-five mayflies (Baetidae, Ephemeroptera) emerged during this period with the very common North American species *Baetis tricaudatus* present as well as the uncommon species *Fallceon quilleri*. Immature blackflies (Simuliidae, Diptera) were observed in the streams in large numbers but were infrequently collected in the emergence traps. *Prosimulium imposter* was the most common blackfly present. Future research should be directed at determining how these insects cope with the long dry periods when no surface water is present. It may be that subsurface flow is maintaining these insects.

METHODS

Emergence traps constructed of shade cloth (Lumite special screen #5103200 from Chicopee Mfg. Co.) with a mesh size of 0.5 mm covered 4m^2 of water surface. Two traps were placed on Bonita Creek and East Whitetail Creek in the Chiricahua National Monument (32_01'18"N, 109_20'19"W and 32_01'15"N, 109_18'44"W). These two streams were at 1627m and 1853m elevation respectively. The site on Bonita Creek is known as the Shake Spring. A seonc site on Bonita Creek was used after the East Whitetail Creek flow stopped on 31 March. The precipitation and stream flow (Table 1) indicate the paucity of water available for this aquatic habitat. Twenty samples were taken between 9 March, 1993 and 15 April 1993. Specimens were aspirated from the inside of the trap and preserved in 70% ethanol. The samples were then returned to Penn State in Erie, PA for sorting and identification. Merritt & Cummins, 1984; Stewart et al 1974) Representative specimens have been deposited at the Chiricahua National Monument.

The Chiricahua National Monument is located in the Southeast corner of Arizona on a tract of 11,985 acres. It was created out of ash from a volcanic explosion some 27 million years ago. The Chiricahua mountains stand at the crossroads of the southern Rocky mountains, the northern Sierra Madre, the Chihuahuan Desert to the east and the Sonoran Desert to the west. Surrounded by deserts and grasslands this "sky island" is the repository of plant and animal species that have retreated to their highlands in the face of gradual climatic change. It is home to plant and animal species more commonly found in Mexico and Central America.

RESULTS AND DISCUSSION

Biotic inventories have not been done for numerous groups and especially aquatic insects. (Stohlgren & Quinn, 1992) Aquatic organisms lead a precarious existence in this habitat and often

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have unique adaptions. The riparian zone may be barren land or in some desert areas composed of tamarisk, willows, cottonwoods, rabbitbrush, sagebrush, mesquite and a variety of low-lying shrubs. Stress of this environment include fluctuating water temperatures, shifting stream substrates, stream bank instability, flash flooding, low water quality and severe, periodic drying up of the water resource or habitat.

One behavioral mechanism for survival is that organisms burrow into the substrate and down into the groundwater areas during periods of surface dewatering. Long slender gills of some organisms add to the interface keeping gills free while burrowing through the sand allowing organisms to obtain oxygen from the water in this habitat and not smoother. Some organisms have strong spines on the head and strong shortened legs which act as tools for breaking up the plating of the benthos and substrate.

Eighteen families of aquatic insects from six orders including 28 taxa were present in approximately 800 specimens collected. (Table 2) Several species collected were uncommon. The life histories of most of these insects are potentially quite unique due to the lack of flowing water for an extended period. Descriptions of the various orders collected follows.

PLECOPTERA (STONEFLIES) emerge as adults in the winter during annual periods of little rainfall and during a time when scouring flash floods do not occur. Mature nymphs crawl up on the edge of the bank, shed their exuviae. and the adult winged form emerges. Adults mate and lay eggs. Eggs hatch before spring run-off and the nymphs burrow down into the sand and are not seen in stream samples until the following winter. (Sagent et al. 1991)

In this study the stoneflies were one of the most abundant insects collected and all from the family Capniidae. *Mesocapnia arizonensis* had 18 males and 33 females at Bonita Creek while at East Whitetail Creek 5 females were collected.

Table 1.—PRECIPITATION in inches measured at the Visitors Center in 1992.

Jan	1.32	Jul	4.14
Feb	0.88	Aug	4.63
Mar	1.14	Sep	1.63
Apr	0.44	Oct	0.76
May	0.18	Nov	0.69
Jun	0.68	Dec	1.31

STREAM FLOW measured in Bonita Creek

1989 - No flow this calendar year.
1990 - Some flow but the amount not recorded, probably minimal.
1991 - 3.0 cm flow 6 Jan.
  4.0 cm flow 4 April
  Some flow last 2 weeks of Dec. but not recorded.
1992 - Flow during the whole month of January but not recorded.
  4.0 cm flow 5 Feb.
  0.5 cm flow 25 Aug.
  0.5 cm flow 2 Sept.
1993 - 5.5 cm flow 8 Jan.
  9.5 cm flow 11 Jan.
  8.5 cm flow 22 Jan.
  10.0 cm flow 29 Jan.
  6.0 cm flow 5 Feb.
  6.5 cm flow 11 Feb.
  5.0 cm flow 19 Feb.
  9.1 cm flow 24 Feb.
  6.1 cm. flow 3 Mar.

Table 2.—Aquatic Insects of Chiricahua National Monument Spring 1993.

- **DIPTERA**
  - **Chironomidae**
    - *Cricotopus* sp.
    - *Orthocladius* sp.
  - **Ceratopogonidae**
  - **Dixidae**
  - **Empididae**
    - *Neoplasta* sp. ?
  - **Psychodidae**
  - **Simuliidae**
    - *Prosimulium imposter* Peterson
    - *Simulium hecti* Vargas, Martinez-Palcios & Diaznajera
  - **Bibionidae**
  - **Ephydridae**
  - **Sciaridae**
  - **Dolichopodidae**
  - **Tipulidae**
    - *Dicranota (Rhaphidolabis)* sp. 1
    - *Dicranota (Rhaphidolabis)* sp. 2
- **EPHEMEROPTERA**
  - **Baetidae**
    - *Fallceon (Baetis) quilleri* (Dodds)
    - *Baetis* sp
    - *Baetis tricaudatus* Dodds
    - *Callibaetis* sp *americanus* or *pictus*
- **MEGALOPTERA**
  - **Corydalidae**
    - *Neohermes* sp
- **ODONATA**
  - **Coenagrionidae**
    - *Argia* sp
- **PLECOPTERA**
  - **Capniidae**
    - *Mesocapnia arizonensis* (Baumann & Gaufin)
    - *Capnia californica* Claassen
- **HEMIPTERA**
  - **Gerridae**
    - *Aquarius remigis* (Say)
  - **Belostomatidae**
    - *Belostoma* sp. or *Abedus* sp.
  - **Veliidae**
    - *Microvelia beameri* McKinstry

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Capnia californica had 4 males and 7 females at Bonita Creek and 9 males and 9 females were collected at East Whitetail Creek. *Mesocapnia arizonensis* is known only from Arizona at elevations of 2000-5000 feet occurring in intermittent streams which dry up during the summer months. Baumann and Gauffin (1970) state that this species emerges in the spring from February to April. Sargent et al. (1991) refer to the genus *Mesocapnia* as tolerant of high mountain streams to lowland streams that are still relatively unperturbed. It may, in this habitat have a fast univoltine life cycle with a summer diapause. *Capnia* is probably similar in its life cycle. The Capniidae function as shredder-detritovores.

EPHEMEROPTERA (MAYFLIES) are common in streams subjected to temporary stress periods. Following a period of stress, small mayfly nymphs tend to reinhabit a stressed area by free-floating downstream from calmer water areas upstream from stress. They have an extremely high reproductive potential. The Baetidae function as collector-gatherers and scrapers feeding on detritus and diatoms in the nymphal stage.

In this study at least 3 species were present. All 25 specimens were collected from the Shake Spring area of Bonita Creek. *Baetis tricaudatus* adults emerge throughout the year. Females crawl under water collapsing the wings onto or alongside the abdomen. Time required for nymphs to mature varies with the area and species. Subimago stage lasts from 7-12 hours. Mating flights take place 6-15 feet over the stream bank in late afternoon or early evening. **CHIRONOMIDAE (midges) DIPTERA**, drift away from a stressed area and reinhabit new areas downstream. Larvae of some species tend to burrow down into the sand and may even spin silken linings to the their burrows.

In this study over 700 adult midges were collected from Bonita Creek with only 33 collected from East Whitetail Creek. At present all specimens appear to be in two genera, *Cricotopus* spp. and *Orthocladius* spp. These species are Orthocladiini with the first genus functioning as a shredder, collector-gatherer as does the latter genus feeding on detritus and algae. **SIMULIIDAE (blackflies) DIPTERA**, may also be present in large numbers, usually on stable substrate such as rock outcrops, fallen logs or vegetation in the streambed. Larvae spin a small net on an object in the direct stream current. Only 3 adults were collected during this study but large numbers of larvae were observed in the stream. Blackflies function as collector-filterers.

TIPULIDAE (craneflies) DIPTERA were collected only at Shake Spring of Bonita Creek with 11 specimens all females. The genus *Dicranota* is in the subfamily Limoniinae and functions as a predator. These craneflies have a brief egg stage and 4 larval stages and a pupal stage that lasts 5-12 days. The entire life cycle may be as short as 6 weeks or as long as 5 years. It would be of interest to know what type of life cycle exists in this habitat.

OTHER DIPTERA (CERATOPOGONIDAE, DIXIDAE, EMPIDIDAE, SCIARIDAE, DOLICHOPODIDAE, BIBIONIDAE, EPHYDRIDAE & PSYCHODIDAE). The biting midges (Ceratopogonidae) were collected only at Bonita Creek, as were the Dixids, dance flies, dark-winged fungus gnats, long-legged flies, March flies, shoreflies, and moth flies. The Ceratopogonidae, Dolichopodidae, and Empididae function as predators. The Dixidae and Psychodidae are collector-gatherers. The Ephydridae may be a shredder. The Bibionidae were an interesting part of the fauna that have been reported to feed on decaying vegetable matter and their presence in an aquatic situation should be further studied. Sciaridae probably are feeding on decaying plant material. **MEGALOPTERA (dobsonflies)**, of the genus *Corydalis* can live successfully in a desert habitat. The life cycle may take 2-3 years to complete. Larvae are hardy and robust so they withstand considerable environmental buffeting and avoid stress by burrowing into substrate and may crawl into pools or under rocks. I believe that the genus *Neohermes* collected during this study has similar features. This genus functions as a predator.

HEMIPTERA (WATER STRIDERS, GIANT WATER BUGS & BROAD-SHOULDERED WATER STRIDERS) Water striders (Gerridae) burrow in the mud or under stones or hibernate when the streams dry up. These insects are unspecialized predators feeding primarily on other insects. The giant water bugs (Belostomatidae) have raptorial front legs that function very effectively as predators. The broad-shouldered water striders also function as predators feeding on both live and dead arthropods.

ODONATA (ZYGOPTERA-damselflies), COENAGRIONIDAE were common at the Shake Spring site on Bonita Creek. *Argia*, the genus present is a predator.

TRICHOPTERA (caddisflies) were not collected as adults but larval cases were observed in the stream. It is surprising that no adult specimens were collected.

At present I am not aware of what happens to these insects during the approximately 9 months when no surface water is present, but there could be subsurface water available. Some of these insects undoubtedly have long periods of dormant stages but it is not apparent at what stage in their life cycle this occurs. Future studies should include sampling of the subsurface areas and periodic sampling to determine the presence of the various life stages throughout the year. Fisher and Gray (1983) reported that most aquatic insects of Sycamore Creek and other Sonoran Desert streams are multivoltine, producing several generations annually.

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Restoration Alternatives for Mexico's Sky Islands: Examples from Guatemalan Forestry

R. Phillips[1], J.G. Mexal[2], and R. Beltranena-Orive[3]

Abstract.—Guatemala is the most populous country in Central America and 63% of the energy consumption is fuelwood. However, land clearing for shifting agriculture, timber harvest, and cattle production have resulted in fuelwood scarcities. Thus, a large percentage of labor and income are devoted to fuelwood gathering. Since 1960, over 48% of the forest has been lost. Without successful management and alternatives to current practices, less than 2% of the original forest will remain by 2010.

The government of Guatemala has entered into a limited but successful partnership with the private sector to reforest many areas. The Guatemala Forestry Law of 1979 which has a fiscal incentive (FI) provision has not only reforested thousands of hectares, but has also provided a viable alternative to continued harvesting of the native forest.

The FI program of Guatemala could be a model for the management of the Sky Islands. Guatemala's successful reforestation programs are: a) restoring deforested sites, b) providing employment, and c) creating alternatives to continued cutting of native forests. Case studies will be examined which represent distinct ecosystems, using both native and exotic tree species, and producing multiple wood products. The environmental, social, and economic benefits of these programs will be discussed in the context of applying these principals to the Sky Islands.

BACKGROUND ON MEXICO

Mexico is the fifth largest country in the Americas and the third most populous. The population is estimated at over 85,000,000 with as many as 30% still living in rural communities (Sharma, 1992). Furthermore, the growth rate is 2.1%, ensuring increasing demands on natural resources. These demands have resulted in serious degradation of native forests over the last four decades (Anon., 1994). Approximately 25% of the landbase of Mexico, or 55,000,000 ha, is classified as forest land. The state of Chihuahua contains 24% of these forests. Since 1960, 30% of the forests in Mexico have been lost. This amounts to 370,000 ha deforested per year. These losses in forests have been attributed to shifting agriculture, illegal harvesting of timber, and forest fires. As a consequence of the deforestation in Mexico, production of forest products has declined 29% since 1989 (fig. 1). Continued demand for wood products will increase the rate of deforestation, threaten the livelihood of indigenous communities, and increase migration to the cities of Mexico and the United States.

The reforestation program in Mexico has been slow to respond to this deforestation. From 1983 to 1988 the reforestation program averaged 42,000 ha/yr. In 1992 and 1993 over 210,000 ha were reforested. While this is a substantial improvement in reforested lands, it does not equal the amount of land deforested nor does it attempt to reclaim the land lost to deforestation over the last four decades. In 1993, the federal government of Mexico developed 23 new nurseries on military reservations. These nurseries produced 123,000,000 seedlings in 1994. These trees are used for reforestation, restoration of disturbed lands, and urban planting programs. However, few attempts to involve industry in reforestation

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programs have been made. Thus, the majority of reforestation activities are either state or federal programs.

BACKGROUND ON GUATEMALA

Guatemala is the third largest country in Central America. With a current population of 10,500,000 people, and a growth rate of 3.3% that will double the population in approximately 22 years (Cooley et al,, 1981), Guatemala is faced with serious demands on limited resources. Agricultural employment, including forestry, accounts for 60% of the employed labor force. The unemployment rate is 6.5%, but underemployment is 30-40% (Anon., 1993a). Much of the population relies on the forest for fuelwood needs. In fact, fuelwood represents 63% of the energy consumption of the country. However, land clearing for agriculture, timber, and cattle production has resulted in fuelwood scarcities.

While Guatemala has the most diverse forest in Central America, with 16 species of conifers and 450 species of broadleaf trees (Cooley et al., 1981), it is quickly depleting these valuable resources. Currently, 71% of the native forest has been lost, and it is estimated that less than 2% of the original forest will remain by 2010 without serious intervention (Anon., 1993c). Serious erosion and flooding have accompanied the destruction of Guatemala's forest. The 125 megawatt hydroelectric plant at Chixoy is threatened by siltation; and the flow of the Rio Motogua, a major river in Guatemala, has been reduced by one-half in the last 20 years due to deforestation (Cooley et al., 1981).

In an attempt to reverse these destructive land use practices, the Guatemalan government enacted the Forestry Law of 1979. This law provides a mechanism for establishing a partnership between the Guatemalan government and the private sector in reforestation. Specifically, the Guatemalan Forestry Law provides financial incentives to encourage reforestation. The fiscal incentive law (FI) provides tax rebates over 5 years to cover the first year establishment costs, and the succeeding 4 years plantation management costs. The program currently funds up to 5,000 ha/yr, but less than 1400 ha have been reforested each year. This level of activity is too small to totally reforest the areas cleared for cattle and shifting agriculture. However, the model is very promising, and may have application in other countries.

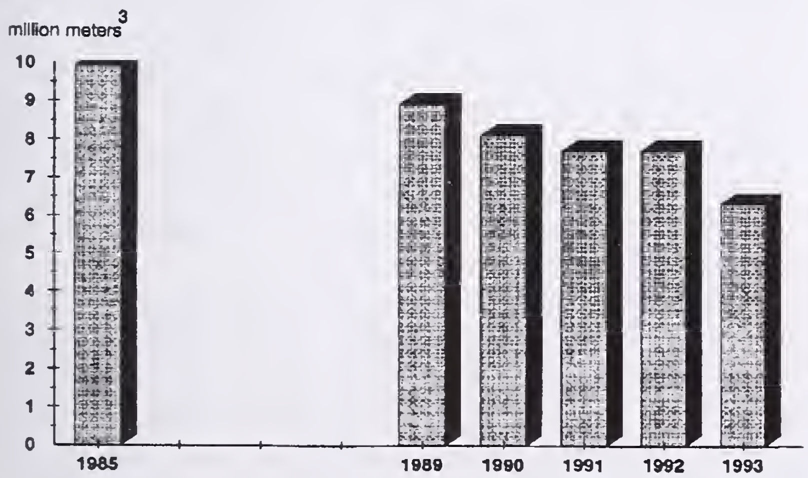

Figure 1.—Changes in harvested roundwood (million cubic meters) in Mexico since 1985 (Anon. 1993).

This government/private sector partnership has resulted in the formation of new reforestation companies (Table 1). Many of these companies are subsidiaries of large Guatemalan corporations. These companies have access to professional specialists and they utilize the organizational skill and financial resources of the parent company to successfully manage their reforestation activities. Since 1979, these reforestation companies have planted over 13,190 ha (fig. 2), requiring an investment exceeding $12,000,000.

The reforestation companies provide technical services to the landowner to ensure successful establishment and management of these plantations. A unique and positive feature of this law is that third parties can invest in reforestation without owning the land. The reforestation company can arrange an agreement between willing landowners and private companies to invest in establishing plantations. The investor provides the funds and receives the tax credits in addition to the favorable publicity associated with successful reforestation. Oversite responsibilities for plantation success and fiscal accountability rest with DIGBOS (Dirección General de Bosque) the Guatemalan forest resource management agency.

REFORESTATION CASE STUDIES

Three examples will be given to illustrate the effectiveness of this program to bring about successful reforestation in Guatemala. AGROBOSQUE is a subsidiary of Cementos Progreso, S.A., one of Guatemala's largest industries. Agrobosque was formed in 1985 with the objective of promoting reforestation by establishing plantations and educating the general public about the need to protect and manage the country's forest resources.

AGROBOSQUE has planted over 1,200 ha across a wide range of sites in the dry region of Guatemala. These sites are characterized by dry, rocky, calcareous soils. The topography is mountainous, the elevation ranges from 760 to 1048 masl and the precipitation is 500 - 1000 mm/yr. AGROBOSQUE has conducted suitability studies with 18 species including; *Eucalyptus, Melia, Pinus, Gmelina,* and *Leucaena*. The most promising species to date is *Eucalyptus camaldulensis*.

AGROBOSQUE has established fuelwood plantations near the primary cement production facility. Cementos Progreso plans to utilize the fuelwood as a substitute for bunker oil for its drying ovens. Their research indicates that 1 m^3 of fuelwood can offset the need for 150 liters of imported bunker oil. They estimate it will require 200-400 ha to produce 40% of the energy required by the cement factory.

AGROBOSQUE also has developed a public education program on the importance of forest resources for Guatemala. Since 1992, Agrobosque has visited 34 schools and conducted environmental and reforestation awareness programs for over 3,200 students. They also have met with 30 communities and 342 community leaders. As part of the community education program, they have donated 150,000 seedlings.

The second example of the FI program is FORESA. FORESA is a subsidiary of Licores de Guatemala, Guatemala's largest distiller, and employs 2,400 people in reforestation efforts (Anon., 1993b). FORESA has reforested over 3,000 ha. It concentrates much of its reforestation efforts on land that had previously been forested but had been cutover to establish pastures for cattle production. These sites are in eastern Guatemala where rainfall averages 850 mm/yr. FORESA has both container and bareroot nurseries producing 250,000 seedlings/yr for reforestation. The major species that they plant are *Pinus caribaea* and *Cupressus lusitanica*. Their objective is to produce saw timber.

Table 1.—Reforestation companies formed in Guatemala as a result of the Fiscal Incentive (FI) law.

Company	Parent Company	Reforested Land (ha)
AFOREST	Polla Campero	1,474
AGROBOSQUE, S. A.	Cementos Progreso	1,218
AGROFOREST	Avon-Colgate-Mixto Listo	1,479
CODEMA	Almacenes Paiz	550
EDCOFIASA	F.P.K. Electronics	250
FORESA	Licoreras de Guatemala	4,125
LA PARADA, S.A.	Bloteca, S.A.	322
MAYA-IZABAL	Marítimas Int'l	200
REFORESTADORA IND.	Cervecería	2,975
REFORVERAPAZ	Agro Industrias Canarias	225

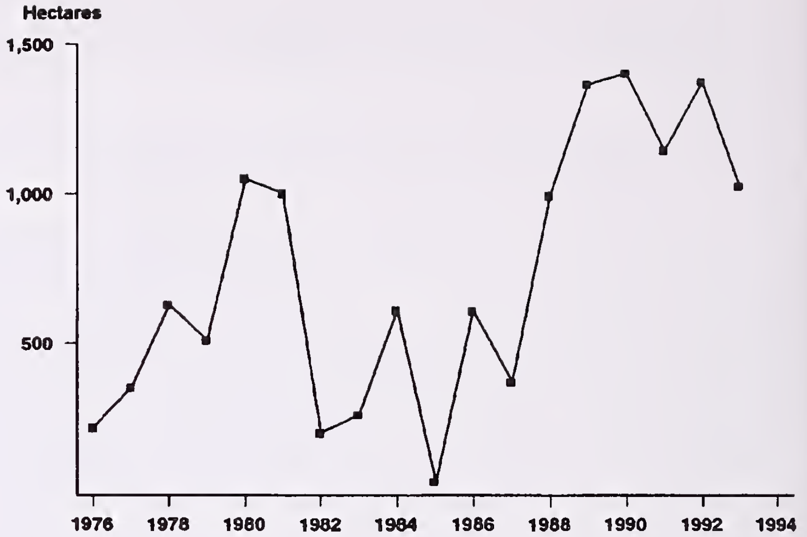

Figure 2.—Annual reforestation in Guatemala under the FI program.

Another positive example of the FI program is AFOREST, which is owned by Pollo Campero, Guatemala's equivalent to Kentucky Fried Chicken. AFOREST is working in the Rio Dulce region of Guatemala. This region, near the Gulf of Honduras, is characterized by high rainfall (4,000 mm/yr). Much of the rainforest that originally dominated the land has been cut for pastures and cattle production. AFOREST has embarked on an aggressive plantation program with *Pinus caribaea*, reforesting 1,500 ha. The major objective is aimed primarily at producing raw material for particle board production in Guatemala City.

These examples of Guatemala's reforestation efforts exemplify the possibilities of constructive partnerships between private industry and the government. Numerous other examples exist where reforestation efforts are being conducted in conjunction with local needs. While some of these programs do not qualify for the FI program, they do illustrate positive efforts in reforestation and an atmosphere of cooperation between industry and the federal government. One example is intercropping subsistence crops such as corn, beans and squash, during the first 2 years of a *Pinus tecunumanii* plantation. This technique provides food and income for the land tenant, and weed control and successful plantation establishment for the reforestation company.

Another positive example involves Simpson Paper Company's investment in fiber plantations in eastern Guatemala. This once richly forested region has been extensively deforested for cattle production. Simpson is working with the Guatemalan government and landowners to establish fiber plantations on depleted cattle pastures. This labor intensive project is providing jobs and needed economic growth and at the same time re-establishing the land in a forest resource.

IMPLICATIONS

Reforestation companies in Guatemala rely extensively on local labor to produce the plants, prepare the sites, plant, weed, prune, and harvest these plantations. These programs represent a major source of employment within an economically depressed region. This labor amounts to 230 days per hectare per year in Guatemala (Reiche et al., 1991). The economic value of this work is $500/ha/yr. Reforestation activities require 0.6 laborers/ha/yr compared to 0.002 laborers/ha/yr for cattle production in this region (Rankin, 1994). Production income varies greatly, with cattle production earning $40/ha/yr verses fiber plantation earnings of $140/ha/yr. Therefore, these activities represent a significant source of employment for a country that has 30-40% underemployment (Anon., 1993a). Expanding the program would not only provide employment for a broad sector of the population, but would also provide needed wood and delay harvest of native forests.

The Guatemalan government has adopted a strategy for reforestation that includes the private sector as a major participant. The private sector has quickly responded to the economic and public relations benefits offered by being associated with this program. The results have been increased and improved reforestation activities, the establishment of new sources of employment in rural areas of the country, and greater public awareness of the importance of forest resources. The Guatemalan model of cooperation should be evaluated throughout Latin America. Similar programs have been successful in Costa Rica and Chile. These programs contribute to the protection of the remaining forests, while simultaneously addressing the growing need for fuel, fiber, timber and other forest benefits. Programs such as these could be useful in Mexico, assuring reforestation of lands and preserving rural communities and indigenous cultures.

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Ecological Conditions in the Overlap Areas of the Pinyon-Juniper and Encinal Woodlands

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Abstract.—Overlap areas between pinyon-juniper and encinal woodlands were evaluated in terms of selected physiographic and vegetative variables at three sites in southeastern Arizona. There were more plots with very stony surfaces in the overlap areas than in either woodland, except for the San Rafael Valley pinyon-juniper woodland where the relationship was not significant. Soil pH was higher in the pinyon-juniper woodlands than soil pH in the encinal woodlands. Studies on the role of soil nutrients, fuelwood cutting, and other factors that might relate to the occurrence of overlap areas between pinyon-juniper and encinal woodlands are needed.

INTRODUCTION

Pinyon-juniper and encinal woodlands are an important natural resource in the southwestern United States and northern Mexico. Not only do the woodlands hold commercial and wildlife values, but they also have cultural, recreational, and aesthetic values important to contemporary society (Propper 1992). In southeastern Arizona, there is growing concern that pinyon-juniper woodlands are encroaching into the more commercially valuable encinal woodlands. A lack of information about the overlap area between the two woodland types limits our understanding of the ecological relationships between them. Relevant baseline data that reflect a variety of existing conditions could be used to predict stand changes on specific sites.

The objectives of this study were to:

1. Describe the overlap area by comparing the characteristics of the overlap area with those of adjacent pinyon-juniper and encinal woodland types. Characteristics included were slope and aspect, and soil characteristics such as surface stoniness, amount of coarse fragments, and pH.
2. Relate the occurrence of overstory trees and regeneration patterns in the overlap area to the physiographic and soil variables, and then compare significant relationships to those of the adjacent pinyon-juniper and encinal woodland types.

STUDY SITES

Three study sites were located within the Coronado National Forest of southeastern Arizona: the San Rafael Valley near Sierra Vista, the Canelo Hills near Sonoita, and Cave Creek on the eastern slopes of the Santa Rita Mountains. The sites were selected for study on the bases of similar vegetative and physiographic features. The main overstory species at the study sites were Emory oak (*Quercus emoryi*), alligator juniper (*Juniperus deppeana*), and border pinyon (*Pinus discolor*). Silver leaf oak (*Quercus hypoleucoides*) was found in some areas of Canelo Hills and Cave Creek, while manzanita (*Arctostaphylos pungens*) was present on all of the study sites.

METHODOLOGY

Tenth-acre sample plots were established from a baseline at each study site. These temporary plots were laid out at random distances from each other along parallel transects that traversed the encinal, overlap, and pinyon-juniper areas. The lengths of the transects varied, depending upon the composition of the vegetation. The distribution of sample plots is shown in table 1.

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Slope and aspect were combined into a single potential solar beam irradiation variable (Frank and Lee 1966); surface stoniness of the plots was described by three classes (not stony, stony, and very stony). Basal area of the overstory was measured by point sampling techniques (Avery and Burkhart 1994).

Basal area was used to determine whether a plot was located in the overlap area, encinal, or pinyon-juniper woodland. If a plot had at least 80 percent basal area of oak or pinyon and juniper, it was considered to be located in that woodland; otherwise, the plot was considered to be in the overlap area. Diameter at root collar (drc) in inches and total height in feet of "in" trees were measured to generate number of trees and volume per acre (cubic feet) estimates. Chojnacky's (1988) equations were used in the estimation of volumes.

A cluster of five one-mil-acre plots was established on each 1/10-acre plot to sample the soil coarse fragments (percent volume) and soil pH at 0 to 6 and 6 to 12 inches depth; soil samples from each of the five one-mil-acre plots at a sampling point were composited (Black 1965) by depth. Regeneration was measured on the one-mil-acre plots in terms of stem counts (per acre) and number of stocked plots. Only sample plots that showed no signs of fuelwood harvests were included for the regeneration analysis. The distribution of the one-mil-acre plots on which regeneration was measured is presented also in table 1.

Tukey's multiple comparison test (Norusis 1991) was used to determine whether overlap areas, pinyon-juniper, and encinal woodlands differed in terms of potential solar beam irradiation, amount of soil coarse fragments, and soil pH. Chi-square tests were used to relate soil surface stoniness to the overlap areas, pinyon-juniper, and encinal woodlands. The counts of the number of 1/10-acre plots were examined by soil surface stoniness class in relation to the overlap area and the adjacent woodlands. Simple regression analysis was used to relate the physiographic measurements with overstory and regeneration measurements; these relationships were compared to determine whether site conditions differed between the overlap areas and adjacent woodlands. All statistical tests were evaluated at a significance level of 10 percent.

Table 1.—Distribution of the number of sample plots among the encinal, overlap, and pinyon-juniper areas by study site.

Study Site	Overlap Area	Encinal Woodland	Pinyon-Juniper Woodland
	Number of Sample Plots		
Distribution of tenth-acre sample plots			
San Rafael Valley	74	41	50
Canelo Hills	78	36	32
Cave Creek	43	33	44
Distribution of one-mil-acre plots on which regeneration was measured			
San Rafael Valley	29	21	16
Canelo Hills	13	7	5
Cave Creek	18	11	7

RESULTS AND DISCUSSION

There was no trend detected among the study sites regarding potential solar beam irradiation values in the overlap area, pinyon-juniper, and encinal woodlands.

Chi-square tests revealed that there were more of the very stony plots in the overlap areas compared to those in the encinal areas (Table 2). With the exception of the San Rafael Valley study site where there was no difference, there also were more very stony plots found in the overlap area than in the pinyon-juniper areas. Other relationships between the overstory conditions and soil surface stoniness, when significant, were site-specific. Therefore, no general trends were evident.

The amount of soil coarse fragments and soil pH at depths of 0 to 6 and 6 to 12 inches varied among the study sites in the overlap areas as compared with those in the encinal and pinyon-juniper woodlands. No consistent trend

Table 2.—Distribution of the number of 1/10-acre sample plots, by stoniness classes, among the encinal, overlap, and pinyon-juniper areas by study site.

	Stoniness Class			
Site	Not Stony	Stony	Very Stony	TOTAL
San Rafael Valley				
Encinal	27a,x	8a,y	6a,y	41
Overlap	26a,x	34b,x	14b,y	74
Pinyon-Juniper	21a,x	21c,x	8ab,y	50
TOTAL	74	63	28	165
Canelo Hills				
Encinal	17a,x	11a,x	8a,y	36
Overlap	7b,x	34b,y	37b,y	78
Pinyon-Juniper	1c,x	12a,y	19c,y	32
TOTAL	25	57	19	146
Cave Creek				
Encinal	11a,x	14a,x	8a,x	33
Overlap	4b,x	15a,y	24b,y	43
Pinyon-Juniper	22c,x	12a,y	10c,y	44
TOTAL	37	41	42	120

Numbers with same letters (a,b,c for columns within a site; x,y,z for rows) are not significantly different (,=0.10).

among the study sites was observed in terms of the relationship between these variables and the occurrences of overlap areas, pinyon-juniper, and encinal woodlands. However, the results of the analyses revealed that soil pH values in pinyon-juniper woodlands were less acidic than those in encinal woodlands.

Neither the overstory density measurements (basal area, number of trees, and volume) nor the regeneration measurements (counts and stocking) of pinyon-juniper and oak were related consistently with the physiographic factors among the overlap area, pinyon-juniper, and encinal woodlands. The variety of relationships between vegetation and physiographic factors suggested that ecological conditions within each of the study sites were unique.

CONCLUSIONS

Soil surface stoniness was the only variable that showed consistent relationships among the overlap areas, pinyon-juniper, and encinal woodlands. Overlap areas had more 1/10-acre plots with very stony surfaces than those of encinal woodlands. Physiography-vegetation variables showed no consistent relationships. Thus, soil surface stoniness and other soil features, perhaps in combination, could influence the occurrences of overlap areas, pinyon-juniper, and encinal woodlands. Studies on the role of soil nutrients, fuelwood cutting, and other factors that might affect the occurrence of overlap areas between pinyon-juniper and encinal woodlands are needed.

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Land in the Balance: A Guide to Ecosystem Management

(Viewer's Guide to Land in the Balance)

George Ruyle[1], Lynn Ketchem[2], Jennifer Ruyle[3], and Jeanne Wade[3]

INTRODUCTION

The Sierra Vista Ranger District of the Coronado National Forest, located in Southeastern Arizona, has initiated an ecosystem management demonstration project. The Lone Mountain/Redrock Canyon Ecosystem Management Area encompasses an area of 130,000 acres, stretching from crest of the Huachuca Mountains on the north to the border of Mexico, and from Montezuma Pass on the east to the Patagonia Mountains on the west. This area has several unique vegetation communities, including madrean oak woodland and plains grassland. There are a number of rare plant and animal species that inhabit the area. The headwaters of two important rivers, the San Pedro and the Santa Cruz, are within the management area boundaries. In addition, the area surrounds one of the largest parcels of privately owned land in Arizona, along with a number of smaller private inholdings. The rural lifestyle of the residents on these lands, defined mainly by cattle production, has been a major contributing factor to the maintenance of open space and the undeveloped appearance of the landscape.

In order to articulate what ecosystem management is and what it means to the local community and other interested people, a video, entitled LAND IN THE BALANCE, was produced by the University of Arizona School of Renewable Natural Resources and the Sierra Vista Ranger District. The primary purpose of the video is to introduce the concept of ecosystem management to the people in the communities involved with the Lone Mountain/Redrock Canyon Ecosystem Management Area. The video includes interviews with various people from the local community, the University of Arizona, the Nature Conservancy, the Santa Cruz county planning and zoning commission, the local Natural Resource Conservation Districts, and the U.S. Forest Service.

Land in the Balance introduces viewers to a road map for the future of this picturesque and biologically diverse region. The Sierra Vista Ranger District and the people who live and work in the Lone Mountain-San Rafael communities have embarked on an exciting and dynamic partnership in the process of developing ecosystem management. In this 20-minute videotape, area residents shared their thoughts about this different approach to land management. And they express their concerns about the future, as they work towards an ecosystem management plan.

Land in the Balance illustrates how the Forest Service is evolving as a land steward. The program also helps viewers understand some key points of ecosystem management: the emphasis on the whole environment of a landscape or a watershed, rather than the individual parts; the critical role of community partnerships; and the integration of current science and technology.

ECOSYSTEM MANAGEMENT BASICS

Rather than a well defined set of practices or an exact science, ecosystem management is a philosophy and an ongoing process that considers individual issues and emphasizes broad objectives. The concept follows four basic principles:

1) Take care of the land.
2) Consider the people of the community.
3) Use resources wisely and efficiently.
4) Strive for balance, equity and harmony between people and land.

DESIRED FUTURE CONDITION

Critical to successful ecosystem management is an agreed upon "desired future condition" for an entire landscape or watershed. This collective picture serves as a guide to management deci-

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[1] University of Arizona

[2] Oregon State University

[3] Coronado National Forest, U.S.F.S.

sions. As communities look to where they want to go, they'll test actions against that picture.

MAJOR COMPONENTS OF A DESIRED FUTURE CONDITION

1) Description and understanding of the land/biological capabilities.
2) Clarification of people's expectations.
3) Understanding costs, benefits, risks and trade-offs.
4) Defining immediate needs of the area driven by present concerns.
5) Recognizing past and present individual and community life-styles.

ROLE OF PARTNERSHIPS

Ecosystem management relies on the willingness of people to communicate, to be actively involved and cooperate on shared visions. Establishing conservation partnerships with communities, agencies, organizations, local government and scientists is a vital aspect of ecosystem management.

POINTS TO REMEMBER

1) Sustain diversity.
2) Work within biological limitations.
3) Look at broad scales (in terms of both time and place).
4) Focus on the end results (desired future condition).
5) Coordinate on common issues.
6) Encourage people to participate.
7) Integrate information.
8) Adapt to change: manage-monitor-research-adapt.

Seed Bank and Tree Fall Gaps in a Mexican Temperate Forest

Carmen Mercado and Laura Arriaga[1]

INTRODUCTION

The southern portion of the peninsula of Baja California Sur bears an oak-pine forest, restricted to the highlands of the mountain range locally called as Sierra de la Laguna, which represents the southwestern limit of the Sierra Laguna component of the Sierra Madrean Woodland Element as part of the Flora Madrotertiary.

This forest presents treefall gaps that are created by three main types of death: dead standing trees (DST), snapped off trees (SNT) and uprooted trees (UPT). When a canopy gap is created, there are changes in the understory. These changes are initially in light, soil moisture, relative humidity, and temperature. Besides this, the type of death, gap area, and severity of disturbance, determine the gap regeneration strategies. The principal aim of this work is to determine the regeneration potential from seed bank in gaps created by these three types of death.

STUDY SITE

The pine-oak forest of Baja California Sur is located between 23°21′ and 23° 42′ N, and 109° 46′ and 110° 10′ W, in the upper woodlands of the Sierra de la Laguna, at an altitude ranging between 1000 and 2200 m.a.s.l. The climate corresponds to a temperate humid one. The total annual rainfall is 762.3 mm. and the mean monthly temperature is 14.5°C.

Structural dominants are *Quercus devia* and *Pinus lagunae* plus *Arbutus peninsularis* and *Nolina beldingii*. The lower layer includes *Calliandra peninsularis, Helianthus similis, Verbesina pustulata,* and *Lepechinia hastata.*

METHODS

Seven sites were selected within the forest, in order to study the seed bank size and floristic composition. Site selection included six gaps (two for each kind of death) created by Kiko's hurricane which occurred in 1989, as well as a mature forest plot (Table 1). During 1991, soil samples were randomly obtained from these sites for the dry and rainy seasons. Soil samples were moved to laboratory conditions and spread into trays, which were watered periodically. Seedling emergence was recorded daily until no further germination was obtained. Additionally, soil physical-chemical analyses were also carried out.

RESULTS

Floristic Composition

The seed bank is constituted by 21 species belonging to 14 families; Leguminosae, Compositae, Euphorbiaceae, and Labiatae were the most representative ones. Eight species that germinated in both seasons (Table 2) comprise the persistent seed bank, while the remainder are part of the transient one. The primary species of this forest (*Quercus devia, Pinus lagunae* and *Arbutus peninsularis*) were not represented in the bank.

Seed Bank Size

Seed density was highest in the mature forest plot that in gaps (fig. 1). Considering those gaps

Table 1.—Some characteristics of the forest plot and gaps

Sites	Species	Area (m2)	Altitude	Rocky (%)	Slope (o)
Forest	------	300	1750	20	21.5
DST1	P.lagunae	34.6	1850	0	6
DST2	P.lagunae	178.5	1700	0	5
SNT1	Q. devia	160.1	1900	30	22
SNT2	Q. devia	236.3	1950	5	8
UPT1	Q. devia	71.0	1750	10	21
UPT2	Q. devia	581.8	2000	0	7

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[1] *Centro de Investigaciones Biológicas del Noroeste, La Paz, B.C.S., México.*

Table 2.—Floristic composition of the seed bank.

Shared species amongst seed bank and stand vegetation:
- *Acalypha comonduana* *
- *Helianthus similis* *+
- *Calliandra peninsularis* *
- *Lepechinia hastata* +
- *Prunus serotina*

Exclusive species from the seed bank:
- *Arracacia brandegii* *+
- *Behria* sp. *+
- *Cosmos* sp.
- *Cyclanthera tamnoides*
- *Cyperus* sp. +
- *Desmodium prostratum* *
- *Eupatorium purpusii* *
- *Euphorbia lagunensis* *
- *Galium microphyllum* +

- *Lupinus lagunensis* *
- *Peperomia umbilicata* +
- *Phytolacca octandra*
- *Piptochaetium fimbriatum*
- *Stachys coccinea*
- *Tagetes lacera* *+
- Solanaceae (1 sp)

Note: Species with asterisk (*) are endemic from Baja California Sur. (+) denote persistent seed bank components.

created by uprooted trees (UPT) and snapped off trees (SNT), biggest gaps presented lower seedling emergence. The contrary occurred in gaps created by dead standing trees.

Species Richness

Species richness was higher in small gaps than in big ones, considering each type of death. The forest plot supports the highest species richness compared with gaps (fig. 2).

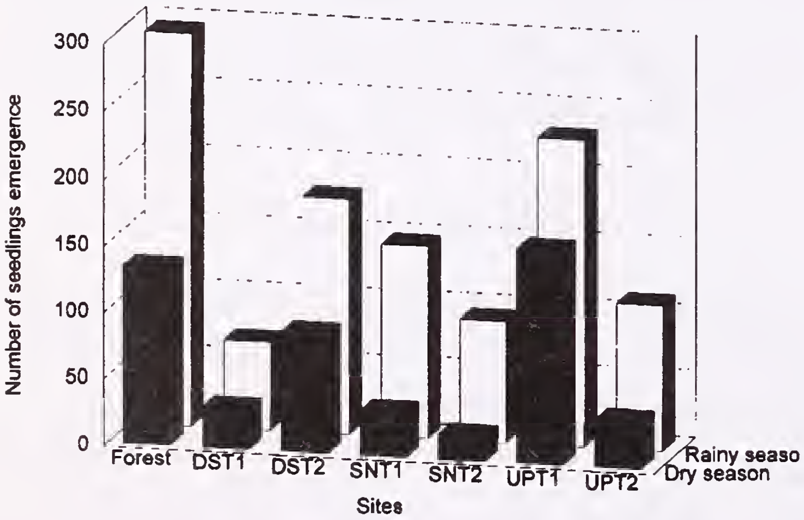

Figure 1.—Seed bank size, considering as the number of germinated seedlings from soil samples.

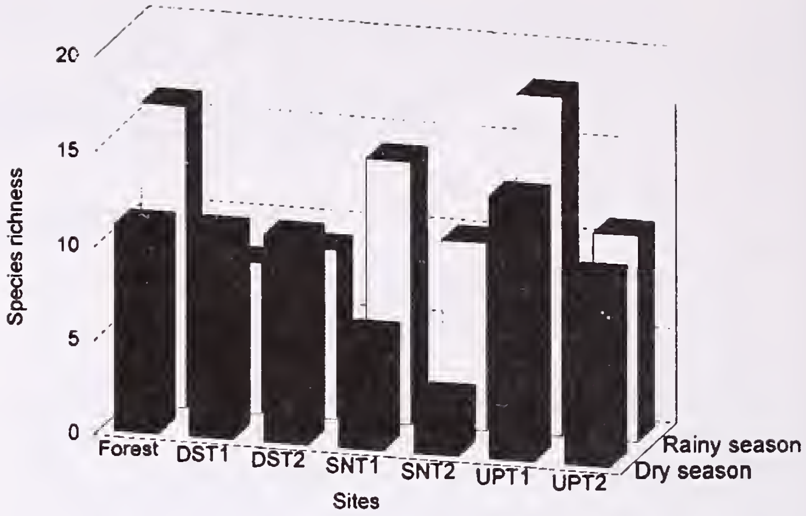

Figure 2.—Species richness in gaps and mature forest plot.

Seasonal Variation

The major number of seedlings germinated in the samples obtained during rainy season, while the contrary ocurred in samples obtained during the dry season (Fig. 3). This result was expected, because of the seasonality of temperate forest.

Soil Analyses

Soil texture is sandy or sandy-loam. Organic matter content was high not only in the forest plot, but also in gaps (higher than to 10% in the first horizon), and pH was acid. Therefore, soil characteristics do not influenced seedling emergency between sites, including forest and gaps.

CONCLUSIONS

The low similarity between buried seeds and floristic composition of the standing vegetation is consistent with other studies. Primary species were not represented in the bank, probably because they regenerate through seedling bank. The seed bank was mainly composed by the shrub and herb layer species with transient seed bank.

The seed bank size and species richness results indicate that gaps created by uprooted trees present the major regeneration potential from the bank. This is because the uprooting process generates pits and mount formation that promote seed removal.

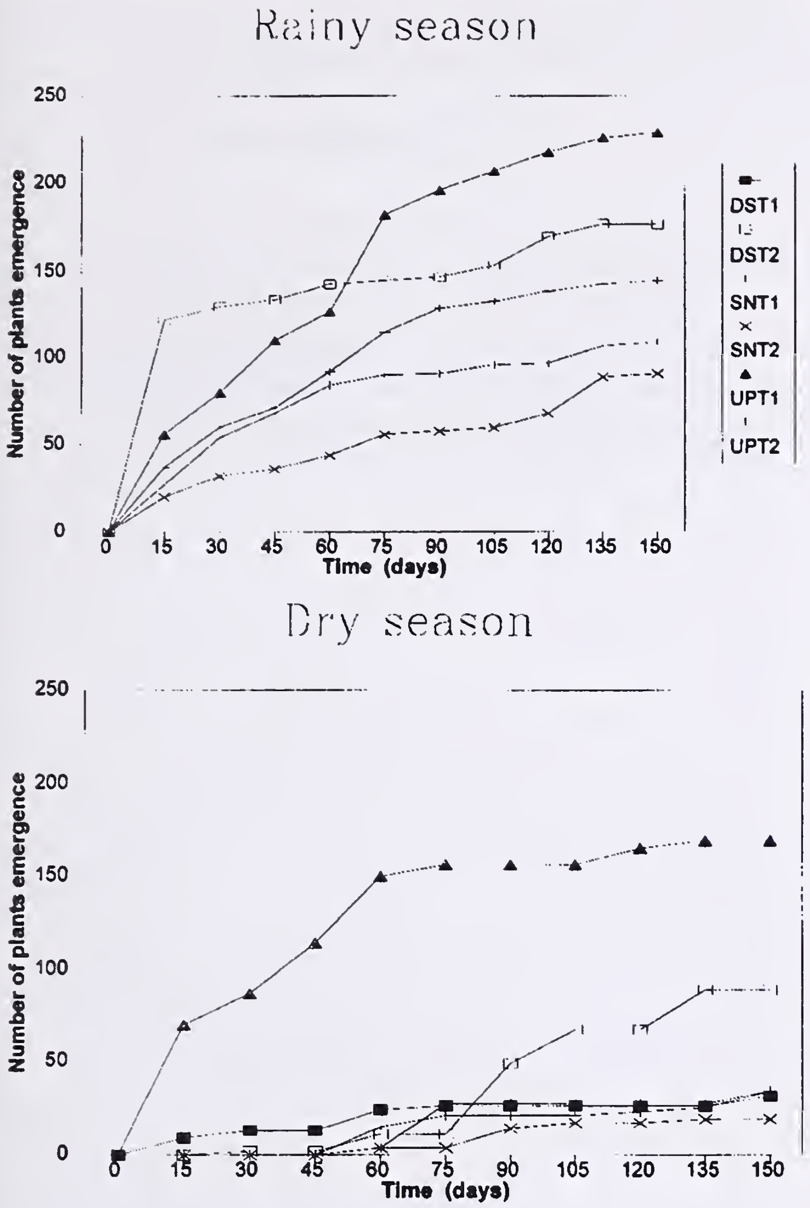

Figure 3.—Temporal variations of the seedlings germination, during dry and rainy seasons.

The Coronado National Forest's Copper Canyon Drainage: A Picture of Biodiversity

William E. Van Pelt[1]

INTRODUCTION

Roughly 10,000 years ago, the southwest resembled a continuous evergreen forest extending hundreds of square miles. However, drier climatic patterns changed this area to more xeric conditions, and eventually, these forests were restricted to the moisture laden mountain ranges creating what is known today as Sky Islands. Many of these mountain ranges straddle the international Mexico-United States border, providing travel corridors as well as suitable habitat for a diverse array of wildlife. Tropical species such jaguarundis and ocelots are at their northern range limits while red squirrels are at their southern range limit. Others, such as the Arizona shrew are restricted to these isolated Sky Islands.

After receiving numerous sighting reports of jaguarundis from the Huachuca Mountain's Copper Canyon drainage, the Nongame and Endangered Wildlife Program (NGEWP) of the Arizona Game and Fish Department (AGFD) initiated efforts to document the presence of this rare feline using remote sensing camera equipment. In addition to camera monitoring, the NGEWP surveyed Copper Canyon for the Arizona shrew (*Sorex arizonae*).

METHODS

A Trailmaster 1500™ remote sensing camera system was installed along the western boundary of the Coronado National Memorial in the Copper Canyon drainage from September 1, 1993 to May 3, 1994. This camera system consists of three parts: an infrared transmitter, a receiver, and an automatic 35-mm camera (Kucera and Barret 1993). The transmitter and receiver were installed along a downed log approximately 1.5 m in length with the beam parallelling the log approximately .09 m above the ground. The beam pulse was set at 0.5 seconds (the amount of time needed for the beam to be broken to count as an event). The camera was strapped to a downed limb located perpendicular to the log at a distance of approximately two meters. The camera was set for a two minute time delay between pictures.

Two types of auditory devices were used to attract wildlife to the remote sensing unit. One unit, the Mini-Squeaker™, resembled the squealing of a wounded rabbit, and the other unit, the Squealing Partner™, sounded like a chirping bird. These two units were re-wired to accept power from a six volt lantern battery. The use of the two attractants were alternated throughout the study.

Pitfall traps used for collecting Arizona shrews consisted of two gallon (7.6 liter) plastic buckets which were buried to the rim. The lids were elevated above the buckets two to five cm, with rocks or woody debris. These pitfalls were placed perpendicular to the water course at distances ranging from 0 to 75 m, and in most cases, were set next to downed logs or limbs.

RESULTS

Although, no jaguarundis were photographed during 244 camera nights, 191 pictures were exposed documenting canyon use by 14 mammalian and four avian species (Appendix 1). Forty-five percent (87) of the photographs contained an animal with 98% of them identifiable to species. Animal size ranged from yellow-eyed juncos (*Junco phaeonotus*) and deer mice (*Peromyscus maniculatus*) to black bears (*Ursus americanus*) and mountain lions (*Felis concolor*). Photographs not containing animals (76) were exposed due to heavy rain or snow fall triggering the infrared mechanism. The other 28 photographs were of people checking the camera set-up.

During the 2184 trap nights expended from May 25 to November 18, 1993, one Arizona shrew (*Sorex arizonae*) was collected in Copper Canyon using pitfalls. Other species captured or observed in the area included deer mice (*Peromyscus maniculatus*), Yarrow's spiny lizard (*Scelopus jarrovi*), Madrean alligator lizard (*Gerrhonotus kingi*), a possible Huachuca tiger salamander (*Ambystoma*

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[1] *Arizona Game and Fish Department, Phoenix, AZ.*

tigrinum stebbeni), and a nesting pair of Mexican spotted owls (*Strix occidentalis lucida*).

DISCUSSION

The use of camera equipment to document nocturnal wildlife has had limited use since 1906 (Garret 1988). These early units were triggered with a trip wire activating both the camera shutter and cartridge blanks which startled the animals. Over time, the variability of the triggering device activating the camera shutter has been as diverse as the subjects themselves. These triggers have ranged from the common household mouse trap (Gysel and Davis Jr. 1956) to pressure pads similar to those used in security systems (Jackson and Hillard 1986). The problem with these different triggering mechanisms is detection by the animals. Jackson and Hillard (1986) expended 561 camera nights in attempting to photograph snow leopards (*Panthera uncia*) in Nepal. Using a pressure pad as a triggering device, 24 cats approached the pad but only three photographs were taken.

Infrared switching devices, like the one used on the Trailmaster 1500™, have advantages over other trigger mechanism because animal activity can be recorded automatically with little disturbance to the subject (Carthew and Slater 1991). In addition, the unit can be installed to collect data on a wide range of animals producing high quality photographs. This monitoring technique allows for numerous applications for wildlife research as well as management (Kucera and Barret 1993). However, wildlife species such as shrews and bats, can not be identified by photographs and must be captured for proper identification.

Arizona shrews have been recognized as a unique species for 17 years, and within that time (prior to this survey), only 15 specimens have been collected. The lack of collections could be related to biologists using Sherman live traps for small mammal surveys instead of pitfalls. Shrews are rarely captured using conventual box traps and Maddock (1992) found mammals weighing less than 25 grams are more frequently caught in pitfalls rather than box traps. Successfully capturing an Arizona shrew during this survey effort suggests that specialized trapping techniques such as pitfalls can yield reasonable success rates for rare species.

The greatest contribution of both these survey techniques is the incidental data collected when in use. Infrared remote camera devices can be used to monitor wildlife species that are difficult to capture or observe while pitfall traps can be used to determine small mammal as well as herptofauna composition. Used in combination, a wide range of wildlife species can be surveyed revealing foraging areas and possible travel corridors within these Sky Islands.

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APPENDIX

Appendix 1. —ist of wildlife species identified or captured during study.

Coati (*Nasua nasua*)
Western spotted skunk (*Spilogale gracilis*)
Striped skunk (*Mephitis mephitis*)
Hog-nosed skunk (*Conepatus mesoleucus*)
Mountain lion (*Felis concolor*)
Bobcat (*Felis rufus*)
Mexican spotted owl (*Strix occidentalis*)
Rock squirrel (*Spermophilus variegatus*)
Gray fox (*Urocyon cinereoargenteus*)
Arizona shrew (*Sorex arizonae*)
Yellow-eyed juncos (*Junco phaeonotus*)
Deer mice (*Peromyscus maniculatus*)
Yarrow's spiny lizard (*Scelopus jarrovi*)
Madrean alligator lizard (*Gerrhonotus kingi*)
Huachuca tiger salamander (*Ambystoma tigrinum stebbeni*)
Mexican spotted owl (*Strix occidentalis lucida*)
Black bear (*Ursus americanus*)
Canyon wren (*Catherpes mexicanus*)
Ringtail (*Bassaricus astutus*)
Collared peccary (*Tayassu tajacu*)
White-throated wood rat (*Neotoma albigula*)
Desert cottontail (*Sylvilagus audubonii*)
Common poorwill (*Phalaenoptilus nuttallii*)

Sustainable Development and Sky Islands: The Baja California Sur Experience

Alfredo Ortega-Rubio, Heidi Romero-Schmidt, and Cerafina Argüelles-Méndez[1]

Abstract.—Development and conservation of natural resources are complementary process in a long term perspective. In Latin American countries, just like Mexico, it is not possible to exclude wide zones from productive activities. It is necessary to search the maximum utilization of the natural resources of the zones for the present inhabitants and the maximum potentiality for the next generations. In this work we discuss the general requeriments in order to attain this compatibility and we analyze an specific case at Baja California Sur.

INTRODUCTION

The Sierra de La Laguna is located at the meridional tip of the Baja California Peninsula, called the Cape Region. Between the parallels 22 ° 50′ N and 24 ° N and by the meridians 109 ° 59′ W and 110 ° 10′ W. (Fig. No. 1). It is a mountainous complex that runs from north to south reaching altitudes up to 2,100 m (Arriaga and Ortega, 1988).

The vegetation of the zone comprises four main physiognomic-floristic associations (León et al., 1988): the desert scrub, the tropical deciduous forest, the oak-pine forest and the pine forest.

The tropical deciduos forest, the oak and oak-pine forests of the Sierra de La Laguna were separated from the mainland during the middle miocene (Padilla *et al.* 1988) allowing thus the establishment of an endemic species evolutionary center, because it is until the pliocene when these mountains were definitively attached to the peninsula which attained its present geographic configuration. This make that zone like a vegetation virtual island.

OBJECTIVE

Through this paper we try to increase the diffusion of several specific alternatives to management of natural resources, for the integral and sustainable use of some faunistic and floristic resources. These alternatives were found by di-

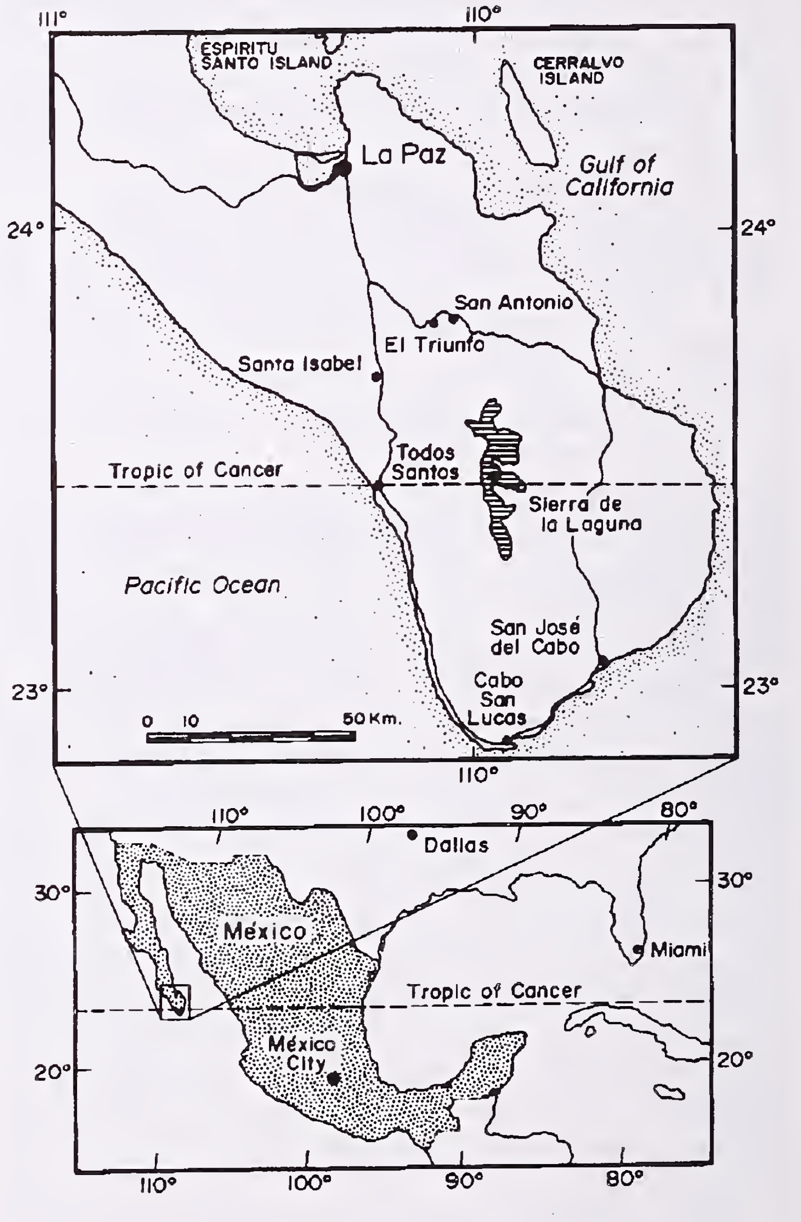

Figure 1.—Location of the Sierra de la Laguna. (from: Ortega, *et al.*, 1992a)

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[1] *Researchers. Centro de Investigaciones Biologicas del Noroeste. Apdo. Postal No. 128. La Paz 23000 BCS. Mexico.*

verse research groups working at CIB and for the specific case of the Sierra de La Laguna. In fact, we are trying to spread to the public attending this meeting, the scientific work developed by many research groups which is concentrated in one specific book (Ortega, 1992).

RESULTS

Since 1986 different research groups of the Centro de Investigaciones Biologicas (CIB) carried out studies not only focused on resources conservation of the Sierra de la Laguna but, searching for different resource management alternatives (Ortega, *et al.*, 1992). Thus, 26 researches and technicians of CIB and 5 more of the other institutions, like the University of Arizona and the Universidad Autónoma de Baja California Sur, have been centered their research in order to find these alternatives. In this work we presented briefly these alternatives generated by different groups of our Center (Ortega, 1992).

AGRICULTURE

Biofertilizers

In the Experimental Biology Division of CIB, a group of researches (Bashan, *et al.*, 1992) have been working on inoculation of plants of importance in agriculture, with beneficial bacteria of the genera *Azospirillum, Bradyrhizobium* and *Pseudomonas* which increased the growth and productivity of these plants. Bashan *et al.*, proposed this modern alternative for the traditional agricultural practice involving chemical fertilizers in the low slopes of Sierra de la Laguna (Bashan, *et al.*, 1992).

Tissue Culture

Another group of researches of the same Experimental Biology Division, works in clonalpropagation techniques, as well as plant tissue culture. These techniques are required to maintain, select and improve the quality of economically important plants. For instance, the Oregano *Lippia palmeri* and the Damiana *Turnera diffusa* are important plants of the Sierra de la Laguna. Alcaraz and Real proposed these methodology for its propagation (Alcaraz and Real, 1992).

Crops

In the Terrestrial Biology Division the researches (Troyo and Salinas, 1992) proposed the utilization of a naturalized bean specie, *Cajanus cajan* (Frijol Gandul). *Cajanus cajan* characteristics allows to the inhabitants of the region to obtain major yield than traditional species and grow up even in saline soils. Troyo and Salinas proposed with this crop to open again culture lands at present useless (Troyo and Salinas, 1992).

Pests

A group of researches (Jimenez *et al.*,1992) have been working in the control of pests. Jimenez *et al.*, have achieved to know the biologic cicle of the fly *Anastrepha ludens* that infest the fruit and on the basis in this study, establish an eradication program (Jiménez, *et al.*, 1992).

VEGETAL RESOURCES

Forest Resources

The Sierra de la Laguna region could be an important source of forest resources (Ffolliott, *et al.*, 1992). Management will have to become more intensive in order to maintain the environmental health of the ecosystems involved (Ffolliott, *et al.*, 1992). While recreation and tourism, watershed protection, and wildlife habitats are of particular concern in the region, the Sierra de La Laguna region also supports woodlands of oak-pine which have potentiales for yielding wood for processing into products such as timber, post fences, charcoal, etc (Ffolliott, *et al.*, 1992). For this reason the research is focused in to optimize such management practices.

Beekeeping Flora

Leon, *et al*, (1992) carried out phenological reproductive studies, in order to evaluate the potentialities of the native flora to take advantages of it for beekeeping practices (Leon, *et al*, 1992). The importance of the beekeeping practices in Baja California Sur are two: for its geographic isolation, perhaps this State will be the last affected by the africanization problems, for this reason Leon, *et al*, proposed to establish centers to grow queen bees for exportation. The other reason from the point of view conservation is the feasibility of obtain a direct economical benefit of the native flora and thus preserve it (Leon, *et al*, 1992).

Forage Resources

Other research group of the Terrestrial Biology Division, Arriaga and Cancino (1992), have analyzed the cattle raising activities and livestock feeding practices, carried out in the tropical deciduos forest in Sierra de la Laguna. Arriaga and Cancino, (1992) gave specific recommendations in order to improve the use of the forage resources of the region promoting the regeneration of the species used to livestock feeding, and for thus avoiding the overexplotation of these resources (Arriaga and Cancino, 1992).

Woody Resources of the Tropical Dry Forest

From the Terrestrial Biology Division, Breceda *et al.*, (1992) analyses the woody and/or commercial species of the tropical dry forest and stream communities of the Sierra de la Laguna, as well as their potential stemwood producction. Breceda, *et al.*, gave specific recommendations in order to improve the forest management practices and the preservation of this forest community (Breceda, *et al.*, 1992).

FAUNISTIC RESOURCES

The White-winged Dove, the Mule deer and the California Quail

Several of the studies carried out by different research groups of the Terrestrial Biology Divisionare focused in the analyses of ecological aspects of the cinegetic species of the Sierra de la Laguna: the White-winged dove *Zenaida asiatica* (Rodriguez, *et al.*, 1992); the Mule deer *Odocoileus hemonious peninsulae* (Gallina, *et al.*, 1992), and the California quail *Callipepla californica* (Llinas, 1992). Each research group proposed the management plan for each specie which involves the local inhabitants participation.

CONCLUSIONS

The Sierra de La Laguna have an incomparable biological richness product of then geographic isolation (Arriaga and Ortega, 1988). The Sierra de La Laguna ecosystems not only harbors the greatest biological diversity of all the State of Baja California Sur, but also in these woodlands, proportionately to their surface, occurs the majority of endemic species and subspecies of all the peninsula (Ortega, *et al.*, 1992a). Each one of these species represent future opportunity to produce new drugs or new materials for industries. The loss of these species represent the non-replace cancellation of such posibilities (Ortega, *et al.*, 1992b).

Research groups of CIB and other institutions, just like the University of Arizona, offers concrete alternatives for the management of natural resources for the integral and sustainable use of faunistic and floristic resources of the zone. The research groups offer reccomendations to improve the agriculture and livestock practices, and pests control in the productive places of the Sierra. The main purpose of these research groups have been to avoid the cancellation of options and opportunities for the future generations (Ortega, *et al.*, 1992b), and to provide rasinable alternatives for present generation (Ortega, 1992).

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Simulation of Changes in Stand Structure of Woodlands in the Madrean Archipelago Region

Peter F. Ffolliott[1] and D. Phillip Guertin[2]

Abstract.—A simulator is available to estimate changes in the stand structure of encinal and pinyon-juniper woodlands in the Madrean Archipelago region. Estimates of changes in stand structure can be simulated for some point in the future under the current management practice. It is planned to expand the capacities of the simulator to obtain estimates of changes in stand structures after the implementation of a proposed management practice. Simulations of changes in the structure, when coupled with applications of stocking equations, are helpful in estimating the anticipated effects of proposed management practices on fuelwood and livestock production, wildlife resources, watershed protection, and recreational opportunities.

INTRODUCTION

A simulator called STAND is available to estimate the growth of encinal and pinyon-juniper woodland stands in the Madrean Archipelago region of the southwestern United States and northwestern Mexico (Ffolliott et al. 1988). These estimates can be simulated for some point in the future under the current management practice. It is planned to expand the capacities of STAND to obtain estimates of changes in stand structures after the implementation of a proposed management practice. Changes in growth, when presented in terms of number of trees (a stand table), basal area, and volume (a stock table) in relation to diameter classes and areas represent changes in the structure of the stands in question. Simulations of changes in stand structure, when coupled with applications of stocking equations, are helpful in estimating the anticipated effects of proposed management practices on fuelwood and livestock production, wildlife resources, watershed protection, and recreational opportunities.

FORMULATION OF THE SIMULATOR

The gross change in number of trees in 2-inch drc (diameter root collar) classes for a projection period is determined by the simulator. It is assumed that the change in a future period will equal that of a past period. The change in number of trees for each 2-inch drc class is multiplied by the average individual tree volume for that class. An estimate of gross growth is obtained by adding the volumes of all drc classes in a stand together. A function describing tree mortality is used to convert the estimate of gross growth into estimates of net growth.

Input Requirements

Input requirements to STAND include site class, individual tree volumes for each 2-inch drc class, and a stand table of growing stock by 2-inch drc classes. Annual drc growth rates are stored in the simulator for the site classes considered. Individual tree volumes are estimated from localized volume tables (Chojnacky 1988), with these values also stored in the simulator. The stand table obtained from inventory data in most instances is entered directly from a computer terminal.

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Simulation Options

A stand table representing current conditions is input to simulate for a one-year period to provide a reference point for subsequent simulations. The stand and stock tables, and basal area distributions obtained represent a snap-shot picture of the current conditions of the stand being considered to serve as a reference point. Tree growth is accumulated for the projection period to simulate the growth of the stand at some point in the future under the current management practice. A stand table that represents the conditions at a start of a year is adjusted to reflect growth during the year for each 2-inch drc class in the projection period. The maximum projection period has been arbitrarily set at 10 years.

It is planned to expand the projection procedure to simulate the growth of a stand after the implementation of a proposed management practices. A change in management is likely to affect the diameter growth of residual trees. Therefore, the relationships that describe annual diameter growth rates will have to be adjusted to reflect the combined effects of site class, intensities of the management change, and years since the proposed management change. These adjustments will be incorporated into the simulator through modifications of the regression coefficients that quantify the annual diameter growth rates as a function of the 2-inch drc classes. Using these adjustments, simulations of the anticipated growth after implementation of the proposed management practice will be obtained. Input requirements to this future option in STAND include the prescribed residual stand table and number of years since the management change.

STOCKING EQUATIONS

Knowledge of changes in stand structure is important in itself in estimating the future effects of time and management. However, this importance is magnified when it is coupled with knowledge of the stocking conditions that determine the feasibility of implementing a proposed management practice to achieve specified management objectives. Solutions of stocking equations provide this information by showing the proportions of a stand that is stocked to density levels that are specified by the proposed management practice.

Development

Stocking equations are developed with different measures of density as the basis. Basal area has been used here for purpose of illustration. Basal area is easily estimated in the field when point sampling techniques are used in inventories (Avery and Burkhart 1994, Husch et al. 1982), and many relationships of wood and livestock production, wildlife resources, watershed management, and recreational opportunities are available with basal area as the independent variable.

The use of a single basal area factor (BAF) in point sampling inventories of the woodlands in the Madrean Archipelago region describes the stocking conditions at a sample point incorrectly, largely because of intermixtures of tree size classes and irregular spacing patterns. If it is not possible to describe the stocking conditions at a sample point correctly with the use of a single BAF, it also is unlikely that the proportion of a stand that is stocked to specified basal area levels can be described. This problem is overcome in many instances through applications of stocking equations. Development of stocking equations is based largely upon two premises.

The first premise is that a sample point is stocked at a basal area level if at least 1 tree is tallied with a BAF corresponding to that basal area level; that is, a sample point is stocked to 10 square feet of basal area per acre if 1 tree is tallied with a BAF of 10. If more than 1 trees are tallied, the sample point is still considered stocked to the basal area level that corresponds to the BAF used. A sampling point is not stocked to the basal area level of the BAF when no trees are tallied with that BAF. Furthermore, the proportion of a woodland stand that is stocked (or not stocked) to the basal area level is estimated from the proportion of sample points stocked (or not stocked) to that basal area level.

The second premise is that the proportions of the stand sampled that are stocked to a range of alternative basal area levels are estimated by the proportions of the points in the sample that are stocked to the basal area levels; this premise assumes that an unbiased multiple-BAF inventory has been made. Such a relationship is a stocking equation, the dependent variable being the proportion of the stand that is stocked to a specified basal area level. The independent variable is the basal area level of interest to management.

Applications

Stocking equations have been developed to represent cutover and virgin ponderosa pine stands in north-central Arizona (Ffolliott and Worley 1973). A mathematical model that approximates a sigmoidal form was selected for their definition. This mathematical model is being used currently to develop stocking equations for the woodlands in the Madrean Archipelago region. Initial expressions of these stocking equations are used here to illustrate the importance of simulating changes in the structure of these woodland stands with the STAND simulator.

Determining Management Feasibility

Suppose that a fuelwood harvesting prescription calls for the removal of a designated amount of wood from a stand, but that the proposed management plan also requires that the stand affected remain stocked to a specified basal area level after the harvesting. Simulation of the anticipated changes in stand structure after the fuelwood harvesting can be made with the STAND simulator. The results from this simulation then become the basis for solving a stocking equation to determine the proportion of the stand that will be stocked to the specified basal area level in the future.

It is often that this solution reveals a stocking condition that is less than that prescribed by management; that is, the stand will not meet the prescribed basal area level in the future. A decision must be made at this time on the feasibility of implementing the original fuelwood harvesting prescription. This prescription might be discarded in favor of an alternative that would place a larger proportion of the stand in the condition represented by the specified basal area level; this could be achieved by harvesting a reduced amount of fuelwood. Regardless of the decision made, it must be a compromise between harvesting the maximum amount of fuelwood that is possible and extending the practice to the largest proportion of the stand in attaining the prescribed basal area level.

Evaluating Multiple Use Impacts

Simulated changes in stand structure and the applications of stocking equations also help to answer questions on the feasibility of the proposed fuelwood harvesting plan in reference to multiple use management. A range management specialist may ask "What proportion of the stand to be affected by fuelwood harvesting will be stocked in excess of a basal area level that is considered the maximum to allow an acceptable level of forage production?" In the absence of information on the "optimum conditions" for recreational activities, a specialist may set arbitrary criteria for casual recreation, asking "What proportion of the stand will support 6-10 trees that are 8-10 inches drc and larger on 1 acre (on the average) 10 years after the harvesting has been completed?" An economist interested in minimizing the costs of management may ask "How much of the stand to be harvested (in fact) will be harvested, and to what intensity does fuelwood harvesting need to be applied, to bring the stand to the specified basal area level in the future?" Answers to these and other questions that are asked ex-ante to the fuelwood harvesting provide a basis to evaluate the proposed harvesting prescription in terms of multiple use impacts before the plan is implemented.

Other applications of stocking equations and the outputs from the STAND simulator include the setting of operating priorities for individual stands within a woodland community, and decisionmaking at the stand, community, and ecosystem levels of interest.

CONCLUSIONS

Estimates of changes in the stand structure of encinal and pinyon-juniper woodlands in the Madrean Archipelago region can be simulated with the STAND simulator. The simulations of changes in the structure, when coupled with applications of stocking equations, are helpful in estimating the anticipated effects of proposed management practices on fuelwood and livestock production, wildlife resources, watershed protection, and recreational opportunities. Heightened pressures necessitate that these multiple uses be given their due consideration in future management of the woodlands in the region.

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Effects of Grazing History on Insect Communities of a Semi-Arid Grassland

Sandra J. DeBano[1]

Abstract.—Insect communities are an essential component of ecosystems. Thus, effective management and conservation of grasslands depends on a basic understanding of how resource uses, such as livestock grazing, affect insect communities. However, most studies on the effects of grazing have neglected insects, and instead have focused primarily on plants and vertebrates. To add to our knowledge of the effects of grazing on insects, a comparative study was performed at the Audubon Appleton-Whittell Research Ranch which has not been grazed for over 25 years, and at surrounding active cattle ranches. Insect communities were sampled with pitfall traps and sweep nets biweekly in the summer of 1993 and 1994 at four ungrazed sites and four comparable grazed sites. This paper reports data collected for two subgroups of insects: grasshoppers collected by sweep netting and insects caught in pitfall traps. Preliminary analyses of the abundance and diversity of these two groups are presented and discussed.

INTRODUCTION

A major goal of conservation biology is understanding the effect of human-caused disturbance on community diversity. In the western United States, livestock grazing is one of the most prevalent of all man-made disturbances, impacting nearly 70% of all federal lands in 11 western states (CAST, 1974). The effect of grazing on populations and communities has generally been hypothesized to be negative, and indeed many studies of birds (e.g., Mosconi and Hutto, 1982), mammals (e.g., Medin and Clary, 1989), and reptiles (e.g., Bock et al., 1990) have shown decreased diversity and densities in grazed areas. However, only a few studies have examined how grazing affects insects (Morris 1967; Jepson-Innes and Bock, 1989), the most numerous and diverse of all animal species. This is true in spite of the fact that insects are vital components of ecosystems, fulfilling important roles in pollination, food webs, and nutrient cycling. Thus the objectives of this study were to:

1. Compare total abundance, species richness, and species diversity in grasshopper communities on grazed and ungrazed sites.
2. Examine relative abundances of each grasshopper species at the two types of sites.
3. Investigate overall trends in species diversity of seven insect orders sampled by pitfall traps.

METHODS

The study was conducted at Audubon's Appleton-Whittell Research Ranch and its surrounding cattle ranches located on the Sonoita Plain, Santa Cruz County, Arizona. The Ranch has not been grazed since 1968. Four 30 X 30 m ungrazed sites on the Research Ranch were paired with four similar sites on surrounding active cattle ranches. Insects were sampled approximately biweekly by sweep netting and by baited pitfall traps three times in 1993 (September - November) and four times in 1994 (June - August). Data from both years were combined because of the non-overlapping temporal distribution of sampling. Data on grasshopper species were collected using sweep netting, and total abundance, species richness, and species diversity were calculated for each site. Richness was calculated as the total number of species present at each site and diversity was measured using the Shannon-Weiner Index, which takes evenness of species abun-

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dances into account. Means for grazed and ungrazed sites were tested for differences using t-tests. Data on species diversity of seven other insect orders were collected from pitfall traps, and species were sorted only to morphological species (i. e., species that are morphologically similar). Means are reported ± one standard deviation.

RESULTS

Grasshopper Communities

A total of 681 adult grasshoppers of 26 species were collected on the Research Ranch and the surrounding cattle ranches in the fall of 1993 and the summer of 1994. Three subfamilies were represented: Gomphocerinae, Melanoplinae, and Oedipodinae. See the Appendix for a list of grasshopper species and their abbreviations. Total abundance of individuals of all species of grasshoppers on ungrazed sites (106.7 ± 53.6 individuals per site) and grazed sites (75.2 ± 45.9 individuals per site) did not differ significantly (t=0.89, P=0.40, n=8). Species richness was actually higher on grazed sites (16.6 ± 2.6 species) than on ungrazed sites (12.5 ± 3.1 species), but this difference was not significant (t=-1.96, P=0.10, n=8). Species diversity as measured by the Shannon-Weiner Index was also not significantly different (t=-1.4, P=0.21, n=8) between the two types of sites (ungrazed sites = 2.07 ± 0.25; grazed sites = 2.28 ± 0.14).

Grasshopper communities did appear to differ in species composition. Species of the subfamily Oedipodinae were more common on grazed areas (fig. 1). Three of five Oedipodinae species were found only on the grazed sites, and the other two species were much more common on grazed sites. However, only one Oedipodinae species differed significantly between sites. Most species of the subfamily Melanoplinae were equally abundant on both grazed and ungrazed sites, but two species were significantly more common on the ungrazed sites (fig. 2). Two species of the subfamily Gomphocerinae were also significantly more common on ungrazed sites, and a third species was collected only on ungrazed sites. In contrast, two other Gomphocerinae species tended to be much more common on grazed sites (fig. 3).

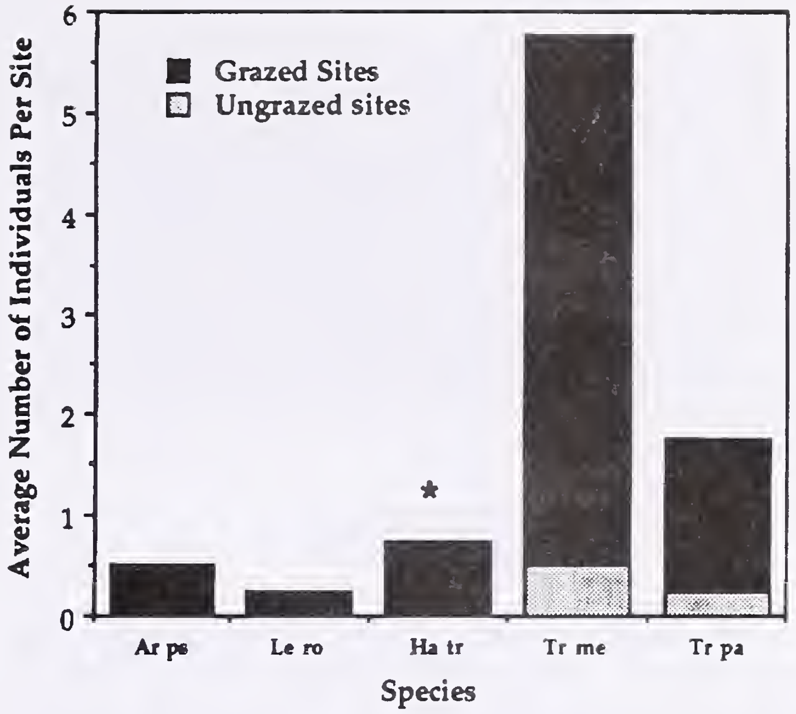

Figure 1.—Average relative abundances of grasshopper species in the subfamily Oedipodinae at grazed and ungrazed sites. An asterisk indicates significance at the 0.05 level (t-test, n=8). See Appendix for key to species abbreviations.

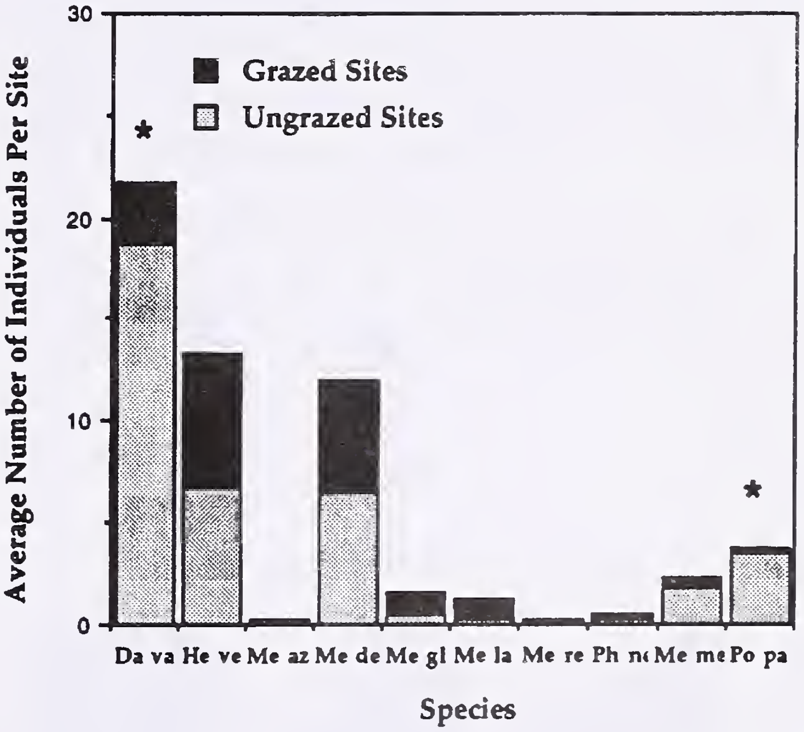

Figure 2.—Average relative abundances of grasshopper species in the subfamily Melanoplinae at grazed and ungrazed sites. An asterisk indicates significance at the 0.05 level (t-test, n=8). See Appendix for key to species abbreviations.

Diversity in Insects Sampled by Pitfalls

Species from seven orders of insects were collected in pitfall traps: Coleoptera, Hemiptera, Homoptera, Hymenoptera, Diptera, Orthoptera, and Lepidoptera. Figure 4 shows the total number of species of each order found on ungrazed and grazed sites. No order differed significantly in species richness or total abundances between grazed and ungrazed sites. However, species composition again appears to be quite different, with a relatively small proportion of species occurring at both sites.

DISCUSSION

The results of this study suggest grazing affects insect communities by affecting species composition of communities, rather than by impacting species richness, diversity, or total abundances. This conclusion is supported by 1) the lack of differences found in grasshopper diversity, richness, and total abundances between grazed and ungrazed sites, and 2) the fact that five grasshopper species were significantly more abundant on one or the other side, and an additional six species were only found on one or the other side. These latter results are consistent with those found by Jepson-Innes and Bock (1989) in their study of grasshopper communities at one pair of sites on the Research Ranch and an adjacent cattle ranch.

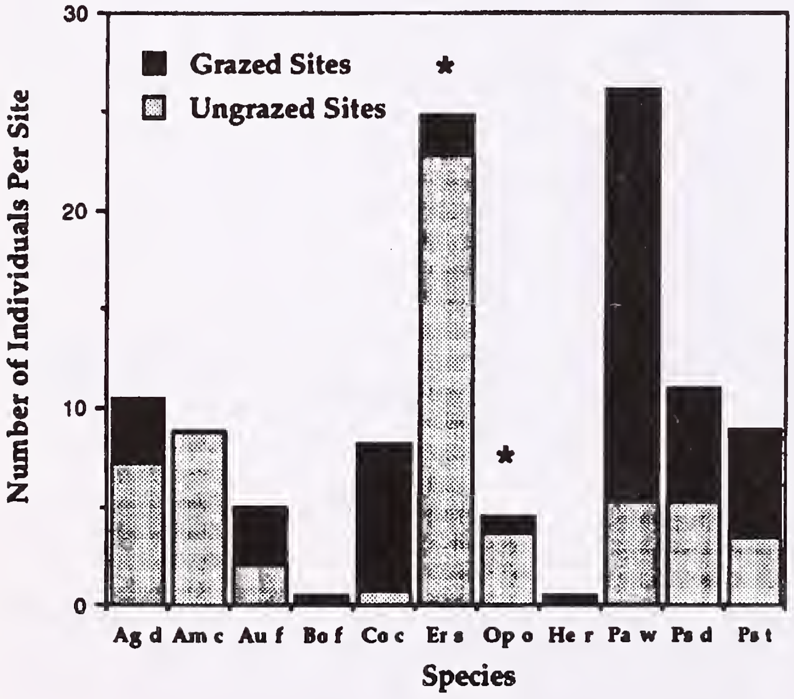

Figure 3.—Average relative abundances of grasshopper species in the subfamily Gomphocerinae at grazed and ungrazed sites. An asterisk indicates significance at the 0.05 level (t-test, n=8). See Appendix for key to species abbreviations.

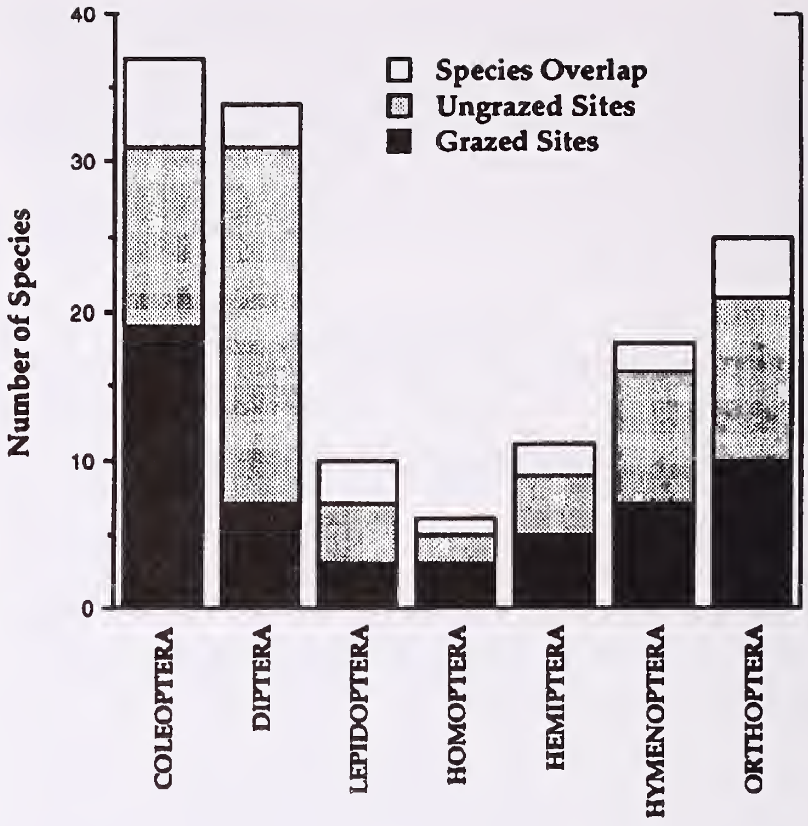

Figure 4.—Total number of species in seven orders found at grazed and ungrazed sites. "Overlap" indicates those species that can be found on both grazed and ungrazed sites. T-tests on average abundance and diversity showed no significant differences between sites.

Species richness and total abundances of seven orders caught by pitfall traps did not differ on grazed and ungrazed sites. However, the small overlap of species that occurs on both grazed and ungrazed sites indicates that species composition of the two communities are quite different. However, these results should be interpreted with caution for two reasons. First, species have only been sorted to morphological species, and await positive identification. Second, the use of pitfall traps may not be an adequate technique for use in comparing two different habitat types. Because vegetation is sparser on grazed sites, odors of baited pitfall traps may carry further, and thus attract more individuals. In addition, insects may be more likely to fall into pitfalls in areas with less vegetation. This is likely to affect abundance estimates the most, but may indirectly affect richness and diversity indices as well. These orders were also sampled with sweep netting, and when analyzed, these results may be more accurate than those obtained by pitfall sampling.

The results of this study suggest that methods commonly used to determine whether human disturbances are impacting communities may not provide enough information to evaluate community health. If disturbed communities do differ primarily in species composition, then simply comparing species diversity or richness may not be sufficient for understanding the dynamics of disturbance.

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APPENDIX

Species of Grasshoppers and Their Abbreviations

Subfamily Gomphocerinae: *Agenotettix deorum* = Ag d; *Amphitorinus coloradus* = Am co; *Aulocora femoratum* = Au f, *Boopedon flaviventris* = Bo f; *Cordillacris crenulata* = Co c, *Eritettix simplex* = Er s; *Helialula rufa* = He r; *Opeia obscura* = Op o; *Parapomala wyomingensis* = Pa w; *Psoloessa delicatula* = Ps d; *Psoloessa texana* = Ps t

Subfamily Melanoplinae: *Dactylotum variegatum* = Da va; *Hesperotettix veridis* = He ve; *Melanoplus arizonae* = Me ar; *Melanoplus desultorius* = Me de; *Melanoplus lakinus* = Me la; *Melanoplus regalis* = Me re; *Phoetaliotes nebrascensis* = Ph n; *Poecilotettix pantherinus* = Po pa

Subfamly Oedipodinae: *Arphia pseudoneitana* = Ar ps; *Hadrotettix trifasciatus* = Ha tr; *Leprus robustus* = Le ro; *Trachyrhachis mexicana* = Tr me; *Trimerotropis pallidipennis* = Tr pa.

Water Requirements and Potential Uses of Pigeonpeas in Agroforestry Systems Appropriate for Sky Islands Management

Enrique Troyo-Diéguez and Federico Salinas-Zavala[1]

Abstract.—A bio-physical model based on the plant-water-climate interactions is proposed to establish the effects of the photosynthetically active radiation (PAR) on the water demand of a field crop. It is shown that a relationship exists between PAR, leaf temperature and the transpiration of regional ecotypes of pigeonpeas (*Cajanus cajan* (L.) Millsp), introduced to Baja California Sur (México) from Asia in the middle of the century. This pigeonpea ecotype was found in the influence area of the Sierra de La Laguna, B.C.S. The proposed relationship was backed by measurements of leaf and ambient temperatures, and PAR, of which the transpiration process is dependent. Given the ample available information on ambient temperatures and solar radiation data in the country, it is concluded that this procedure is useful to establish the expected level of transpiration of pigeonpeas and its minimum water requirements. The observed phenotype suggests the usefulness of pigeonpeas in Sky Islands ecosystems; yield of grain was near 6 $Mg \cdot ha^{-1}$. This results enable us to design appropriate agroforestry systems in the villages of Sierra de La Laguna and similar Sky Islands; these low inputs systems could include understorey horticultural species and pigeonpeas.

INTRODUCTION

Numerous studies on plant physiology and plant-climate interactions are being performed because of the growing necessity to racionalize water in agroecosystems (Penman, 1963). The urge to know the minimum water requirements is strongly related to rural characteristics of arid and semiarid zones, where water is scarce and expensive, and the global scheme of social and agricultural development depends on the acquisition and distribution of available water through some empirical methods.

This is the case for several crops in the area of influence of the Sierra de La Laguna, the only oak-pine forest in the most arid state of Mexico: Baja California Sur. This sky-island ecosistem was declared in July 1994 a Biosphere Reserve because of its endemic flora and its role as a hydrological reservoir for the Cape Region.

In order to insure the ground water reservoirs for next generations, it is proposed to perform more accurate estimates of the water volumes required for the cultivation of traditional and improved agroecosystems. The matter is of considerable importance for this Reserve because of the fragile conditions of the water reservoirs and the possibility to recover wide extensions of lands already closed to agriculture as a consequence of water scarcity.

Goals. The aim in this work was to develop a simple mathematical model for the relationship between pigeonpeas transpiration and photosynthetically active radiation (PAR), for incorporation into an empirical water-demand model. The proposed plant-climate relationship would be the key to adequate the water use in the rural agricultural villages, acording to its availability, nearby the Sierra de La Laguna B.C.S. oak-pine forest, a new Biosphere Reserve in Northwest México.

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Other goal was to explore a possible association between pigeonpeas (*C. cajan*) and traditional horticultural and spice crops in the study area. By means of such association, we expect to provide a feasible option to rationalize the inputs required in local agroforestry systems, as well as the water distribution and other commonly used inputs, in the influence area of the Sierra de La Laguna Biosphere Reserve.

SITE DESCRIPTION

This work was conducted at P.E. Calles agricultural village, at the proximities of Sierra de la Laguna oak-pine forest. The study site was located on the Pacific Ocean side at 23°20'N and 110°05'W, 120 Km south La Paz city, in the southweastern part of the Baja California Peninsula (fig. 1.). The soil of the site was a sandy-loam type with low content of organic matter (0.7%); the volumetric moisture contents at field capacity (FC) and permanent wilting point (PWP) were 12.5 and 7% respectively.

Climate in this region is BW(h')hw(e) type, which means a very dry weather with a principal rainy season in summer and a secondary one in winter; rains are in general scarce all year long; winter precipitation is less than the summer one. It can be considered as a warm climate, with annual thermal oscillation from 7 to 14°C (García and Mosiño, 1968).

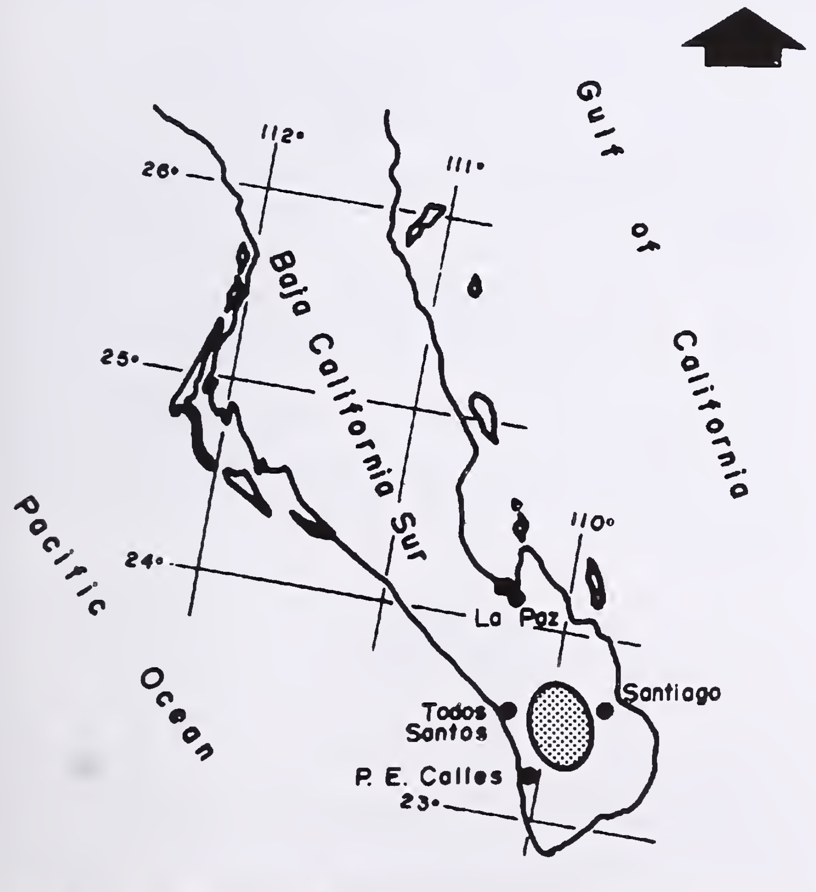

Figure 1.—Geographic location of the pigeonpeas experimental site; the shaded area is the oak-pine subtropical forest.

METHODS

After finding a well adapted 'roustic' ecotype of pigeonpea (*C. cajan*) in the influence zone of the Sierra de La Laguna Biosphere Reserve, an institutional project was developed in order to determine the adaptability and productive potential of this species in the marginal areas of the Sierra de La Laguna 'Sky Island' ecosystem.

An experimental plot was established in the agricultural village 'P.E. Calles' in the southwestern portion of the influence zone. The phenology and phenotype variations of the ecotype under study were recorded. Water relations were measured by means of a portable porometer and a Scholander type pressure chamber. Microclimatic variables were recorded simultaneously.

Direct radiation (G_M) values (Galindo and Chavez, 1977) were considered for the time of transpiration measures. Maximum G_M in the study area occurs in June (0.540 $kW.m^{-2}$), in the beginning of the summer season, and a minimum in December (0.387 $kW.m^{-2}$); according to these data, annual mean G_M is 0.487 $kW.m^{-2}$, among the highest in Mexico.

MEASUREMENTS AND COMPUTATIONS

As PAR approximates to the interval 0.4 to 0.7 μm of wide wavelength band (Rao, 1984), and its spectral intensity varies all day long, it is expected in all cases that: a) $0 \leq PAR << 1$, and, b) although G varies in a known way all day long [$G=g(t)$], the variation of PAR will be different than that of G [$PAR \approx f(t)$, where $f(t) \neq g(t)$]. Since variation G(t) is well known, in this work we intend to describe f(t) and estimate the proportional adjustment factor PAR_M, in an analogous way to G(t); such equation could be represented by the expression:

$$PAR(t) = PAR_M \, f(t)$$

The incident solar radiation related to the transpiration of a crop, can be associated with the defined integral of PAR(t) according to the equation:

$$Ir = ko \int_{0}^{q} PAR(t)\ G(t)\ dt$$

Where Ir is the required irrigation for the cultivated crop per square meter during the time q, and ko is an empirical adjustment factor; ko becomes a constant parameter for each crop and particular region.

A typical distribution of PAR(t) is presented in fig. 2. Points were obtained from experimental data using a pyranometer integrated within a porometer. Note that the curves adjust to the sinus curve, similar to the G(t) function:

$$G(t) = G_M \operatorname{Cos}^{ß} (pi \cdot {}^{t}/_{L})$$
$$ß = 1.2$$

G_M is the maximum value of radiation at midday; it has been considered as a numeric constant for any month. Similarly, the value of L, the number of astronomic light hours, can be obtained out of astronomic charts, computer programs or estimated for any month and study site through theoretical equations (Monteith, 1973). Dimensionless values of PAR are represented in fig. 3 using the function:

$$PAR = PAR_M \operatorname{Cos}^{n}(pi \cdot {}^{t}/_{L})$$

Where PAR_M is the maximum value of PAR, at midday, and the exponent n=5. For the study period, G_M = 0.52 kW.m^{-2} and L=12.8 h (46,080 s). The function PAR(t) was obtained by dividing the sinus curve with better fitting to the measured data of PAR by the function G(t) for the same period of time. If PAR_M is fixed as the maximum value of PAR(t), at midday, in this case 0.313 kW.m^{-2}, f(t) can thus be decribed through the following computations.-

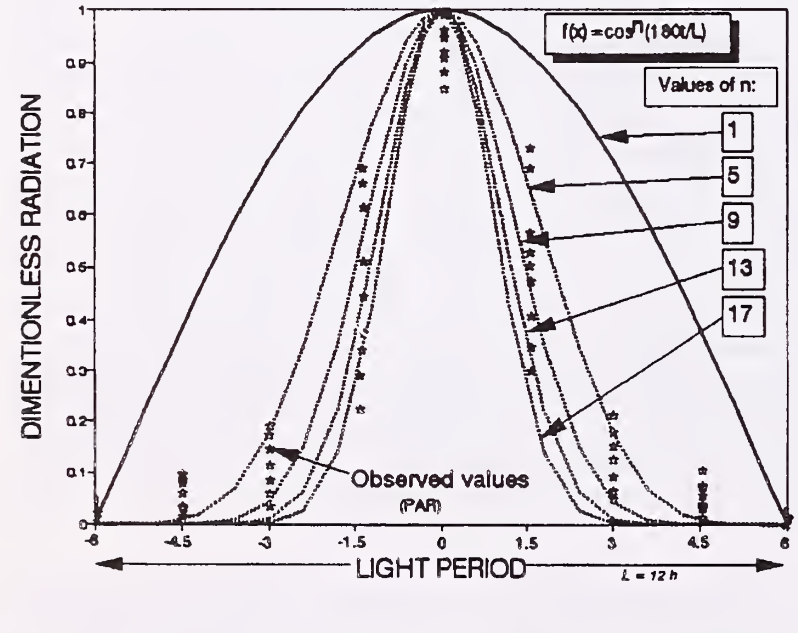

Figure 2.—Graphic representation of PAR measurementsand a set of sinus curves.

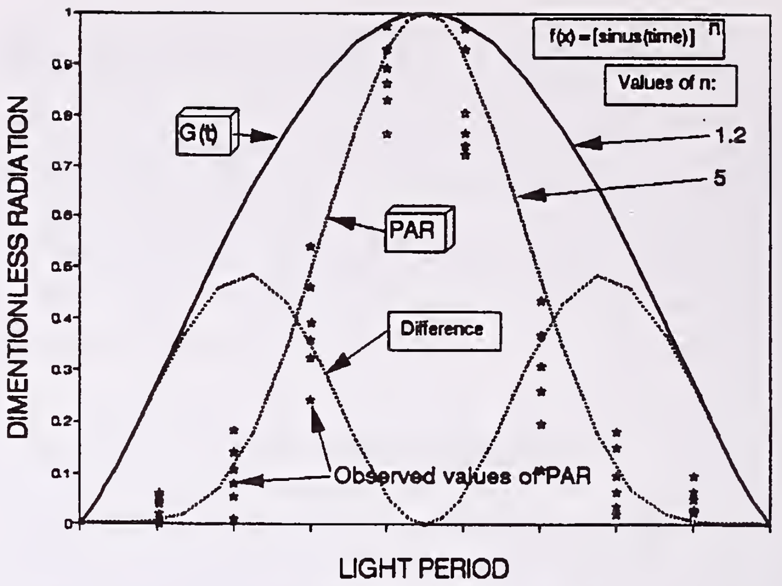

Figure 3.—Comparison between G(t) distribution and the proposed function for PAR, received by a pigeonpea plot.

Considering the following definitions:

$$PAR = PAR_M\, f(t)$$
$$G(t) = G_M \operatorname{Cos}^{B}(pi \cdot {}^{t}/_{L})$$
$$PAR = PAR_M \operatorname{Cos}^{n}(pi \cdot {}^{t}/_{L})$$

Then, the equations for PAR_M and G_M can be reexpressed through the following expressions:

$$PAR_M\, f(t) = \left(\frac{PAR_M}{G_M}\right) \frac{\operatorname{Cos}^{n}(pi \cdot {}^{t}/_{L})}{\operatorname{Cos}^{B}(pi \cdot {}^{t}/_{L})}$$

After solving the above equation for f(t), it is obtained:

$$f(t) = \left(\frac{PAR_M}{PAR_M\, G_M}\right) \frac{\operatorname{Cos}^{n}(pi \cdot {}^{t}/_{L})}{\operatorname{Cos}^{B}(pi \cdot {}^{t}/_{L})}$$

From observational data, we define for the environmental conditions associated to the experimental ecotypes of pigeonpea the next relationships:

$$K_1 = \frac{PAR_M}{PAR_M G_M}$$

$$T = (pi \cdot {}^{t}/_{L})$$

Then, after simplifying it follows that:

$$f(t) = K_1(\operatorname{Cos}^{n} T \;/\; \operatorname{Cos}^{1.2} T), \text{ and}$$

$$f(t) = K_1(\operatorname{Cos}^{m} T)$$

Where exponent m is calculated by: $m = n - B$
If $n=5$ and $B=1.2$, then $m=3.8$.

After manipulating the above equations K_1 is calculated as $PAR_M/(PAR_M.G_M)$; the argument T is $(pi \bullet {}^t/_L)$. Similarly, f(t) can be expressed as:

$$f(t) = K_2(\cos^m T)$$

Frequently, several meteorological parameters are fitted to a sinus type function; in this sense, the validity of the procedure lies on common methodologies. Solving Ir for the interval 0 to q and estimating a crop coefficient K_c, the whole procedure can be simplified into the model:

$$Ir = 24(K_c)(G_{max})(PAR_{max})$$
$$K_c = Tr_{max}/PAR_{Trmax}$$

Where Ir is the minimum irrigation requirement in mmH_2O/day, G_{max} is the maximum G in $kW.m^{-2}$, PAR_{max} is the maximum value of PAR in $kW.m^{-2}$, 24 converts units per h into units per day, K_c is the adimentional crop coefficient, in this case $K_c = 0.7$; Tr_{max} is the maximum recorded transpiration rate in $g.h^{-1}.m^{-2}$, and PAR_{Trmax} is the simultaneous value of PAR.

RESULTS

High correlation ($r=0.89$) was found between PAR and transpiration of regional ecotypes of pigeonpeas (*Cajanus cajan* (L.) Millsp), measured in typical days. It was found that the transpiration shows a growing tendency with PAR, but after reaching a limit value the rate of transpiration is again reduced. The nonlinear relationship implies that other factors influence transpiration. Growing values of PAR, from sunrise to noon under normal conditions, promotes transpiration in crops as a natural response, but when radiation reaches extreme high values, it follows a closure of stomata with a gradual reducing of transpiration rate. Such was the case for the influence zone of the Sierra de La Laguna, in the south part of the Baja California Peninsula, where extreme values of solar radiation occur in summer, from June through September. As a consequence, the natural cooling system of the leaf (transpiration) loses efficacy and thus leaf temperature reaches higher values. This is one of the physiological mechanisms that causes frequent crop collapses in the region, where water is insufficient to fulfill the demands.

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Tropical Dry Forest of the Sierra de la Laguna: A Phytogeographical Analysis

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INTRODUCTION

The tropical dry forest of southern Baja California represents the northwestern extreme of the present distribution of this type of vegetation. In the Peninsula of Baja California this vegetation is restricted to the southern extreme, growing over the Sierra de la Laguna foothills. According with the origin and evolution of the Sonoran Desert (Axelrod 1958, 1979) this vegetation evolved from the Madro-Tertiary Geoflora, mainly from the Arid Subtropical Scrub Complex and some species belong to the Sierra Madrean Element (Axelrod 1950). The arid subtropical scrub remains as the ancient vegetation (Miocene-Pliocene) which was widely distributed in North America and was confined to more southerly regions in response to an increasing cold and reduction of summer precipitation. Since the last glaciation deserts have been expanding (Axelrod 1979) reducing the area of the Tropical Arid vegetation to the Cape Region in the Baja California Peninsula and particularly the tropical dry forest to the Sierra de la Laguna.

Ever since that time the geographic and climatic isolation of this community have been one of its outstanding characteristics, therefore its current floristic relationships arise interesting questions. What are the level of endemic taxa?, Which are the main geographical affinities of this flora?, Is the Sonoran Desert the main source of its floristic composition or the tropical areas of mainland Mexico?.

METHODS

To approach this questions we obtained the geographic distribution of the families and genera of the tropical dry forest of Baja California Sur (Willis 1973, Puig 1989, Villaseñor *et al.* 1988). At a species level the geographic-floristic affinity groups were defined according to a regionalization proposed by Rzedowski (1991). These are based in the natural distribution of endemic taxa in Mexico and adjacent areas. To obtain the affinities patterns for the most characteristic family of this vegetation, the distribution of the Leguminosae species were also analyzed. The genera and species of the tropical dry forest in Baja California Sur were also compared with the floras of the Sonoran Desert (Shreve & Wiggins 1964) Rio Mayo (Gentry 1942), Sinaloa (Vega Aviña 1991), Chamela (Lott 1993), and Chiapas (Breedlove 1986)

RESULTS

For the tropical dry forest of Baja California Sur 500 species, 303 genera and 86 families have been recorded. The ratio genera/family and species/genera are 3.5 and 1.6 respectively. The endemic element include : 2 genera, 48 species and 7 minor categories, which are equivalent to 9.6% of all the species. This percentage could be considered as moderate, it is smaller than the 23% reported for the entire peninsula of Baja California (Wiggins, 1980), and is also smaller than the endemic level of the Cape Region, which is 17% of endemic (León de la Luz pers. comm.).

The tropical dry forest in the Peninsula of Baja California has pantropical and neotropical affinities (table 1). These elements include more than 70% of all the genera. At a specific level the ascription of the distribution of the taxa according to the regionalization proposed by Rzedowski (1991) (fig.1), shows that the distribution of most of the species (54.6%) in the tropical dry forest are restricted to Mexico and its nearest zones (table 2). The Mexico region is the area which contains the major number of species. The second place corresponds to Megamexico I which includes parts of the arid zones of the southern United States, the distribution of a group of endemic species with xeric features is restricted to this area. The third place corresponds to Megamexico II, which comprises the area of natural distribution of species

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with tropical features. Finally the Megamexico III is the region with lower number of species.

The geographical distribution of the 54 species of Leguminosae shows four patterns (fig.2). Most of the species (18) are distributed in the western coast of Mexico, 15 species are found in the southwest of the United States, 3 species are restricted to the Sonoran Desert and 18 species and subspecies are endemic to the Cape Region.

The comparison between the flora of the tropical dry forest in the Baja California Peninsula, the Sonoran Desert, and the flora of some tropical areas in mainland Mexico shows (fig.3) that the tropical dry forest of Baja California Sur has the highest numbers of common taxa with the Sonoran Desert and Chiapas (table 3).

Table 1.—Phytogeographic affinities of the families and genera of the tropical dry forest in Baja California peninsula.

	Families		Genera	
	No.	%	No	%
Cosmopolite	40	46.5	60	19.8
Pantropical	38	44.2	114	37.6
Neotropical	2	2.3	103	34.0
Neoarctic	5	5.8	16	5.3
American	1	1.2	8	2.6
Endemic	0	0.0	2	0.7
Total	86	100	303	100

We also use some similarity indices to compare the flora of the studied region with those mentioned above. Sorensen's, Preston's and Jaccard's indices for these species are shown in the table 4. There are different values according with each type of index, nevertheless for all of them the Sonoran Desert has the highest value, the close relationship between these areas is due to their geographical closeness. According to the Soren-

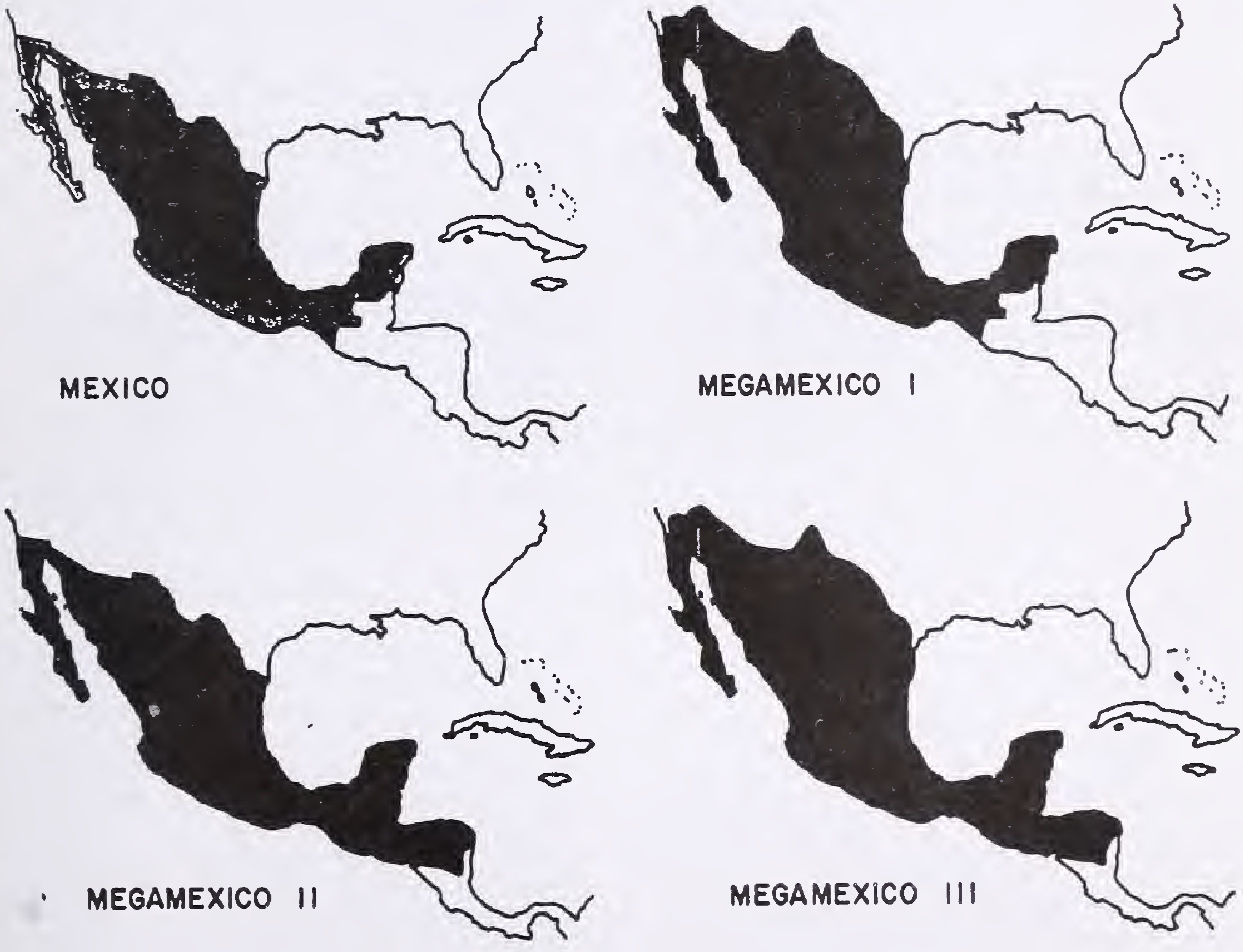

Figure 1.—Mexican regions proposed by Rzedowski (1991).

sen's and Jaccard's indices, Sinaloa is the next area bearing a high relationship with the tropical dry forest of Baja California Sur; Rio Mayo and Chamela have similar coefficient values and finally Chiapas has the lowest coefficient of similarity. The values of the Sorensen's and Jaccard's indices show a tendency which can be related to a geographical position, the Sonoran Desert is the nearest area to the Sierra de la Laguna, and Chiapas represents the southern extreme of all of them. This tendency implies an environmental gradient, the Sonoran Desert is the xeric extreme, Sinaloa and Rio Mayo are a xeric and tropical mixture while Chamela and Chiapas have typical tropical floras.

The Preston's index shows a different tendency. This is related with the total number of common species between the tropical dry forest and each one of the analyzed floras. According to this values the Sonoran Desert has the highest coefficient; Chiapas is the next one, Sinaloa the third, and Rio Mayo and Chamela the last ones.

Table 2.—Geographic distribution of the species in the tropical dry forest of Baja California peninsula(following Rzedowski's classification).

Region	Species No.	Species %
Megamexico I	67	13.4
Megamexico Ii	27	5.4
Megamexico Iii	25	5.0
Mexico	154	30.8
Endemic	45	9.0
Other Regions	182	36.4
Total	500	100

Figure 2.—Geographical distribution of 54 species of leguminosae.

Figure 3.—Genera and species common to the tropical deciduous forest of the Sierra De La Laguna and a natural province, two localities, and two states of the west coast of Mexico.

Table 3.—Number of genera and species common to the TDF of Baja California peninsula and the other sites.

	Desierto Sonorense	Sinaloa	R.mayo	Chamela	Chiapas
Genera	248	232	204	201	256
Species	253	157	117	111	176

Table 4.—Coefficients of similarity between the species of the TDF of Baja California Sur and other regions.

Index of Similarity	Desierto Sonorense	Sinaloa	R. Mayo	Chamela	Chiapas
IS Sörensen	16.1	15.8	13.2	13.7	4.7
IS Preston	50.8	31.8	23.9	22.9	35.2
IS Jaccard	8.1	7.9	6.6	6.8	2.3
No. Species	253	157	117	111	176

CONCLUSIONS

The high proportion of the pantropical affinities of the tropical dry forest of Baja California Sur suggests that, at a generic level, the major relationship exists with the tropics of the world rather than with the American tropics. Maybe this result is due to the pristine condition of this area. Nevertheless, the proportion of the endemic genera (0.4%) is very poor to sustain this conclusion. On the other hand, the pantropical elements seem to have a generalistic distribution pattern, thus the recent plant colonization of southern Baja California was maybe done by these components. The relative high proportion of cosmopolitan elements supports this assumption.

The low ratio genera/family and species/genera found in the tropical dry forest are similar to those recorded in islands. This could be the result of the geographical isolation. However, the moderate number of endemic taxa suggests that the geographic isolation is not as effective as we would expect, it is possible that a slow, but progressive, species incorporation from the Sonoran Desert, and from mainland Mexico, particularly from Sinaloa is occurring, through the Sonoran Desert .

The distribution patterns of the Leguminosae as well as the Preston's coefficient of similarity, and the total number of common species shared between the dry forest community of Baja California and the analyzed floras, reveal that the flora of the tropical dry forest of Baja California Peninsula is composed by numerous xeric species. Notwithstanding the disjunction with the tropical mainland communities, still the flora of Baja California has a close floristic relationship with the dry mexican tropic. The tropical dry forest of the Cape Region summarizes the same condition magnified for the whole the country. It represents the limit between the arid and the tropical element and its floristic composition is a mixture of both of them.

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Life Histories and Demographics of Long-lived Organisms: Implications for Management and Conservation

Justin D. Congdon[1], Arthur E. Dunham[2], Richard C. van Loben Sels[3], and Josiah T. Austin[4]

Abstract.—Populations of Blanding's turtles (*Emydoidea blandingii*) and snapping turtles (*Chelydra serpentina*) have been studied on the University of Michigan's E. S. George Reserve for 30 of the past 40 years. Adults of both species are long-lived and populations of both species are essentially stable. Cohort generation times for snapping turtles (25.4 years) and Blanding's turtles (37.5 years) are associated with the following life history traits: 1) long delays in sexual maturity, 2) extended reproductive lifespans, 3) high adult survival and 4) extended longevity. Cohort simulations were made using data from long-term studies of stable populations. Simulations were used to examine the relationships between annual juvenile and adult survival when a single demographic trait is allowed to vary. Analyses indicated that annual juvenile survival between age 1 and first reproduction must average over 76% to maintain a stable populations of these turtles. The severity of impact of harvesting adult snapping turtles from a population increases as younger adults are harvested. Since the youngest adult snapping turtles weigh approximately 2 kg, it is probable that unregulated harvests would almost certainly include the youngest females.

INTRODUCTION

Studies at the genetic, developmental, physiological, biomechanical, behavioral, and life history level all provide evidence that there are constraints on the breadth of functions that a single organism can perform. Suites of life history trait values coevolve a result of constraints and processes that occur at the individual level, and these traits interact with environmental factors to produce demographic traits of populations (Dunham et al., 1989a). Life history studies in general are labor and time intensive, and problems that impede life history and demographic studies are magnified when species being studied are long-lived (Tinkle, 1979). As a result development of conservation programs pertaining to long-lived organisms often must proceed without adequate life history data on target species.

A life history feature common among long-lived vertebrates is delayed sexual maturity (Charlesworth, 1980; Charnov, 1990; Dunham et al. 1988). Benefits attributed to delaying the onset of reproduction include increased quality of young produced, increased number of young per reproductive bout, decreased costs associated with reproduction, and decreased risk of mortality as an adult (Bell, 1977; Gadgil and Bossert, 1970; Stearns and Koella, 1986; Tinkle et al., 1970; Wiley, 1974). Theoretically, such benefits combine to result in higher lifetime reproductive success of individuals that delay sexual maturity than that attained by individuals maturing earlier. Costs of delaying sexual maturity include increased risk associated with death prior to first reproduction, and lengthened generation times.

An often overlooked inter-generational life history feature associated with delaying sexual maturity is the substantial increase in annual sur-

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vival of juveniles required to maintain a stable population (Dunham et al., 1989). Even with high annual fecundity, values of alpha approaching 20 years require annual juvenile survivorships that are greater than those reported for most extant vertebrates (Dunham et al., 1988; Turner, 1977; Wilbur and Morin, 1988; Ricklefs, 1973) to maintain a stable population.

We combined the results from studies of Blanding's turtles (*Emydoidea blandingii;* Congdon et al., 1993) and common snapping turtles (*Chelydra serpentina;* Congdon et al., 1994) to demonstrate how: 1) life history traits values may constrain potential responses to disturbances of populations, and 2) co-evolved life history traits should be of particular concern when formulating conservation and management programs for long-lived organisms.

MATERIALS AND METHODS

An intensive mark-recapture study of Blanding's turtles and snapping turtles has been maintained on the University of Michigan's, E. S. George Reserve (ESGR) for 29 (*E. blandingii*) and 20 (*C. serpentina*) of the past 39 years (Table 1). Data on clutch size, reproductive frequency, and age at maturity (alpha) are taken from Congdon et al. (1983, 1987, 1993, 1994), and Congdon and van Loben Sels (1990, 1993).

Each year from 1975 through 1986 and in 1990 intensive aquatic trapping was carried out from early May through early-September, and drift fences were usually monitored from April through June and during September and October. From 1987 through 1989 the study was conducted only from early May to early July. Each turtle was individually marked by notching the margins of the carapace, weighed, and measured (straight line plastron length and carapace length), and then released at the point of capture. Clutch size was determined from X-radiographs taken of all gravid females captured from 1978-1992.

Age class zero was assigned to the period from egg laying to emergence from the nest which occurred from late August to early October. Age class 1 began at emergence from the nest and covered the hatchlings' first fall, winter, and first full activity season. Turtles that were first captured with fewer than 19 or 12 growth rings (*E. blandingii* and *C. serpentina*, respectively) were assigned an age based on the assumptions that growth rings were laid down annually in juveniles and young adults.

Life tables were constructed from long-term means of all parameters except for annual survivorship (s_x) of juvenile Blanding's turtles between age one and 13 years; juvenile survivorship values were estimated to obtain values resulting in a stable population (Table 2). For the life tables, fecundity (m_x) was defined as the number of female eggs produced annually (i. e., average clutch size / 2, which adjusts for production of males by making an assumption of an equal primary sex ratio, and then multiplied by clutch frequency).

To examine the consequences of reproduction in survivorship of juveniles or adults, we set the population parameters of models at values slightly increased over long-term means to minimize the probability that required juvenile survival necessary to maintain a stable population would be overestimated. We explored the impact of changes in life history parameters on population stability by examining which combinations of the demographic variables (age at maturity, fecundity, nest survivorship, and juvenile and adult survivorships) would permit population persistence (i.e., $r \geq 0$, r is the solution to Euler's equation:

$$1 = \sum_{x=0}^{\infty} e^{-rx} l_x m_x$$

where l_x is the survival from birth to age x, m_x is the expected fecundity of a female of age x, and e is the base of natural logarithms).

RESULTS

Populations of Blanding's turtles and snapping turtles on the ESGR are essentially stable (Congdon et al., 1993, 1994: Table 3). Therefore, results from cohort analyses should accurately reflect population attributes of each species. Cohort generation times for snapping turtles (25.4 years) and Blanding's turtles (37.5 years) are primarily the result of the following life history traits: 1) long delays in sexual maturity, 2) extended reproductive lifespans, 3) high adult survival and 4) extended longevity. Coupled with the above traits, analyses of Blanding's and snapping turtles indicate that annual juvenile survival between age 1 and first reproduction must average over 80% and 76% to maintain a stable population (Fig 1a,b; 2a,b;3a,b). Although we could not actually determine the survival of Blanding's turtle hatchlings, measured survival of snapping turtle juveniles were close to the levels originally estimated.

Table 1.—A summary of mark recapture records and reproductive data on two species of turtles from the E. S. George Reserve.

	Individuals Marked	# of Recaptures	# X-radiographs	# Nests
E. blandingii	711	2,968	342	193
C. serpentina	1,576	3,922	202	378

Table 2.—A summary of values used in construction of life tables for *E. blandingii and C. serpentina* on the E. S. George Reserve in southeastern Michigan.

	E. blandingii	*C. serpentina*
Reproduction:		
Min Alpha	14 yrs	11 yrs
Mean Alpha	17.5	14.0
Mean clutch size	10.2	28.0
Clutch frequency	0.80	0.85
Annual fecundity	4.0	12.0
Survivorships (l_x)		
Nest (age 0)	0.44	0.23
(age 1)	0.78	0.45
Mean (age 2 - 12)	0.78	0.77
Adult females	0.96	0.93

Table 3.—Life tables for *Emydoidea blandingii* and *Chelydra serpentina* on the E. S. George Reserve. Data are long-term mean fecundity and survivorships for each age class of the population. S_x is the age-specific probability of survival, l_x is the probability of survival from age x to age x + 1, m_x is the expected fecundity of a female age x, Ro = net reproductive rate or the sum of l_xm_x, r = the intrinsic rate of population increase or the implicit solution of 1 = the sum of $l_xm_x^{e-rx}$, and T_c is the cohort generation time for the population. Population parameters are: *E. blandingii* R_o = 0.995; r = 0.0001, and T_c = 37.5 years; *C. serpentina* R_o = 1.009; r = 0.0004, and T_c = 25.4 years, Doubling Time = 1959 years.

Age	s_x	l_x	m_x	l_xm_x	s_x	l_x	m_x	l_xm_x
0	0.2610	1.00000	0	0.0000	0.230	1.00000	0	0.0000
1	0.7826	0.26100	0	0.0000	0.470	0.23000	0	0.0000
2	0.7826	0.20426	0	0.0000	0.810	0.10810	0	0.0000
3	0.7826	0.15985	0	0.0000	0.650	0.08756	0	0.0000
4	0.7826	0.12510	0	0.0000	0.650	0.05691	0	0.0000
5	0.7826	0.09790	0	0.0000	0.750	0.03699	0	0.0000
6	0.7826	0.07662	0	0.0000	0.740	0.02775	0	0.0000
7	0.7826	0.05996	0	0.0000	0.810	0.02053	0	0.0000
8	0.7826	0.04693	0	0.0000	0.770	0.01663	0	0.0000
9	0.7826	0.03672	0	0.0000	0.800	0.01281	0	0.0000
10	0.7826	0.02874	0	0.0000	0.820	0.01024	0	0.0000
11	0.7826	0.02249	0	0.0000	0.820	0.00840	4	0.0336
12	0.7826	0.01760	0	0.0000	0.820	0.00689	6	0.0413
13	0.7826	0.01378	0	0.0000	0.930	0.00565	8	0.0452
14	0.9600	0.01078	1	0.0108	0.930	0.00525	10	0.0525
15	0.9600	0.01035	2	0.0207	0.930	0.00489	12	0.0586
16	0.9600	0.00994	3	0.0298	0.930	0.00454	12	0.0545
17	0.9600	0.00954	4	0.0382	0.930	0.00423	12	0.0507
18	0.9600	0.00916	4	0.0366	0.930	0.00393	12	0.0472
19	0.9600	0.00879	4	0.0352	0.930	0.00365	12	0.0439
20	0.9600	0.00844	4	0.0338	0.930	0.00340	12	0.0408
21	0.9600	0.00810	4	0.0324	0.930	0.00316	12	0.0379
22	0.9600	0.00778	4	0.0311	0.930	0.00294	12	0.0353
23	0.9600	0.00747	4	0.0299	0.930	0.00273	12	0.0328
24	0.9600	0.00717	4	0.0287	0.930	0.00254	12	0.0305
25	0.9600	0.00688	4	0.0275	0.930	0.00236	12	0.0284
26	0.9600	0.00661	4	0.0264	0.930	0.00220	12	0.0264
27	0.9600	0.00634	4	0.0254	0.930	0.00205	12	0.0245
28	0.9600	0.00609	4	0.0244	0.930	0.00190	12	0.0228
29	0.9600	0.00584	4	0.0234	0.930	0.00177	12	0.0212
30	0.9600	0.00561	4	0.0224	0.930	0.00164	12	0.0197
31	0.9600	0.00539	4	0.0215	0.930	0.00153	12	0.0184
32	0.9600	0.00517	4	0.0207	0.930	0.00142	12	0.0171
33	0.9600	0.00496	4	0.0199	0.930	0.00132	12	0.0159
34	0.9600	0.00477	4	0.0191	0.930	0.00123	12	0.0148
35	0.9600	0.00457	4	0.0183	0.930	0.00114	12	0.0137
36	0.9600	0.00439	4	0.076	0.930	0.00106	12	0.0128
37	0.9600	0.00422	4	0.0169	0.930	0.00099	12	0.0119
38	0.9600	0.00405	4	0.0162	0.930	0.00092	12	0.0110
39	0.9600	0.00389	4	0.0155	0.930	0.00086	12	0.0103
40	0.9600	0.00373	4	0.0149	0.930	0.00080	12	0.0096
45	0.9600	0.00304	4	0.0122	0.930	0.00055	12	0.0066
50	0.9600	0.00248	4	0.0099	0.930	0.00039	12	0.0046
55	0.9600	0.00202	4	0.0081	0.930	0.00027	12	0.0032
60	0.9600	0.00165	4	0.0066	0.930	0.00019	12	0.0022
65	0.9600	0.00134	4	0.0054	0.930	0.00013	12	0.0016
70	0.9600	0.00110	4	0.0044	0.930	0.00009	12	0.0011
75	0.9600	0.00089	4	0.0036	0.930	0.00006	12	0.0008
80	0.9600	0.00073	4	0.0029	0.930	0.00004	12	0.0005
85	0.9600	0.00059	4	0.0024	0.930	0.00003	12	0.0004
90	0.9600	0.00048	4	0.0019	0.930	0.00002	12	0.0003
95	0.9600	0.00040	4	0.0016	0.930	0.00001	12	0.0002
100	0.9600	0.00032	4	0.0013	0.930	0.00001	12	0.0001
105	0.9600	0.00026	4	0.0011	0.930	0.00001	12	0.0001
110	0.9600	0.00021	4	0.0009				

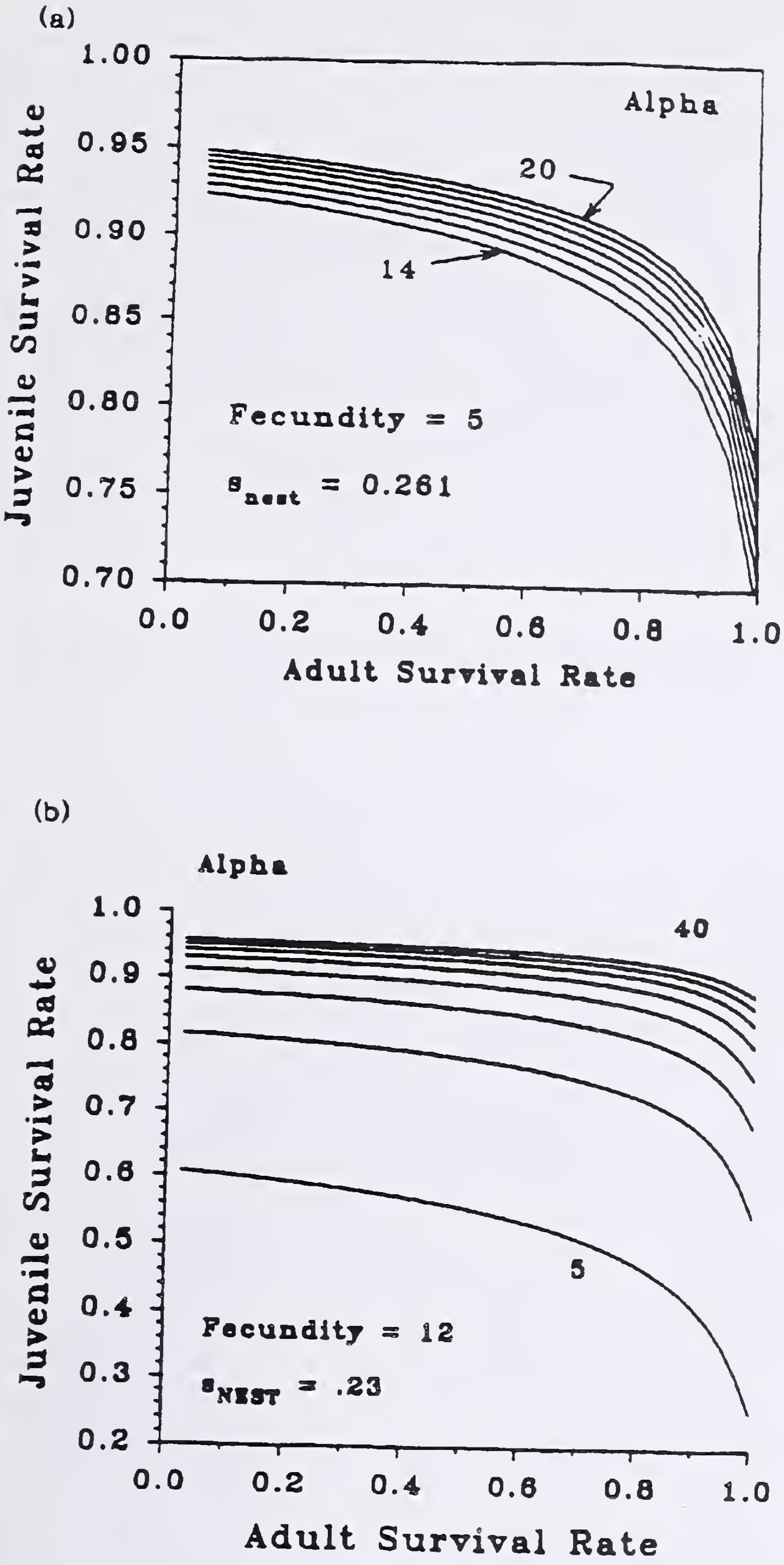

Figure 1.—The relationship between adult survival rate and juvenile survival rate while average age at sexual maturity (alpha) is allowed to vary from 14 to 20 years (*Emydoidea blandingii*) and from 5 to 40 years (*Chelydra serpentina*). Values for fecundity and nest survival are fixed.

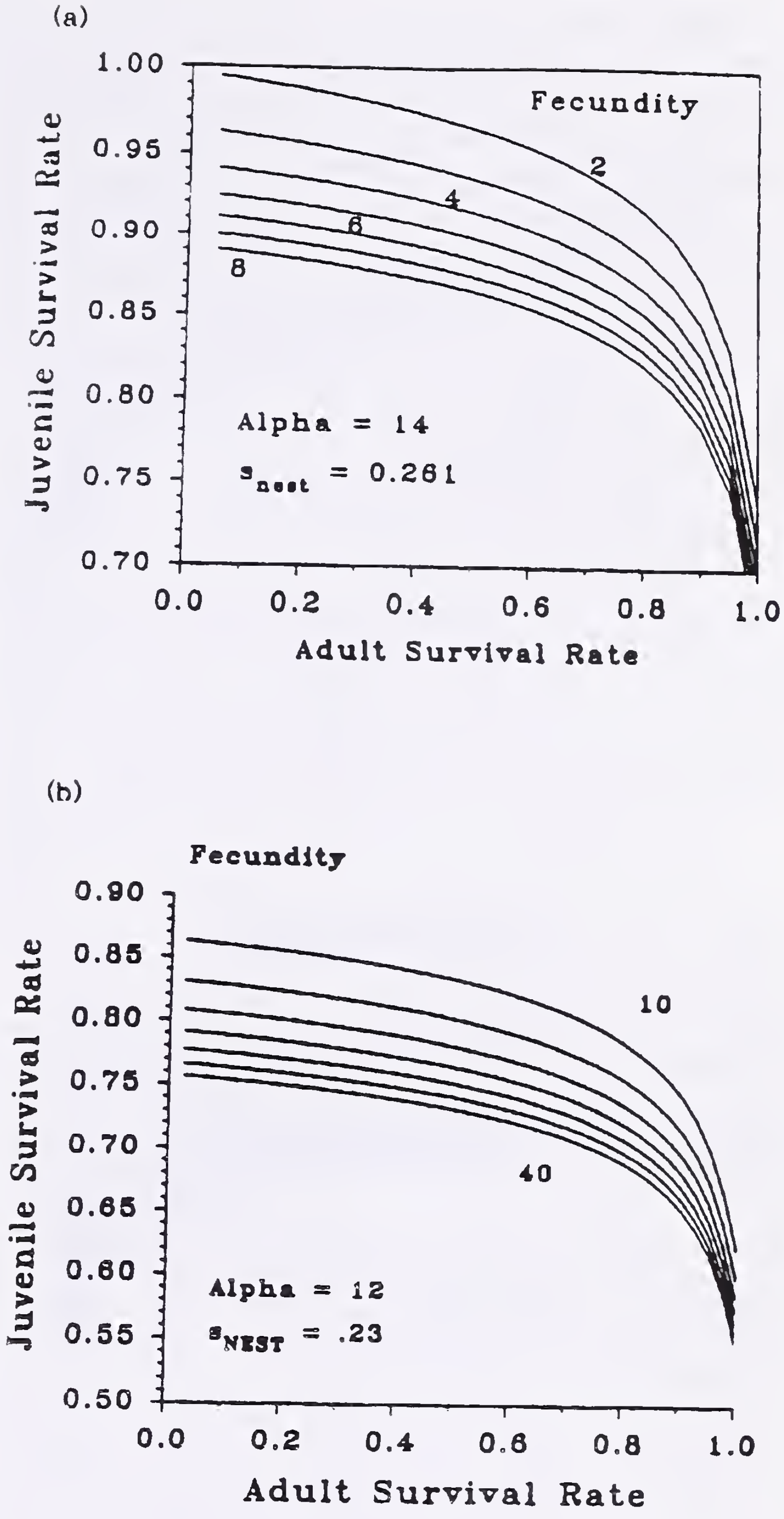

Figure 2.—The relationship between adult survival rate and juvenile survival rate while annual average fecundity is allowed to vary from 2 to 8 (*Emydoidea blandingii*) and from 10 to 40 (*Chelydra serpentina*) female producing eggs per adult female. Values for alpha and nest survival are fixed.

Snapping turtles are large bodied animals with females and males attaining maximum body masses of 6 and 14 kg, respectively, on the ESGR. The impact of harvesting adult snapping turtles from a population is dependent on the ages of the adults harvested (fig. 4). The younger the adults harvested the larger the impact on the population. since the youngest adult snapping turtles weight approximately 2 kg, it is probable that unregulated harvest would include the youngest females.

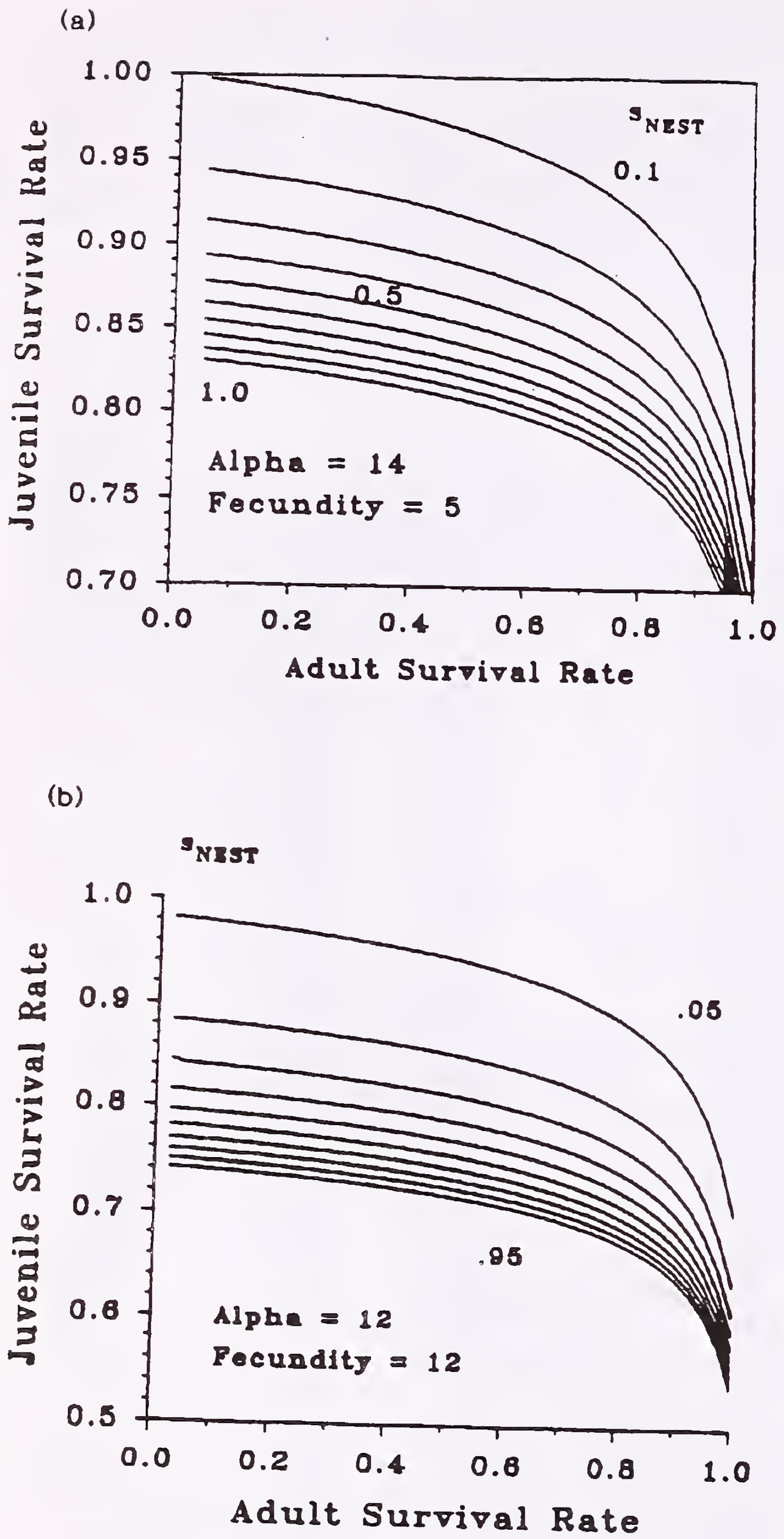

Figure 3.—The relationship between adult survival rate and juvenile survival rate while nest survivorship is allowed to vary from 0.1 to 1.0 (*Emydoidea blandingii*) and from 0.05 to 0.95 (*Chelydra serpentina*). Values for alpha and fecundity are fixed.

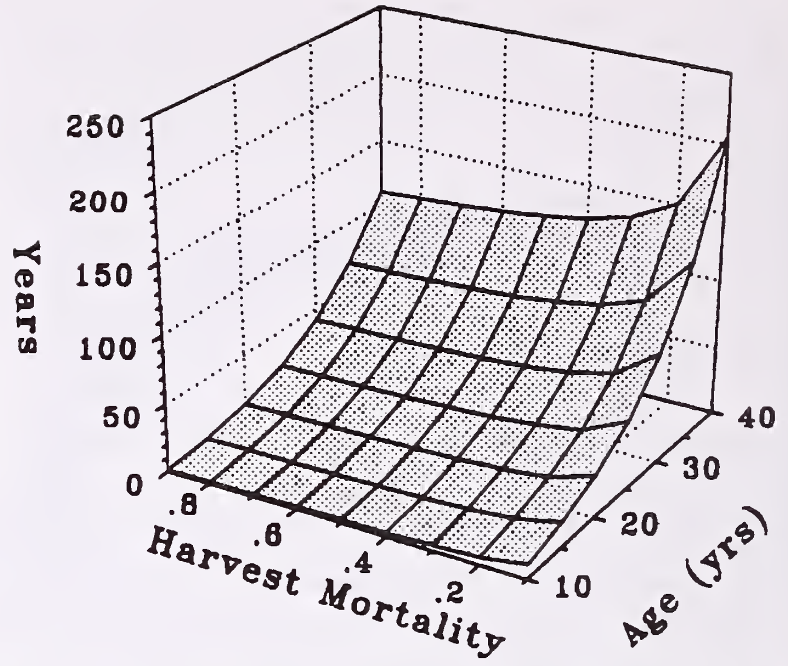

Figure 4.—The relationships among years taken to remove half a population and increased annual mortality due to harvesting adult *Chelydra serpentina* ranging in ages from 10 to 40 years.

DISCUSSION

Blanding's turtles are among the longest-lived freshwater turtles for which data are available from the field (Brecke and Moriarty, 1989). Some individuals marked on the ESGR as adults in the mid-1950s remain in the population, are now approaching a minimum of 60 years of age, are still reproductive, and exhibit no obvious signs of increased mortality or reproductive senescence (Congdon and van Loben Sels, 1993). Annual survival rates of adult Blanding's turtles and snapping turtles on the ESGR are among the highest reported for freshwater turtles (Brooks et al., 1991; Frazer and Gibbons 1990; Frazer et al., 1991; Gibbons and Semlitsch, 1982; Mitchell, 1988).

Our analyses indicate that the high average annual survival rates of juvenile turtles required to maintain a stable populations of Blanding's and snapping turtles are higher than juvenile survivorships reported for animals without parental care. It is important to note that the high average annual survival of juveniles does not need to be constant across all ages of juveniles or cohorts as long as the long-term mean (e. g., a minimum time span for a long-term mean would be equal to the minimum age at sexual maturity) among cohorts maintains the average required to maintain a stable population. However, values that fall below the mean survival values of juveniles in an age group or cohort will require increases in other age groups or cohorts of juveniles. Harvesting populations for the pet trade would in most cases include the taking of juveniles. In addition, without density dependent compensation of some type, harvesting of adults from a population will also require an increase in juvenile survival to maintain a stable population.

One long-lived chelonian of conservation concern in Arizona and California is the desert tortoise. Although adequate data on life history trait values are lacking, the desert tortoise shares many general life history traits with Blanding's and snapping turtles (delayed sexual maturity, iteroparity, and high adult survival rates). Desert tortoises reach sexual maturity between 12 and 20 years (Turner, et al., 1987 have clutch sizes that average 4 - 5 eggs and some females are capable of producing more than one clutch; however, some adult females do not reproduce every year (Turner et al., 1984; Turner and Berry, 1986). As a result, fecundity in desert tortoises is approximately 3 to 4 female eggs and is similar to Blanding's turtles. Desert tortoises have also been recently subjected to higher mortality associated with habitat destruction, upper respiratory tract disease, increased raven predation on hatchlings and young juveniles, harvesting for pets, and poaching (Berry, 1986). Since desert tortoises have life histories similar to Blanding's turtles, they will share the same demographic constraints demonstrated in this study, and management plans will need to address the problems related to high survivorship required by juveniles as well as adults.

The model and data from Blanding's and snapping turtles point out that in long-lived organisms in general, and desert tortoises in particular, chronic reduction in survival of adults requires an increase in the already high level of survivorship of juveniles to maintain a stable population. The probability that juvenile survival can increase, through compensatory release from density dependence, enough to offset even a relatively small chronic decrease in survival of adults in long-lived organisms seems very low (Brooks et al., 1991).

Some general conclusions from this study are that the suite of life history traits that coevolve with longevity results in populations that are severely limited in their abilities to respond to chronic increases in mortality of neonates and even less so to increased mortality of juveniles or adults. Headstarting hatchlings in many cases will have little effect if there is not concomitant reduction in the causes of mortality of older juveniles and adults. Effective management and conservation programs (Frazer, 1992) will be ones that recognize the integrated nature of life histories and the extreme limitation that the evolution of longevity has placed on the ability of populations of long-lived organisms to withstand and respond to increased reduced fecundity or increased mortality at any life history stage. In addition, programs developed to aid in the recovery of depleted populations of long-lived organisms must recognize that there will be long delays before population responses can be detected.

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Dendroclimatological Study in the Sierra de La Laguna, B.C.S. México

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INTRODUCTION

To manage a natural resource area adequately, it is necessary to have a clear knowledge of its communities, and their relationship to the environment. Climate is a participate environmental factor which determines species occurrence in a comunity, its variations produce diversity and abundance changes. If we could know the future climate trends, we could foresee the community changes and the management of the natural resources could be optimized.

To construct a climate prediction model it is necessary a wide range of climatic data. Unfortunately, the existing climatological records are too short to detect long-term climatic variability and changes.

The dendrochronology can produce information about past environments. If the climate estimates can be verified with independent climatic measurements, its estimates can be considered valid (Fritts, 1987). This way, it is possible to extend predictions for future and past climatic changes for undocumented time periods.

OBJETIVE

The principal aim of this work is to analyze the available climatic information for the Sierra de La Laguna mountain range, as well as the tree-ring climatic information. A climate trend prediction was constructed for this region, by means of dendroclimatological techniques, and its usefulness for management purposes of the natural resources of this area are discussed.

STUDY SITE

The study was carried out in the Sierra de La Laguna, a mountain range located in the southern portion of the Baja California Peninsula (fig. 1). Its geographical position and its altitudinal range produce marked climatic differences, which allow the establishment of different life forms, that are unique compared to those that occurred in the rest of the state. The upper portion, between 1,800 and 2,000 m.a.s.l., harbors the only oak-pine woodlands of the state. These represent the southwestern portion of the Sierra Madrean element, where an endemic conifer, *Pinus lagunae*, grows. This pine species constituted our main subject of study, with which we carry out the present dendrochronological study.

METHODOLOGY

Two increment cores were obtained from each of 80 selected pines from the oak-pine forest of the Sierra de La Laguna . Dendrochronological procedures and techniques with these cores were used to analyze radial growth. The procedures included cross-dating, measurements of the ring widths, and standardization of these measurements in order to obtain an index series from each tree. A master chronology was obtained by simple averages of the indices series. The dendrochronology computer program library (Holmes, 1992) was used to standardized and to obtain the master chronology.

The master chronology for the Sierra de La Laguna was compared with other chronologies of southwestern U.S.A. and Baja California state in Mexico concerning Sierra Madrean woodlands.

The regional climatic series (aridity series) was obtained by Díaz *et al.* (1994), who estimated a Martone's aridity index (1926) with the precipitation and temperature records of nine meteorological stations located at the low and middle lands of the Sierra de La Laguna.

Subsequently, both series were correlated and the best correlated model was selected for the aridity reconstruction. The model was used to verify the aridity estimations. Finally the aridity was reconstructed, and with these wide period of aridity data a Fourier analysis and a periodogram

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(Box and Jenkins, 1976) was obtained to test for the presence of persistent cycles.

RESULTS

The master obtained chronology included the period between 1804 and 1990. It was compared with other chronologies from California and the Sierra de San Pedro Martir, but no significant correlations were obtained between them.

Since linear regression model was to be used, dendrochronology and aridity series were first tested for normality and the significantly deviates values from the general fitted model were replaced with their corresponding unweighted moving five terms averages.

Single and multiple regressions were tested between the chronology of the next year (dependent variable) and temperature, precipitation, and aridity (independent variables). The best fitted model was a simple linear regression one relating aridity and chronology as follows: $Y = 2.988X + 65 (X)$; where: Y, is the chronology; X, is aridity; $r = 0.523$; and $p \leq 0.05$.

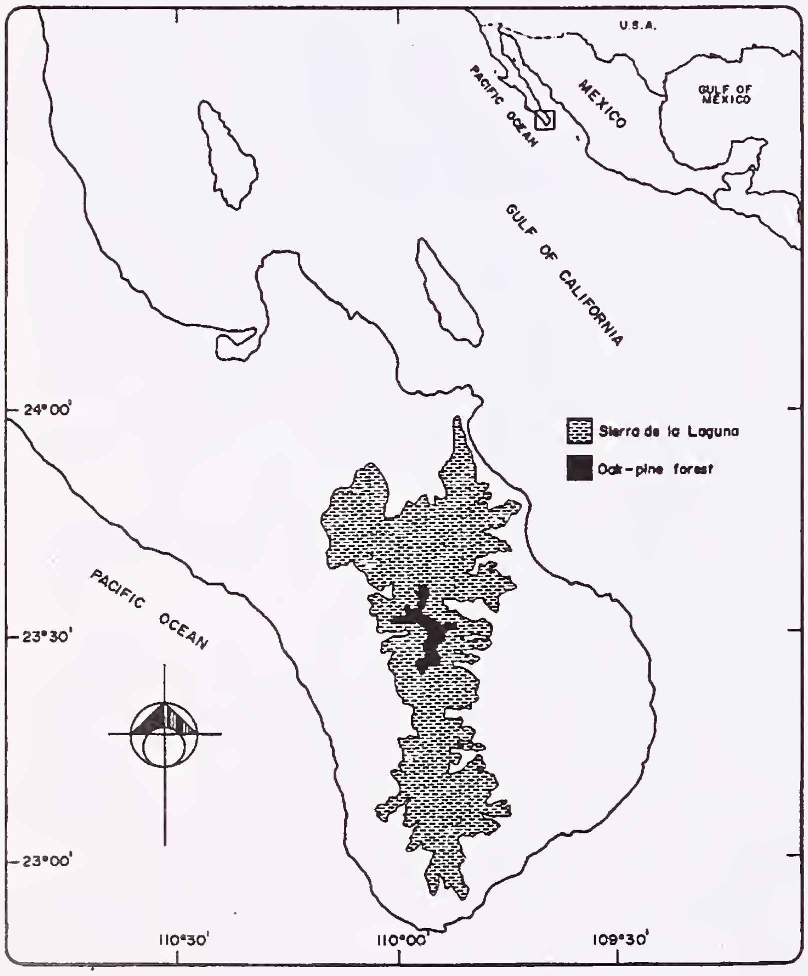

Figure 1.—Sierra de La Laguna localization.

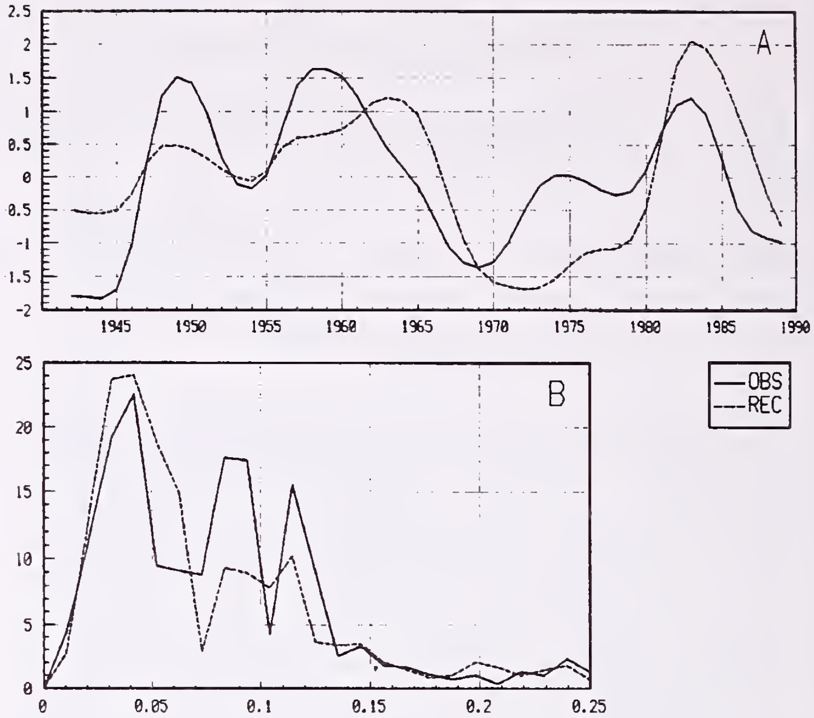

Figure 2.—A. Aridity series observed and recalculated. B. Aridity series Periodogram.

Aridity index was reconstructed from the regression equation and the values were compared with the actual aridity index values for the 1940-1989 period (fig. 2). It seems evident that the aridity interdecadal trends grossly correspond in both series.

The series obtained (fig. 3a) shows the occurrence of a high variability and high aridity period that goes from 1810 to 1890. This was interrupted by few years of very low aridity during de mid 1840's. From 1900 to the mid 1950's there was a remarkable stable period of intermediate aridity values. Recent years are highly variable, where a first decrease in aridity occurred during the mid 1960's, a maximum during the early 1970's. Another decrease in aridity also occurred during the mid of 1980's.

The aridity series obtained was examined with Fourier analysis techniques. Figure 3b shows the periodic graph in which six significant frequency values can be seen: 46, 37, 28, 20, 20, and 18 year periodicity.

DISCUSSION AND CONCLUSION

The results of low significance correlation between the master chronology for the Sierra de La Laguna and the other chronologies coincide with the observations of Rueda (1983). He stated that this low correlation is due to the variation in the precipitation patterns obtained for these zones.

The chronology-aridity correlation was found not to be equally correspondent maybe because there are not long climatic records available for this woodland area. Thus, we could only use the climatic data of the nearby meteorological stations. These stations are at a much lower altitude than the forest area. Besides the pine biological response to interannual variability in aridity may be "filtered"; if so, chronology may reflect better long sustained trends than interanual variations, as it is observed.

Despite limitations, aridity reconstruction was intended for the last two centuries based on chronology data. It reflects a sustained trend similar to those presented by the meteorological records for the nearby areas for the last decades variations.

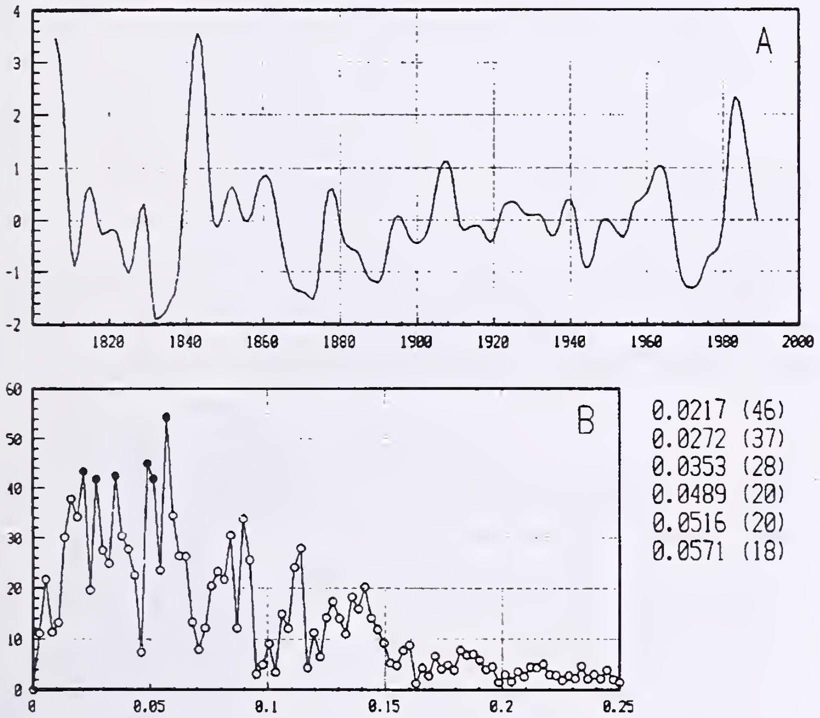

Figure 3.—A. The aridity series reconstructed. B. Periodogram for the aridity series reconstructed.

The frequencies of 24-year periodicity (fundamental frequency) in the aridity series obtained by Diaz *et al.* (1994), also were found in the aridity series calculated (Fig. 2b). Nevertheless, the time frequencies obtained in the series present a lot of noise.

It is concluded that *Pinus lagunae* is a sensitive species to long climatic variations. Therefore, further studies concerning future global climatic changes could be done using this species as a possible reference of how plant resources respond within this area.

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Remote Sensing and Geographic Information Systems Research in Southeastern Arizona

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Abstract.—The Advanced Resource Technology Program (ART) is an interdisciplinary research and service program in the School of Renewable Natural Resources, University of Arizona. ART was created to work with local, state and federal natural resource management agencies to create computer-based tools to efficiently solve natural resource problems in the southwestern United States. ART has been active developing new remote sensing and geographic information system (GIS) techniques for resource management. ART projects in Arizona, California, and Mexico, with groups such as the National Park Service, U.S. Fish and Wildlife Service, Arizona Game and Fish Department, Pima County, U.S. Forest Service, Bureau of Land Management, Arizona Department of Environment Quality and National Science Foundation. Examples of ART projects pertinent to southeastern Arizona include the Arizona GAP Analysis Project to assess how well different wildlife habitats are being protected in Arizona, vegetation mapping and GIS database development at Chiricahua National Monument, and development GIS-based fire management applications.

INTRODUCTION

The Advanced Resource Technology Program (ART), in the School of Renewable Natural Resources, University of Arizona was started in 1988 to provide advanced computer technology and expertise to researchers so they can develop computer-based tools for natural resource and agricultural assessment and analysis. Over this time ART has grown from several personal computers and a digitizing tablet to over $100,000 in equipment and a million dollars in outside research.

Most of this research has been conducted in the southwest and has a direct bearing on resource and environmental problems in the Madrean "Sky Islands" Archipelago. ART currently has research projects with the National Park Service, U.S. Forest Service, U.S. Fish and Wildlife Service, U.S. Navy, U.S. dir b: Air Force, Agricultural Research Service, National Science Foundation, and numerous state and local agencies. Several of these projects are located in southeastern Arizona, in the heart of the Archipelago.

The purpose of the poster paper is to review the work that has been done at ART in southeastern Arizona. The objective is to provide an understanding of the potential of using advanced computer technology to address research and management problems in the Archipelago.

ART ACTIVITIES

ART is an interdisplinary program with extension and education, as well as research responsibilities. ART has active research and service projects in several areas; use of remote sensing and global positioning systems for mapping, monitoring and inventory of resources, use of geographic information systems (GIS), models, and artificial intelligence in resource analysis, and the integration of different computer technologies such as GIS, models, and database management systems, to solve resource problems. ART pro-

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vides training and advice to outside groups and has an active educational program for graduate and undergraduate students at the University of Arizona. One criteria for accepting a project in ART is its educational and training potential. This includes providing students with database development and analysis experience.

Remote Sensing Applications

Researchers at ART have been developing procedures to integrate different types of remote sensing imagery, such as aerial photography, aerial videography, and satellite imagery, for resource mapping and monitoring (Myhre et al. 1991; Graham 1993). The techniques are being used to develop a state-wide vegetation map, at a scale of 1:100000, as part of the Arizona GAP Analysis Project, funded by the U.S. Fish and Wildlife Service. The analysis will combine, in a GIS, the vegetation map with known animal distributions, available water sources, and land ownership. The GAP Project will assess how well different wildlife habitats are being protected in Arizona. These techniques also are being used by GAP Analysis Projects in other states, as well as to map riparian vegetation in Arizona, and to map irrigation systems in Mexico.

Several studies have been conducted which examine the potential of different types of remote sensing imagery for resource mapping and monitoring. Qi (1994) used several types of imagery, satellite, videography and historical aerial photography to investigate changes in riparian vegetation in the Gila Box National Riparian Conservation Area in Arizona. Qi's work shows the potential of using remote sensing, including videography of monitoring riparian condition. Potter (1993) evaluated the use of several types of imagery for developing GIS databases of urban land use for hydrological modeling in the southwest. Potter found that high resolution imagery did not improve the modeling results and that the use of SPOT imagery was adequate for urban hydrological applications in the southwest.

Kunzmann et al. (1994) has integrated several computer based technologies in order to map vegetation at Chiricahua National Monument and surrounding areas. Using a 1:24,000 scale, true color, rectified mosaic of digital aerial photographs as a base, vegetation polygons were delineated using on-screen digitizing. GPS-Geolink linked airborne video point sampling (50 m horizontal swath width in full zoom), historical data, and a GIS with elevation, aspect and slope information were used to help classify the vegetation polygons. The vegetation classification plots were then measured, using procedures proposed by Krajina (1969) and Braun-Blanquet (1965), where sampling points within polygons were located using a global positioning system. Field vegetation measurements were then used to develop a neural network model to assist in the classification of all identified GIS vegetation community polygons into an ecologically based Brown, Lowe and Pase (1982) classification system. The results were then compared to a historical vegetation map for the area, done by Roseberry and Dole in 1939. Using a GIS, coincidence and spatial-temporal predictability analyses were conducted to describe changes in vegetation between 1939 and the present.

GIS Applications

A major limiting factor in the development of GIS applications is the lack of high quality spatial (GIS) databases. The creation and processes used to create high-quality databases, that can be used in application development, are an important part of the research effort. Importantly, in resource management, monitoring the effects of management actions in a timely and cost effective manner is essential, and is thus another important research topic dealing with database development (Walters and Holling 1990). Databases can be developed by keyboard data entry, hand digitizing, remote sensing technique, automated mapping using global positioning systems, traditional field surveying techniques, or a combination of several methods. Over the last several years ART has created several GIS databases in the Madrean Archipelago; Pusch Ridge Wilderness in the Santa Catalina Mountains, Saguaro National Monument (East), Chiricahua National Monument, Walnut Gulch Experiment Watershed, Santa Rita Experimental Range, Buenos Aires National Wildlife Refuge, and San Rafael/Huachuca Mountain area of the Coronado National Forest.

ART researchers have been active, designing, developing and testing computer-based applications to solve natural resource problems. One area of research has been the development of tools for fire management. This work has included the development of a GIS-based fire spread model FIREMAP (Ball and Guertin 1992; Vasconcelos and Guertin 1992). FIREMAP can simulate and display the spread of fire over time over complex terrain and varying weather conditions. FIREMAP also has been linked to tree mortality probability functions, of species found in northern Arizona, so the effect fire on stand dynamics can be simulated (Kunzmann et al. 1991). Vascocelos and Zeigler (1993) developed a technique to model spatial dynamic ecological processes by linking discrete-event simulation methodology (Zeigler 1990) with geographic information systems. With this technique Vasconcelos and Zeigler could simulate the evolution of different landscape patterns under varying fire regimes.

Ball (1994) used neural networks to map fire fuel parameters (fuel moisture and loading) in semiarid grasslands. The neural network model takes environmental variables, such as soil type, aspect, and slope, and points of known fire fuel characteristics and then predicts the fuel moisture in unsampled locations. The results may help fire managers create GIS map layers for fire management applications.

ART has been working closely with the National Park Service for several years at several units; Chiricahua National Monument, Organ Pipe Cactus National Monument, Petrified Forest National Park, Saguaro National Monument (East), Tonto National Monument, Casa Grande National Monument, Wupatki National Monument and Montezuma Castle National Monument. A number of GIS applications have been developed for these units; an archeology site prediction model and a cumulative erosion model for Petrified Forest (Kunzmann et al. 1994a), evaluating the effect of roads on wildlife mortality at Organ Pipe, investigating vegetation change at Chiricahua (Kunzmann et al. 1994b), and addressing visual quality concerns at Tonto (Christoperson et al. 1993). Current projects include investigating landscape biodiversity under different grain sizes at Organ Pipe National Monument and developing a paleo-site prediction model for Petrified Forest National Park.

Other applications that have been developed at ART include: GIS-based habitat modeling using logistic multiple regression for the Mt. Graham red squirrel (Pereira and Itami 1991), evaluating the effects of GIS database grid size on hydrologic simulation results (Hu and Guertin 1991), developing tools for recreation and visual quality management (Colvin and Gimblett 1991; Gimblett et al. 1987). At the Santa Rita Experimental Range, ART researchers have develop a spatial modeling approach to predict forage production and utilization in semidesert grasslands for range management (Wissler and Guertin 1991). Wissler and Ritter (1992), working with the Arizona State Museum, assessed the archaeological sensitivity of Arizona stream reaches. ART has also been working with federal agenices to define GIS program needs for small resource management units (Potter et al. 1992).

ART researchers also have been developing new computer programming procedures for simulating spatial dynamic processes (Ball and Gimblett 1992). In cooperation with the Department of Electrical and Computer Engineering, ART is currently developing algorithms the utilize new computer architectures for simulating complex natural systems (Gimblett et al. 1994).

SUMMARY

Holistic management of the Madrean Archipelago requires the use of computer-based technology to make it a functional reality. Remote sensing is used to inventory, and importantly, monitor the resources and the affect management has on the resources. Geographic information systems (GIS) are not only used for spatial data management, but with cartographic modeling techniques to perform spatial analysis to help evaluate resource problems (Berry 1986). Models will need to be designed or adapted to use the new power of GIS and be capable of assessing the cumulative effects of our management actions. Importantly, field research is needed to validate the models. In the future, global positioning systems will be very important not only for efficient resource mapping and inventory, but for delineating and locating research sites. Work in these areas is just beginning. The ART Program will continue to facilitate the development of resource management computer-based tools.

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Lizards of the Sierra de La Laguna, Baja California Sur, Mexico

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INTRODUCTION

The southernmost portion of Baja California south of the Isthmus of La Paz is known as the Cape Region. This region had an origin related to but separate from that of the remainder of the peninsula and throughout its evolution had an interesting climatic and phytogeografic history.

The origin of lizard species (and Herpetofauna species in general) distributed in the Cape Region and in the Sierra de La Laguna particularly are different and varies according to the autors (Savage 1960, Murphy, 1983, Grismer 1994). Most of these species have their origin in the southwest coast of México, in fact, Murphy (1983) proposed that as the Cape Region broke away from mainland México it carried with it a representative herptetofauna of southwestern México.

When the distribution of species are studied its necessary to analize their habitat usage. According with Rose (1976), the factors could contribute to differences between and within species in habitat usage are species-specific preferences, competitive exclusion, physical characteristics of habitats, and behavioral flexibility.

The central aim of this paper is to describe and analyse the distribution and habitat use of lizards and their habitat use at Sierra de La Laguna.

METHODS

Lizard's observation were made at Sierra de La Laguna (fig. 1) throughout "La Zorra" canyon (East side, near Santiago) and "La Burrera" canyon (West side, near Todos Santos) (fig 1).

Habitat and microhabitat niche breadth were calculated using a standardized measure of Simpson's diversity index (Ds) to range between 0 (only one sort of habitat used) to 1 (equal frequencies over all the habitats) (Levins, 1968).

Habitat and microhabitat niche overlaps between species were measured using Pianka's index (O_{jk}) (Pianka, 1973).

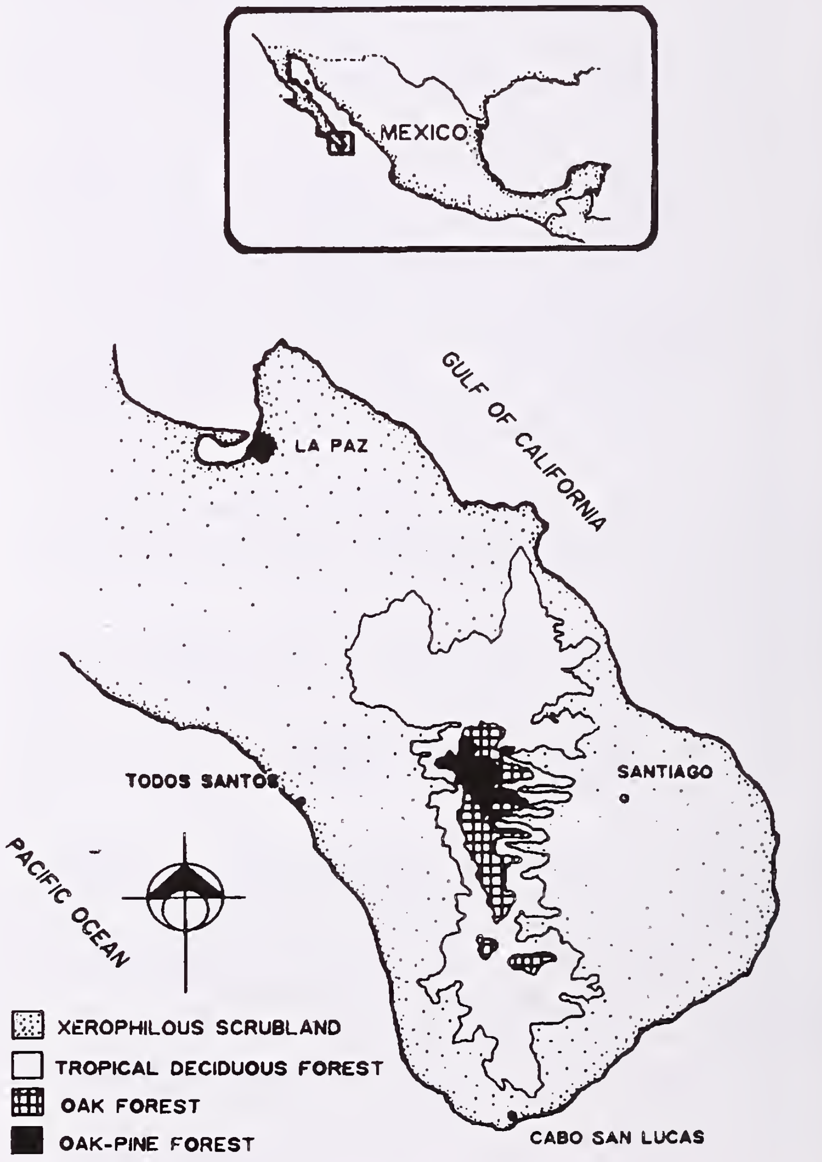

Figure 1.—The location of the Sierra de La Laguna, Baja California Sur, México.

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RESULTS

A total of eighteen species were observed along the transects. Five of these species are endemic for the Cape Region, as well as four subspecies (Table 1).

Table 2 shows the Sierra de La Laguna Lizard taxonomic composition, as well as the found number of individuals by vegetation association.

These observations have made possible to define the distribution of the species along the altitudinal gradient of Sierra de La Laguna. Figure 2 exhibits the vertical distribution of lizard species. As it is possible to observe the most widely distributed species are *Urosaurus nigricaudus* and *Sceloporus zosteromus*, in spite of them the individuals of the last one are scarce.

Table 1.—Lizard endemics present at Sierra de La Laguna.

BAJA CALIFORNIA SUR ENDEMICS

Species	Subspecies
Eumeces lagunensis	*Phyllodactylus xanti xanti* *Ctenosaura hemilopha hemilopha*

CAPE REGION ENDEMICS

Species	Subspecies
Phyllodactylus unctus	*Callisaurus draconoides draconoides*
Sceloporus licki	*Petrosaurus thalassinus thalassinus*
Sceloporus hunsakeri	*Xantusia vigilis gilberti*
Sceloporus zosteromus	*Elgaria paucicarinata paucicarinata*
Cnemidophorus maximus	

Table 2.—Taxonomic composition and number of lizard censused in each vegetation type.X.S.= Xerophilous Scrubland, T.D.F.= Tropical Deciduous Forest, O.F. = Oak Forest, O.-P.F. = Oak-Pine Forest, Ds = Standarized niche breadth (Simpson's Index standarized).

FAMILY	SPECIES	X.S.	T.D.F.	O.F	O.-P.F.	Ds
GEKKONIDAE	*Phyllodactylus unctus*	4	2	-	-	0.226
	Phyllodactylus xanti	3	3	-	-	0.333
	Coleonyx variegatus	5	-	-	-	0
XANTUSIIDAE	*Xantusia vigilis*	-	-	18	22	0.326
SCINCIDAE	*Eumeces lagunensis*	-	-	-	1	0
TEIIDAE	*Cnemidophorus hyperythrus*	51	7	-	-	0.089
	Cnemidophorus maximus	31	5	-	-	0.104
ANGUIDAE	*Elgaria paucicarinata*	-	5	7	18	0.420
PHRYNOSOMATIDAE	*Callisaurus draconoides*	33	20	-	-	0.295
	Petrosaurus thalassinus	2	31	9	14	0.508
	Phrynosoma coronatum	6	-	-	-	0
	Sceloporus hunsakeri	3	25	2	2	0.198
	Sceloporus licki	5	29	4	2	0.268
	Sceloporus zosteromus	4	1	2	2	0.746
	Urosaurus nigricaudus	45	27	12	20	0.759
	Uta stansburiana	32	-	-	-	0
IGUANIDAE	*Dipsosaurus dorsalis*	30	-	-	-	0
	Ctenosaura hemilopha	12	2	-	-	0.108

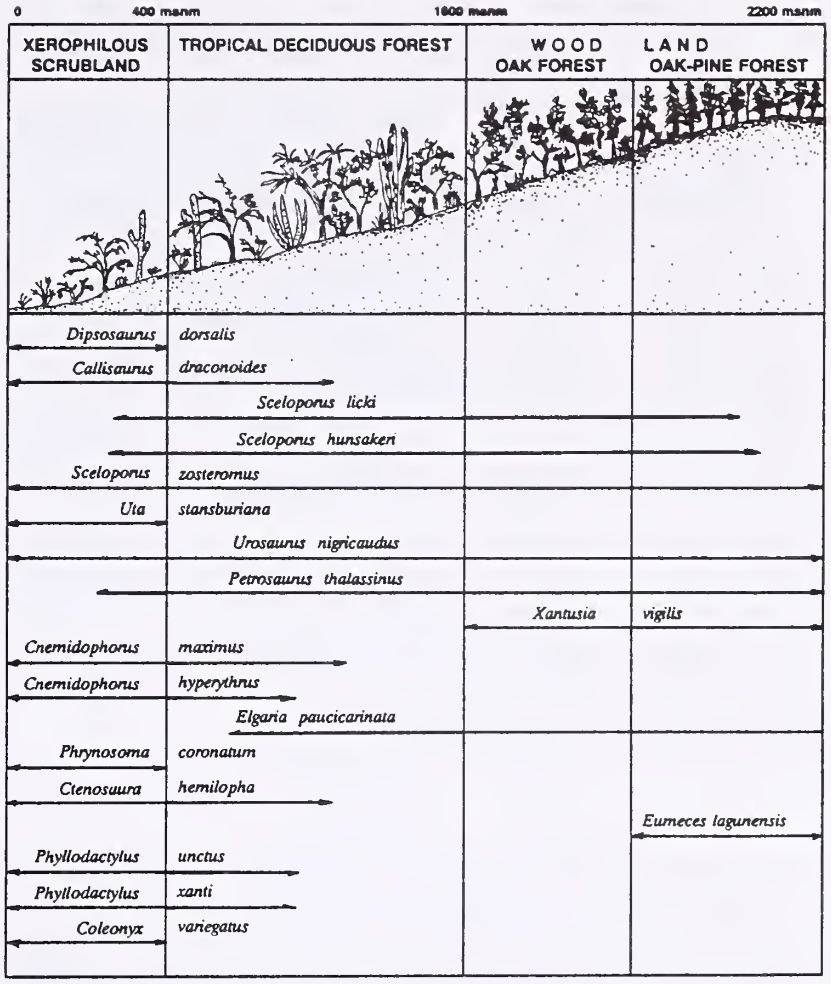

Figure 2.—Altitudinal distribution of the lizards of the Sierra de La Laguna, Baja California Sur.

At microhabitat level there exists different preferences: Table 3 shows the substrate utilization by the 11 more abundant species. The species with highest diversity of microhabitat use were *Sceloporus licki* and *Urosaurus nigricaudus*.

Individuals of *Diposaurus dorsalis, Callisaurus draconoides, Cnemidophorus hyperythrus* and *Cnemidophorus maximus* spent most of their time on the soil. *C. draconoides* is found mostly on sandy soils.

Petrosaurus thalassinus exhibit a marked preference by rocks bigger than 2 m and rocky wells. *Sceloporus hunsakeri, S. licki* and *Urosaurus nigricaudus* are found on rocks smaller than 2 m and the last two species could be found, with the same frequency, on trees. *Xantusia vigilis* individuals were only found below fallen trunks in the forest.

Habitat interspecific overlap values are showed at Table 4 (lower part) and the microhabitat at the upper part. Table 5 shows the average of both values.

Table 3.—Distribution of species by microhabitat (relative occurrence). Ds= Standarized niche breadths, Sp.= SPECIES : D.s.= Dipsosaurus dorsalis, C.d.= Callisaurus draconoides, S.l.= Sceloporus licki, S.h.= Sceloporus hunsakeri, U.s.= Uta stansburiana, U.n.= Urosaurus nigricaudus, P.t.= Petrosaurus thalassinus, X.v.= Xantusia vigilis, C.m.= Cnemidophorus maximus, C.h.= Cnemidophorus hyperythrus, E.l.= Eumeces lagunensis.

Sp.	sandy	consolidate	< 1m	1-2m	> 2m	< 30 cm	> 30 cm	log	stone	fallen log	rock	Ds
D.d.	0.467	0.533	-	-	-	-	-	-	-	-	-	0.099
C.d.	0.736	0.264	-	-	-	-	-	-	-	-	-	0.063
S.l.	-	-	0.125	0.125	0.225	0.200	0.225	-	-	0.100	-	0.447
S.h.	-	-	0.219	0.406	0.313	-	-	-	-	-	0.031	0.221
U.s.	0.125	0.469	0.125	-	-	-	-	-	-	0.281	-	0.202
U.n.	-	0.058	0.163	0.115	0.038	0.221	0.192	-	-	0.212	-	0.470
P.t.	-	-	-	0.107	0.588	-	-	-	-	-	0.304	0.181
X.v.	-	-	-	-	-	-	-	0.545	0.455	-	-	0.098
C.m.	0.305	0.667	-	-	-	-	-	0.028	-	-	-	0.085
C.h.	0.293	0.673	-	-	-	-	-	-	-	0.034	-	0.085
E.p.	-	0.667	-	-	-	-	-	0.200	-	0.133	-	0.099

Table 4.—Habitat (lower part of the table) and Microhabitat (upper part of the table) niche overlaps values between species (O_{jk}). The abbreviation are the same that Table 3.

Ojk	*D.d.*	*C.d.*	*S.l.*	*S.h.*	*U.s.*	*U.n.*	*P.t.*	*X.v.*	*C.m.*	*C.h.*	*E.p.*
D.d.	-	0.874	0	0	0.757	0.104	0	0	0.957	0.951	0.707
C.d.	0.854	-	0	0	0.480	0.046	0	0	0.698	0.684	0.317
S.l.	0.167	0.649	-	0.620	0.178	0.849	0.509	0	0	0.010	0.044
S.h.	0.118	0.613	0.997	-	0.085	0.401	0.655	0	0	0	0
U.s.	1	0.854	0.167	0.118	-	0.445	0	0	0.832	0.856	0.859
U.n.	0.783	0.913	0.640	0.600	0.783	-	0.123	0	0.126	0.150	0.019
P.t.	0.057	0.505	0.927	0.925	0.057	0.649	-	0	0	0	0
X.v.	0.069	0.095	0.215	0.186	0.069	0.486	0.531	-	0.029	0	0.216
C.m.	0.987	0.926	0.321	0.274	0.987	0.848	0.196	0.079	-	0.998	0.865
C.h.	0.990	0.917	0.290	0.252	0.990	0.840	0.176	0.078	0.999	-	0.870
E.p.	0	0.129	0.351	0.344	0	0.504	0.667	0.933	0.039	0.034	-

Table 5.—Average of Habitat-microhabitat niche overlaps values between species (O_{jk}).

Ojk	*D.d.*	*C.d.*	*S.l.*	*S.h.*	*U.s.*	*U.n.*	*P.t.*	*X.v.*	*C.m.*	*C.h.*	*E.p.*
D.d.	-	0.864	0.084	0.059	0.875	0.444	0.029	0.034	0.972	0.971	0.354
C.d.		-	0.325	0.307	0.667	0.480	0.253	0.048	0.812	0.801	0.223
S.l.			-	0.811	0.173	0.745	0.748	0.108	0.161	0.155	0.197
S.h.				-	0.102	0.502	0.818	0.093	0.137	0.126	0.172
U.s.					-	0.614	0.029	0.035	0.910	0.923	0.430
U.n.						-	0.393	0.243	0.487	0.495	0.365
P.t.							-	0.266	0.098	0.088	0.334
X.v.								-	0.054	0.039	0.575
C.m.									-	0.998	0.452
C.h.										-	0.452
E.p.											-

DISCUSSION

Lizard community, at La Sierra de La Laguna, seems to be spatially subdivided - at vegetation association level - in different subsets of only 4 o 5 species. Each subset is further ecologically subdivided at microhabitat utilization level, as well as by foraging strategies or food specializations.

Most of them, in fact, show various substrat specialities. Such specializations are well-known in lizards (Pianka, 1966; 1986) but they are not necessarily nor likely to be a competitively induced phenomena as previously has been discussed (Rose, 1976, Barbault and Maury, 1981; Barbault et al., 1985).

Higher spatial overlap values are found at the desert scrub at the soil level. However, among these species it is possible to find different foraging strategies and food specializations, which could contribute to reduce potential competition pressures. For example, *Dipsosaurus dorsalis* and *Callisaurus draconoides* have high spatial overlap, nevertheless *D. dorsalis* is primarily herbivorous mean while *C. draconoides* is insectivorous. On the other hand in the case of *Cnemidophorus hyperythrus* and *C. maximus,* the variation of size determined the differences in the diet.

According to Asplund (1967), lizards of several species (or species complexes) appear to be less restricted in habitat occurrence in the Cape than in more xeric habitats peripheral to and within the Sonoran Desert.

CONCLUSION

Lizard community at La Sierra de La Laguna is very rich, such in species diversity as well as in endemic occurrence. These richness is product of the complex geologic history of the region, as well as the variability of vegetation, topography and substrate at the zone.

The species of this lizard community are ecologically differentiated in the use of the habitat and microhabitat. There exists conspicuous preferences in the use of spatial resources. Such specializations, however, are not necessarily produced by interspecific competition pressures, but it could be evolved in the context of complex combination of selective pressures (Ortega *et al.*, 1982) such as predator escape, reproductive success and thermoregulatory behavior.

Because the biological importance of La Sierra de La Laguna, and because the pressures of human activities on their natural resources, it is necessary to develop further studies concerning the key communities and species of the region. Certainly, lizards of La Sierra de La Laguna must be deeply studied in order to guarantee its conservation.

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Multiscale Analysis in Ecosystem Management for the Lone Mountain/San Rafael Valley Ecosystem Management Area

Carrie Christman[1] and William J. Krausman[2]

Differing scales of spatial data provide different kinds of information about an ecosystem area. By using data ranging from very small scale to very large scale, important information can be represented regarding land use patterns and habitat distribution. This information is an essential tool for effective ecosystem management. This poster displays varying scales of remotely sensed data encompassing the Lone Mountain/San Rafael Ecosystem Management Area. Advance Very High Resolution Radiometer (AVHRR) and Thematic Mapper (TM) satellite imagery, high altitude photography, resource photography, and on-site photography are used to show examples of different scales of data.

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RESUMENES EN ESPAÑOL

Alfredo Ortega, Heidi romero-Schmidt, Jesus Acevedo, y Dolores Vazquez

01. La Importancia ecológica del Archipielago Madreano de las Islas en el Cielo: Una Visión Mundial.

Peter Warshall, Office of Arid Lands Studies, College of Agriculture, University of Arizona, Tucson.

Los trabajos previos sobre aislamiento biogeográfico se han referido a la cadena de islas oceánicas, islas asociadas con continentes, archipiélagos marginales y cuerpos de agua tales como el sistema de lagos africanos, el cual funciona como "islas acuáticas". Este artículo examina las "islas continentales" y las compara con el Archipiélago Madreano de las islas en el cielo. El contexto geológico, hidrológico y climático de los archipiélagos Afroalpino, Guyana, Páramo, y Desierto alto y bajo de la Gran Cuenca (Great Basin), se comparan en cuanto a áreas fuente, número de islas, mecanismos de aislamiento, ecosistemas interactivos e historia evolutiva. La historia de la exploración científica y el trabajo de campo para el Archipiélago Madreano y su estatus único entre todos los archipiélagos del planeta, se resumen.

02. La Importancia de la Sierra Madre Occidental en la Diversidad Biológica de México.

Robert Bye., Director del Jardín Botánico, Instituto de Biológia, Universidad Nacional Autónoma de México, México, D.F.

Las cinco provincias montañosas morfotectónicas de México están cubiertas con bosques de coníferas-encino, aunque éstos bosques ocupan cerca del 21% de la superficie terrestre de México (la segunda después de los desiertos), ellos alojan el tipo de vegetación mas diverso, que contiene la mayor riqueza (7,000 especies o 24% de la flora) y endemismos (4,000 especies, 32% de la flora) de las plantas vasculares. La Sierra Madre Occidental es la extensión más norteña de la principal cadena montañosa Mexicana. Constituye el principal centro de diversidad de plantas tales como el madroño *(Arbutus)*, frijoles silvestres *(Phaseolus)*, y maguey *(Agave)*. Las plantas endémicas de la Sierra Madreana, no solamente se derivan a través de la radiación de especies en los hábitats fragmentados a lo largo de escarpados gradientes ecológicos, sino que también son elementos relictuales de migraciones anteriores de plantas (e.g.*Picea parnassia*) y de progenitores de diversos taxa contemporáneos (e.g. *Ceanothus*). Los beneficios de los bosques Madreanos pueden ser medidos en términos locales y nacionales. Aunque las políticas actuales tienden a enfatizar estos bosques heterogéneos como una fuente de material genético primario para madera y pulpa, los residentes de los bosques, quienes han vivido por varias generaciones ahí, reconocen y utilizan una amplia serie de productos vegetales con propósitos domésticos y comerciales. Por ejemplo, de las casi 300 especies de las plantas medicinales, cerca de una sexta parte de ellas llega a los mercados regionales y nacionales. Ciertas especies medicinales (por ejemplo *Lingusticum porteri, Psscalium decompositum*) son cada dia más escasas con el cambio en las prácticas del uso del suelo, mientras que algunos endemismos (e.g.*Packera Candidissima)* se han incrementado con la apertura de los bosques. El reconocimiento de los valores biológicos, culturales y utilitarios, actuales y potenciales, de la flora de la Sierra Madre Occidental, deben ser integrados en las políticas futuras de manejo para la región.

03. Interrelaciones Entre Investigaciones y Manejoen el Archipielago Madreano.

Peter Ffolliott, School of Renewable Natural Resources, University of Arizona, Tucson; Leonard F. DeBano, Rocky Mountain Forest and Range Experiment Station, c/o School of Renewable Natural Resources, University of Arizona, Tucson; y Alfredo Ortega Rubio, Centro de Investigaciones Biológicas del Noroeste, La Paz, B.C.S. México.

Una clave para el éxito de ésta conferencia es el analizar adecuadamente las relaciones de la investigación y el manejo de ecosistemas en el Archipiélago Madreano. Al hacer esto nosotros esperamos ilustrar cuales son los eslabones entre la investigación, no importa cúan ampliamente esté definida, y el papel del manejo necesario para mantener la biodiversidad. Los componentes de los ecosistemas representados pueden ser vistos como procesos circulares con numerosos mecanismos de retroalimentación. Esto es, la investigación efectiva se formula principalmente en respuestas a los deseos de la gente de implementar un mejor manejo, y a su vez un mejor manejo desarrolla la generación de nuevos descubrimientos obtenidos de investigaciones sensibles. Al colocar los eslabones entre investigación y manejo en una perspectiva para los participantes de esta conferencia nosotros presentaremos una representación modular de los principales componentes del Archipiélago Madreano (población, agricultura, industria, recursos naturales y contaminación) dentro de una red integral de conexiones de retroalimentación. Nosotros sostenemos que esta representación es una herramienta útil en el intento de comprender donde hemos estado, donde estamos en el presente y donde debemos proceder para asegurar que las preocupaciones de la gente en relación a las caracteristicas de la biódiversidad del Archipiélago Madreano se encuentran propiamente consideradas. Es imperativo que la comunidad de investigadores, manejadores y sociedad, desarrollen una confianza mutua y propia para comprender y manejar la biódiversidad del Archipiélago Madreano.

04. Una Visión de la Flora de las Islas en el Cielo: Sureste de Arizona, Diversidad, Afinidades e Insularidad.

Steven P. McLaughlin. University of Arizona, Office of Arid Lands Studies, Tucson.

La región de la "Islas en el Cielo" del sureste de Arizona coincide aproximadamente con el Distrito Apacheano de la Provincia Florística Madreana. La región se extiende de las Montañas Pinaleno y Galiuro en el norte y hacia las Montañas Baboquivari en el oeste. La flora total de la región incluye de 2000 a 2100 especies de la cuales cerca de 160 son no nativas; las familias más grandes en orden descendiente son la Asteraceae, Poaceae, Fabaceae, Cyperaceae, Scrophulariaceae, y Euphorbiaceae. Las montañas más grandes que se extienden dentro de la región de las Islas en el Cielo - Santa Catalina, Rincons, Chiricahua y Huachucas- tienen floras locales que poseen cerca de la mitad de la flora regional. Para su tamaño y rango altitudinal las Montañas Pinaleno se encuentran comparativamente paupérrimas. Basadas en sus distribuciones dentro del oeste de los Estados Unidos, las especies nativas pueden ser clasificadas como Madreanas (58%) Cordilleranas (17%) Sonorenses (14%), Californianas (6%) e Intermontañas (5%). El elemento Madreano es un grupo heterogéneo de especies encontradas principalmente en el sur de la frontera internacional y alcanzando su límite norteño de distribución en el sureste de Arizona; incluyendo especies endémicas con afinidades Chihuahuenses, Sinaloenses y tropicales así como Apacheanos (Islas en el Cielo). En comparación con floras realmente insulares, la región de las Islas en el Cielo muestra un grado comparativamente bajo de endemismos locales y regionales, un grado comparativamente alto de similaridad entre islas y un bajo porcentaje de especies exóticas. En contraste con el sureste de Arizona, se conoce muy acerca de la flora de ésta porción de la región de las Islas en el Cielo del noreste de Sonora y noroeste de Chihuahua o cómo la flora de la región de las Islas en el Cielo se relaciona con la de la Sierra Madre Occidental como un todo.

05. Un Puente Hacia los Trópicos: Los árboles de la Región Madreano-Apacheana del Sureste de Norte América.

Richard S. Felger, Drylands Institute, University of Arizona, Tucson; and, Matthew B. Johnson, Desert Legume program, University of Arizona, Tucson.

Casi 230 especies de árboles existen en la regiones montañosas Madreano-Apacheanas del este de Sonora, oeste de Chihuahua y en las Islas en el Cielo de Arizona-Nuevo México. Aunque comprenden solamente 3 a 5 % de la flora, éstas son especies-clave de plantas para las áreas. Originalmente, los árboles formaron un dosel casi cerrado de bosque tropical deciduo (BTD) en las bajas altitudes de la parte sureste de la región. Los BTD se extienden en una diversidad reducida hacia el margen sureste de la región de las Islas en el Cielo en el noroeste de Sonora. El BTD ripario del sureste de Sonora y adyacente a Chihuahua es especialmente rico con árboles tropicales, muchos de ellos alcanzan alturas de 20 a 30 m. El BTD del noroeste de México contiene la más rica flora de árboles en el sureste de Norte América. En el extremo norteño de la reión, el BTD es eliminado por el incremento en sequía y el clima congelante y da paso al Desierto Sonorense, el Desierto Chihuahuense y a los pastizales donde los árboles son principalmente riparios. La interposición de elementos templados norteños entre las floras tropicales produce conjuntos de especies únicas en el mundo. Diversos bosques de encino y bosque de coníferas se extienden a través de la región en altas elevaciones. Estos bosques exhiben diferencias altitudinales, y específicas de nicho del norte al sur. El carácter de éstos hábitats está producido por una cierta contigüidad de comunidades bióticas en un gradiente altitudinal y norte-sur. Conforme uno se mueve hacia el norte, existe la tendencia de una reducción en la estatura y una reducción de las especies tropicales, géneros y familias enteras. Más de una docena de familias de origen tropical alcanzan sus límites norteños (al menos en la América del Norte Occidental) en Sonora y Chihuahua. Muchas especies templadas norteñas de árboles penetran al interior de América Latina en las altas elevaciones de montañas. Sin embargo, proporcionalmente pocas especies encuentran sus límites sureños en la región. Desafortunadamente, los enormes bosques BTD del noreste de México están amenazados por la irreversible desertificación debida principalmente a la deforestación y a la introducción del pasto Buffel. La fragmentación de éstas áreas está ocurriendo a un ritmo muy rápido y está destruyendo la contigüidad de los bosques que una vez llegaron hasta Sudamérica. El potencial para otros usos de los BTD por las comunidades locales está disponible. Métodos de explotación y agroforestales de los productos del bosque usando técnicas menos destructivas deberán ser exploradas.

06. El Muestreo de la Diversidad Biótica en el Archipiélago Madreano: Lecciones de Inventarios Regionales.

Tony Burgess, Desert Laboratory, University of Arizona; Julio Betancourt, Desert Laboratory, U.S. Geological Survey; and, John Busby, ERIN Unit, Australian National Parks & Wildlife Service.

El muestreo y monitoreo adecuado son el núcleo de una comprensión y manejo efectivo. El fenómeno de las Islas en el Cielo implica fuertes contrastes de vegetación o una alta diversidad beta en cortas distancias. Nuestra experiencia en crear bases de datos sobre distribución de las plantas en el Desierto Sonorense, en el suroeste de Norteámerica y al norte de Australia, han revelado problemas fundamentales con la intensidad del muestreo requerido para presentar adecuadamente la biodiversidad regional. Por medio de curvas de área-especies nosotros mostramos el efecto de la intensidad del muestreo sobre nuestras estimaciones de diversidad. Los problemas de muestreo se empeoran por la escala local de variante biótica y la dificultades de acceso inerentes a situaciones montañosas. La representación inadecuada de la diversidad biótica es probablemente una traba en la caracterización de patrones y predicciones de las consecuencias del manejo. Las estrategias de muestreo dependerán de la delineación del área a ser caracterizada. Existe una polémica con respecto a los límites del Archipiélago Madreano. Nosotros comparamos diferentes delimitaciones fisiografícas y geógraficas y discutimos como éstas se relacionan a los "continentes" hipotéticos de la Sierra Madre Occidental, Sierra Madre Oriental, las Montañas Rocallosas, el Mogollon Rim, y la Sierra Nevada. Modos efectivos de censos bióticos seran los tópicos centrales en el mandato para desarrollar el inventario nacional biológico.

07. Historias de la Evolución del Paisaje y de la Formación del Suelo como los Determinantes Primarios de la Biodiversidad dentro de los Pies de Montaña de las Islas en el Cielo

Joseph R. McAuliffe, Desert Botanical Garden, Phoenix, AZ; and, Tony L. Burgess, The Desert Laboratory, Tucson, AZ.

Los bosques que cubren las más altas elevaciones de las Islas en el Cielo están franqueadas por extensos piés de montaña. Las pendientes suaves de estos piés de montaña difrazan su considerable complejidad en geomorfología y edafología. El entendimiento de la variación de los suelos y de la respuesta de la vegetación asociada, se aumenta grandemente a través del conocimiento de la evolución geomórfica de estos paisajes. Los complejos patrones espaciales de los suelos se producen a través de los diferentes orígenes de esas geoformas (por ejemplo, sedimentos contra depósitos aluviales) y las amplias variaciones de las edades de esas geoformas. La escala espacial de la existencia de geoformas de diferentes edades está controlada por diferentes factores que incluyen la litología, y las fluctuaciones a nivel base del fondoo de la cuenca. La formación del suelo implica el desarrollo de horizontes arcíllicos (ricos en arcilla) y horizontes cálcicos en materiales parenterales no cálcicos, y es en parte dependiente del paso del tiempo. La fuerza de horizonación del suelo (particularmente del horizonte arcíllico) es determinante principalmente de la cantidad, tiempo y distribución vertical del agua en suelos en estos piés de montaña semiáridos. La estabilidad de algunas geoformas por lapsos de tiempo, del orden de decenas de miles a más de millones de años, contribuye al desarrollo de los suelos con horizontes arcíllicos fuertemente desarrollados. Regímenes " hyper-estacionales" de humedad del suelo en tales suelos, llevan al predominio de especies de plantas generalmente con raíces superficiales (por ejemplo, pastos perennes y suculentas activas durante el verano) capáces de tratar con esta variación extrema temporal en la abundancia de agua en el suelo. Las partes menos estables del paisaje y los depósitos extremadamente jóvenes carecen de un desarrollo del suelo tan fuerte; plantas leñosas con raíces muy profundas y desarrollo de vegetación de tipo chaparral son las que se encuentran típicamente favorecidas en tales suelos. La biodiversidad en cualquier elevación simple, surge como una consecuencia de éstos complejos geomórficos y mosaicos edáficos en los piés de montaña, que pueden ser equivalentes a aquellos que resultan a través de cambios a pequeña escala en el clima, debido a los cambios altitudinales. Las pendientes de los piés de montaña que flanquean las laderas del Noreste de las Montañas Santa Catalina proporcionan un ejemplo del grado en el cual los patrones edáficos y complejos geomórficos son responsables de la considerable diversidad de la vegetación.

08. Un Sistema de Clasificación y Mapeo de las Comunidades Bióticas de Norteamérica.

David E. Brown and Frank W. Reichenbacher, Southwestern Field Biologists, Tucson, AZ.

Las comunidades bióticas (Biomas) son comunidades regionales de plantas y animales dentro de las regiones bióticas y florísticas. Utilizando la terminológia existente de biológos, ecológos y biogeógrafos, hemos desarrollado un sistema de clasificación jerárquico y un mapa para las comunidades bióticas de Norteamérica. Actualmente en uso por el Grupo de Investigación en Ecosistemas Aridos de la Agencia de Protección Ambiental (EPA), del Programa de Monitoreo y Evaluación Ambiental, éste sistema de clasificación está formulado en criterios naturales y reconoce adaptaciones particulares evolutivas de climas regionales así como los efectos limitantes de la temperatura mínima y de la humedad sobre la estructura de las comunidades bióticas. Para ilustrar la aplicabilidad de este sistema, la EPA financió la preparación de un mapa a colores 1:10,000,000 ilustrando las principales comunidades bióticas de Norteamérica usando un esquema de colores ecológicos donde se muestran gradientes de humedad del suelo disponible, calor y frio. Universal y compatible con computadoras, la jerárquica naturaleza del sistema facilita inventarios bióticos y evaluaciones, la delineación y clasificación de hábitats y la conservación de la biodiversidad. Tratamientos ejemplo de Biomas que caracterizan el Archipiélago Madreano se enfatisan.

09. Flora de la Sierra de los Ajos, Sonora: Un Reporte de Trabajo en Curso Sobre la Flora de las Islas en el Cielo Madreano.

Mark Fishbein, Department of Ecology and Evolutionary Biology and Herbarium, University of Arizona, Tucson, AZ; Richard Felger, Drylands Institute, Tucson, AZ; and, Florentino Garza, Centro Ecológico de Sonora, Hermosillo, Sonora, México.

Las Islas en el Cielo son paradójicamente una de las bioregiones más diversas biológicamente y más pobremente estudiadas en la América del Norte templada. A la fecha sólo la Sierra del Tigre en Sonora, las Montañas Rincon y parte de las Montañas de Santa Rita en Arizona tienen publicaciones de floras razonablemente completas. Adicionalmente las Montañas Pinaleno y las

Montañas Huachuca en Arizona han sido colectadas intensivamente y las publicaciones de la flora de esos sitios se encuentran en preparación. Cada uno de los sitios probablemente contienen cerca de 1,000 especies de plantas vasculares -más del total del este del Río Mississippi de América del Norte templada .- Con el objeto de documentar y analizar la diversidad de la región de Islas en el Cielo, nosotros comenzamos un inventario florístico de la Sierra de los Ajos en 1992. La Sierra de los Ajos es un tema adecuado para estudios florísticos en la región por varias razones: 1) está situada en el centro de la Provincia Florística Apacheana, como las Montañas Huachuca 30 millas al norte, esto la hace ser probablemente la más diversa entre las cadenas montañosas; 2) a diferencia de las Huachucas, colinda con la Provincia Florística de Sonora hacia el sur a lo largo del Río Sonora, incluyendo especies desérticas no encontradas en las Huachucas; 3) a diferencia de las Hucahucas, a las cuales se parecen topográfica y geológicamente, no han experimentado supresión de incendios durante los últimos cien años, proporcionando así un "experimento natural" de los efectos de los incendios sobre los bosques de las Islas en el Cielo; Los datos florísticos son un prerequisito para ésta clase de estudios. Nosotros hemos colectado casi 500 especímenes documentando la existencia de más de 300 especies en solo siete días de colecta en una área actualmente protegida del sitio. Nosotros esperamos mucho más de 1,000 especies en esta flora. Hemos documentado a la fecha la primera población conocida de limon lily (*Lilium parryi*) y de chiricahua dock (*Rumex orthoneurus*) en México, ambos en la categorIa de candidatos número uno para la lista como especies el peligro en los Estados Unidos. Hemos documentado las poblaciones más norteñas de *Gutierrezia alamanii* y *Rudbeckia mexicana* (Asteraceae), *Tinantia erecta* (Commelinaceae), los encinos *Quercus mcvaughii* y *Q. viminea* (Fagaceae), *Sisyrinchium sacabrum* (Iridaceae) y *Penstemon campanulatus* (Scrophulariaceae) y las poblaciones más sureñas (las únicas localidades en México) de el junípero de la Montañas Rocallosas (*Juniperus scopolorum*), *Antennaria marginata* (Asteraceae), *Arenaria stricta* (Caryophyllaceae) y *Lathyrus arizonicus* y *Thermopsis montana* (Fabaceae). Nosotros hemos documentado los primeros registros Sonorenses del algodoncillo *Asclepias nyctaginifolia* (Asclepiadaceae) y *Desmanthus cooleyi* (Fabaceae).

10. Flora de la Montañas Huachuca, Condado Cochise, Arizona.

Janice E. Bowers, U.S. Geological Survey, Tucson, AZ; and, Steven P. McLaughlin, University of Arizona, Office of Arid Lands Studies, Tucson.

Las Montañas Huachuca en el Condado Cochise, Arizona son una de las casi dos docenas de "Islas en el Cielo" en el sureste de Arizona. El registro de un herbario revela que antes de 1989, 801 especies habian sido documentadas para las montañas huachuca. Nuestro trabajo de campo desarrollado entre 1990 y 1993 ha sumado otras 173 especies a la flora conocida; otros colectores han documentado adicionalmente 15 especies. En total 989 especies en 458 generos y 106 familias son ahora conocidas para las Huachuca. De éstas, 56 especies son no nativas, los elementos florísticos Apacheano y Madreano dominan la flora comprendiendo 78.5% de todas la especies nativas. El elemento Sonorense (18.3 % de todas la especies nativas) está pobremente representado, relativamente, en las Huachuca comparado con rangos de montañas más áridas en el sureste de Arizona. la flora de las Huachuca es comparativamente rica para una flora local de Arizona, con 35-45 % más especies que lo esperado, basandose en su rango altitudinal e historia de colecta. La complejidad del sustrato y la presencia de muchos hábitat de cañones muy húmedos y manantiales contribuyen a la alta diversidad de especies.

11. La Flora de los Bosques de la Sierra de La Laguna, B.C.S., México

José Luis León de la Luz, Raymundo Domínguez Cadena, Miguel Domínguez León, Rocío Coria Benet. División de Biología Terrestre, Centro de Investigaciones Biológicas del Noroeste, La Paz, Baja California Sur, México.

Los bosques de las montañas de la Sierra de La Laguna, fueron considerados por Axelrod para su clasificación de la flora Madro-Terciaria como parte del Elemento de Bosques de la Sierra Madreana y específicamente como el componente de la Sierra de La Laguna. Las especies leñosas actuales de los géneros *Arbutus, Pinus, Ilex, Populus, Garrya, Rhus* y *Quercus*, tienen vicariantes con sus correspondientes en rangos de California y Arizona, así como con la Sierra de Sonora y de Sinaloa en México. La Sierra de La Laguna, es la principal cadena de altas montañas en la porción sureste de la árida península de Baja California. La Sierra es alta y estrecha levantándose abruptamente de las zonas costeras con muchos precipicios y pendientes rocosas. Sus picos alcanzan hasta 2,100 metros. Por arriba de los 1 500 metros la Sierra se encuentra ocupada por la única comunidad montañosa de bosques en el Estado y se cree que ha sido una isla en los sentidos estricto y biológico, las zonas bajas consisten de vegetación xérica, de vegetación árida. Otros bosques similares se encuentran localizados a cientos de kilómetros. El bosque de encino y el bosque de encino-pino comprenden cerca de 250 a 300 Km^2 en superficie, el bosque de pino-encino comienza a formarse a elevaciones que van desde los 1,000 metros hasta los 1,500 metros, éste último ocupa hasta las cumbres más altas. El bosque de encino se caracteriza por la presencia de individuos dispersos del "roble", *Quercus tuberculata* y muchas especies de el bosque de encino-pino y de las partes bajas. Las especies dominantes del bosque encino-pino son los endémicos *Pinus cembroides* var. *lagunae, Arbutus peninsularis, Nolina beldingii*, and *Quercus devia*. Nosotros hemos diferenciado cuatro diferentes habitats en esta última comunidad, cada una de ellas manteniendo una composición distinta de especies: valles, fondos de arroyos, el bosque propiamente y las áreas abiertas. La participación de especies arroja 238, de las cuales las hierbas perenes son las principales formas de vida; proporciones similares se encuentran en el bosque de encino.

12. Bosques de la Islas en el Cielo: Características en Pié y prescripciones silvícolas.

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Las altas montañas del Archipiélago Madreano contienen ecosistemas de bosques de pino y de bosques mezclados de coníferas. Los bosques de encino, de junípero-piñonero y de pino-encino son comúnes en elevaciones más intermedias. Numerosos tipos de hábitat de bosques (asociaciones de plantas) han sido identificados en las principales cadenas montañosas del Archipiélago. Muchos de los bosques más altos son representativos de la flora en las Montañas Rocallosas, mientras que los bosques de pino, bosques de encino y juníperos de más bajas elevaciones son de origen Madreano. Los patrones climáticos locales y regionales han influenciado el establecimiento y supervivencia de las asociaciones. El uso de los bosques por los humanos a cambiado con el tiempo. La industria de productos tradicionales del bosque ha declinado mientras que la demanda de leña y de otros productos de los bosques bajos se han incrementado en las regiones donde la población ha aumentado. Ambos tipos de vegetación son importantes para la protección de la vida silvestre y de las cuencas. La demanda e impactos del uso recreacional son críticas en algunas áreas y su magnitud se está incrementando. Las prescripciones silvícolas pueden ser desarrolladas para asegurar la sustentabilidad y proporcionar salud para los bosques. También pueden ser usadas como una herramienta de manejo de múltiples recursos para enfatizar el hábitat de la vida silvestre y la producción de especies herbáceas para el ganado y las especies silvestres. La prescripciones deben dar como resultado una adecuada regeneración de los árboles para sustentar la asociación. Los métodos de selección pueden ser apropiados en bosques donde una estructura de edades no uniforme es necesaria para la vida silvestre o por consideraciones estéticas. Los métodos para edades uniformes puden ser necesarios donde existen enfermedades o problemas de insectos. Los métodos para sotobosques parecen ser los mejores en bosques dominados por encino. Las prescripciones silvícolas deben ser relacionadas con la información del tipo de hábitat y las capacidades del suelo y del sitio cuando estén disponibles. Los tratamientos deben ser programados para mantener las diversidades biológicas espaciales y temporales de los ecosistemas.

13. Pinos Templados del Norte de México: Su Uso, Abuso y Regeneración.

J.T. Fisher, P.A. Glass, and J.T. Harrington, College of Agriculture, Department of Agronomy and Horticulture, Mora Research Center, New México State University, Las Cruces.

Los pinos del norte de México contribuyen ampliamente a la economía regional y a la biodiversidad. Esté artículo examina su distribución, régimen de propiedad y usos principales. También explora su integridad presente y futura en función de las prácticas presentes y proyectadas. En particular, esté papel enfoca la necesidad de desarrollar estrategias efectivas de regeneración de los bosques las cuales no disminuyan la diversidad genética. Algunos de estos pinos tienen un papel potencial en el mejoramiento comercial genético, reservorios genéticos selectos mantenidos en los Estados Unidos. Entonces, los esfuerzos cooperativos para establecer plantaciones *Ex situ* para conservar el germoplasma merecen atención especialmente en el caso de especies en peligro.

14. Dinámica de los Manchones de Paisajes en los Bosques Viejos de Mont Graham, Arizona.

Duncan T. Patten and Juliet C. Stromberg, Center For Environmental Studies, Arizona State University, Tempe.

Los bosques viejos del Monte Graham de las Montañas Pinaleno del este de Arizona, están compuestos de manchones de bosque más que ser de una composición homogénea. Estos manchones reflejan la heterogeneidad de las perturbaciones que ocurren en las montañas. Las dos perturbaciones primarias han sido los incendios y el viento, aunque el aclaramiento y desmonte para la construcción de caminos y recientemente para el observatorio astronómico han sido también perturbaciones importantes. Los manchones de bosques representan diferentes estadíos en la sucesión de bosques siguiendo la perturbación. Los manchones pueden describirse como bosque abierto, límite del bosque, bosque maduro y bosque viejo. Dentro de éstas categorías la composición y la demografía de las especies dominantes de árboles varían. La variabilidad resulta de el éxito relativo de las especies pioneras de árboles y de la consecuente invación de otras especies. Estos patrones están demostrados por los siguientes ejemplos: en los bosques de picea-abeto (*Picea engelmannii - Abies lasiocarpa* var. *arizonica*) los bosques maduros estan caracterizados por piceas con edades hasta de 180 años y con un sotobosque de abetos jóvenes (hasta de 40 años). Los bosques viejos tiene piceas hasta de 380 años de antiguedad con abetos de por lo menos 200 años y dominando las clases de edad más jovenes. Estos patrones indican el éxito de la piceas como una especie pionera siguiendo una perturbación, con el abeto invadiendo según como el microambiente se va moderando. Un patrón similar de desarrollo se encuentra en los bosques de transición de coníferas mezcladas pero con el abeto de Douglas (*Pseudotsuga* *menziesii* var. *glauca*) como un co-pionero con las piceas y apareciendo solamente como árboles viejos en muchos de los manchones de los bosques viejos y maduros. Los límites del bosque dentro de la zona picea-abeto tienden a tener números relativamente grandes de abetos maduros que en el interior del bosque, mientras que los manchones abiertos tienden a ser dominados por piceas. La tasa de crecimiento de los árboles en los manchones abiertos es cerca de cuatro veces más grande que el los bosques viejos. Esto produce rápidamenten un dosel que crea un ambiente adecuado para el desarrollo posterior de los bosques de coníferas de altas elevaciones.

15. Los Factores que Afectan la Distribución de *Agave chrysantha* Peebles y *Agave palmeri* Englem. (Agavaceae).

Liz. Slauson, Desert Botanical Garden, Phoenix, AZ.

El genero *Agave* es un importante componente vegetal de los ecosistemas del Archipiélago Madreano, sin embargo, los procesos de especiación, reproductivos y ecológicos del *Agave* se encuentran pobremente comprendidos. La historia evolutiva de *A. Chrysantha* es de interés por varias razones; es difícil de separar de la estrechamente emparentada *A. Palmeri* en las áreas donde las dos especies se traslapan, exhiben un síndrome de polinización intermedio entre las abejas y los murciélagos y tienen un área de distribución limitada en el sureste y centro de Arizona dentro de una gran variedad de hábitats. Se desarrollaron estudios biosistemáticos para determinar si *A. Chrysantha* representa una raza subespecie de *A. Palmeri* la cual se ha diferenciado a lo largo de gradientes ambientales, o alternativamente, está significativamente aislada como especie y las zonas de contacto son meros ejemplos de hibridización introgresiva. Se desarrollaron estudios de la biología de la polinización para determinar a los polinizadores y sus tasas de polinización, la producción de polen y néctar y la efectividad de los polinizadores diurnos contra los nocturnos medidos por colectas de semillas y frutos. Varias poblaciones que fueron localizadas sugieren la introgresión entre *A. chrysantha* y *A. palmeri* y *A chrysantha* y *A. parryi*. Esta tendencia de filogenia reticular en *Agave* parece ser debida a una falta de aislamiento reproductivo entre los taxas reconocidos a nivel específico. Las fluctuaciones climáticas del ciclo glacial-interglacial durante el Pleistoceno pueden haber dado como resultado repetidos períodos de expansión del rango de distribución y de intercambio genético entre las especies de agave, seguidos por periodos de contracción de rangos y aislamiento en pequeñas poblaciones distintas, dentro del Archipiélago. Este repetido contacto puede haber sido suficiente para prevenir el desarrollo de barreras reproductivas. Aunque *A. chrysantha* exhibe varias caracteristicas que sugieren la polinización de las plantas (por ejemplo, la dehiscencia nocturna de las anteras y producción de nectar, flores que emiten un olor "a murciélago", concentraciones de azúcar en el néctar de 18 a 20 %), las abejas (*Apis y Bombus*) fueron los visitadores primarios. No se observaron murciélagos visitando las inflorescencias y la mayoría de las poblaciones se encuentran localizadas por debajo del rango de distribución de los murciélagos comedores de néctar. El conjunto de frutos de umbelas expuestos solamente a polinizadores diurnos fue de 23 % , a polinizadores nocturnos 17% y para los controles 23%. Estos rasgos "murciélago-adaptados" pueden ser sólo una ventaja para los insectos y otros animales de microclimas calientes y áridos donde los picos de actividad son cerca del ocaso y del amanecer.

16. Conservación de la Biodiversidad y el Desarrollo de Proyectos Forestales Regionales en México.

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El desarrollo de proyectos forestales regionales ha sido propuesto para manejar los bosques y expander las industrias comerciales forestales y los asentamientos en México. Como un requisito de la Legislación Ambiental Mexicana y de las políticas multilaterales de los bancos de desarrollo, las evaluaciones ambientales (EAs) son obligatorias para evaluar los impactos de tales proyectos. Para la conservación de la biodiversidad, las EAs deben integrar las prioridades de conservación con estrategias regionales de desarrollo. Este artículo examina dos proyectos regionales de desarrollo forestal en México: (1) Guerrero y Oaxaca, y (2) Chihuahua y Durango. Se concluye que la EAs no fueron incluídas adecuadamente en los planes de desarrollo regional forestal debido a fallas en los procedimientos institucionales así como a los inventarios biológicos incompletos y sesgados. Por lo tanto, la EAs deben identificar las áreas potenciales de conflictos entre la conservación y la extracción de recursos. Adicionalmente, este artículo presenta un método para localizar tales áreas dentro de las limitaciones de la EAs en México.

17. Persistencia de Plantas Raras Cryopédicas en los Bosques Forestales de Picea-Abeto de las Montañas Chiricahua.

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Existen pequeñas poblaciones de plantas boreales que persisten en los bosques de picea-abeto. Veinte años después de que fueron por primera vez registradas por el autor, plantas tales como *Lonicera utahensis, L. involucrata, Sorbus scopulina, Vaccinium myrtillus y Rubus parviflorus,* sobrevivieron a la caliente década de los años 1980'tas. Los bosque de picea-abeto no están bien estructurados en capas de herbáceas y arbustos como se encuentran en cualquier lugar en Arizona y Nuevo México. En cambio, éstas plantas del sotobosque de regímenes de temperatura de suelo heladas, se encuentran donde existe poca competencia de otras plantas y donde existen factores compensatorios en los micrositios. En 1993 la mayoría de las poblaciones estuvieron cercanas a sus niveles de 1974 o se incrementaron. Este ambiente de cima de montaña se encuentra dentro de los criterios de temperatura del bosque de picea-abeto tal como lo indican éstas especies de plantas. Tendría que haber un calentamiento climático considerable para forzar a las especies cryopédicas hacia la extinción local a pesar de sus bajos números poblacionales.

18. Las Características y Consecuencias de la Invación del el Suroeste Arido de los Estados Unidos por el Arbusto de Resina Dulce *Euryops multifidus*.

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Euryops multifidus (Arbusto de resina dulce), una compuesta arbustiva nativa de Sudáfrica, fué introducida el suroeste árido de los Estados Unidos en 1935 por el USDA Inventario de Conservación del Suelo (Soil Conservation Survey). La expansión de éste arbusto representa una de las amenazas más serias a la integridad ecológica y al valor económico de varios ecosistemas en el suroeste semiárido. En el sureste de Arizona éste arbusto invadió rápidamente los pastizales semiáridos vegetacionalemente intactos, y eventualmente forman monocultivos virtualmente ininterrumpidos en los que los pastos, arbustos y suculentas nativas se encuentran casi completamente excluídos. El estudio de las respuestas de las plantas hacia el frente de avanzada de éstas áreas ocupadas por el arbusto de resina dulce, indican que la mortalidad y la exclusión de especies nativas se deben a mecanismos competitivos, posiblemente de inhibición química. Estas dramáticas alteraciones de la vegetación son persistentes y conducen a una variedad de cambios adicionales negativos, incluyendo un marcado incremento en la erosión del suelo. Nosotros nos encontramos actualmente identificando las características climáticas, de vegetación, elevación y suelos de los sitios que son suceptibles a la invación por *E. multifidus*. Hemos encontrado que en el sureste de Arizona el arbusto de resina dulce puede existir en vegetación que varía desde el Desierto de Sonora y de vegetación dominada por la creosota de las bajas elevaciones (850-1060 m) hasta pastizales, chaparrales y bosques de altas elevaciones (más de 1300 m). En los pastizales, éste arbusto puede invadir áreas con un amplia variedad de tipos diferentes de suelo, variando desde los suelos cálcico-limosos típicamente ocupados por conjuntos de grama negra (*Bouteloua eriopoda*) hasta pesados suelos arcillosos ocupados por la tobosa (*Hilaria mutica*) y el mezquite rizado (*H. berlangeri*). Nosotros mostraremos que una significativa cantidad de tierras públicas y privadas del suroeste se encuentran dentro del rango de ésta especie invasora. Nuestros resultados preeliminares demuestran las consecuencias catastróficas de la invasión por el arbusto de resina dulce en el suroeste de los Estados Unidos.

19. 100 Años de Vicisitudes: Cambios en la Distribución de Aves Terrestres y de Mamíferos en el Suroeste Americano, 1890-1990.

David E. Brown, Department of Zoology, Arizona State University, Tempe;, and, Russell Davis, Department of Ecology and Evolutionary Biology, University of Arizona, Tucson.

Los cambios de distribución en los pasados 100 años se encuentran documentados para un número de aves y mamíferos terrestres en Arizona y Nuevo México. Al menos 39 especies aparentemente han sido extirpadas o han sufrido restricciones en su distribución geográfica, mientras otras 55 han experimentado expansiones de su rango de distribución. Aún cuando las especies exóticas no son tomadas en cuenta, la bíodiversidad de endotermos es ahora más grande que en 1890. No sorpresivamente, Las filas de los "perdedores" contienen un número desproporcionado de grandes predadores y especies asociadas a los pastos. Como punto de contraste, la mayoría de los "ganadores" fueron especies adaptadas a los bosques y a los matorrales. Demás aplicación a este estudio fué el hecho de que más del 70 porciento de los "ganadores" fueron especies cuya afinidad biótica primaria es de la frontera entre México y Estados Unidos. Unas pocas especies de Rocky Mountain, Great Basin or Great Plains han incrementado su distribución. Las razones posibles para este fenómeno se discuten incluyendo los efectos potenciales del incremento de la temperatura mínima invernal, sobre la distribución de las plantas y la abundancia de invertebrados.

20. La Declinación del Borrego Cimarrón en las Montañas de Santa Catalina, Arizona.

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El borrego cimarrón (*Ovis canadensis mexicana*) es un componente importante de la bíodiversidad de las montañas de Santa Catalina, Arizona. Desafortunadamente, la población a decrecido de más de 200 en los años de 1940, a menos de 25 en los años de 1990, y su distribución está limitada a una pequeña en el área silvestre de Pusch Ridge Wilderness. El declinamiento en número y distribución se ha atribuído a las actividades humanas incluyendo el desarrollo de caminos y sendas; la construcción de casas y lugares de recreación; paseos; perros; y supresión de incendios. La supresión de incendios, efectivamente ha alterado la vegetación de áreas que tal modo que ahora no son adecuadas para el borrego cimarrón. La invación humana en el hábitat remanente puede ser también demasiado severa para que la población se incremente. Las enfermedades, la depredación y la cacería también pueden haber contribuído al declinamiento reciente pero su influencia no ha sido evaluada. Previo a cualquier esfuerzo de reintroducción, se requiere comprender totalmente los factores que han causado ésta declinación. El público apoya las opciones de manejo incluyendo aquellas que restringen el uso de ciertas áreas, y la prevención de perros en el hábitat del borrego cimarrón. Todos los asociados con esta histórica manada del borrego cimarrón deben involucrarse en los esfuerzos de recuperación, incluyendo a los cazadores, excursionistas, público interesado y agencias de manejo (por ejemplo U.S. Forest Service y Arizona Game and Fish Departament.)

21. Predadores Introducidos en Humedales del Archipiélago Madreano y Pastizales del Sureste de Arizona.

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Reportamos detalles de la distribución de ranas nativas y predadores exóticos que aparecen impactando a éstas, enfocados en las regiones de las Montañas Chiricahua y Huachuca. Las poblaciones de ranas nativas leopardo, *rana Chiricahuensis* , *R. Blainri, R. Yacapaiensis*, y ranas arbolrícolas de montaña *Hila Eximina* se encuentran actualmente en decline que puede ser acentuado por recientes tendencias en la precipitación pluvial. Observaciones realizadas durante cuatro decadas correlacionan el declinamiento con la expansión de sapos toros introducidos, los cuales predan y posiblemente compiten con los anuros nativos. En adición, peces depredadores introducidos, particularmente la trucha de Brook en las montañas y los bagres y centrárquidos en los pastizales -pueden estar impactando a las ranas nativas como ha sido reportado en California. Finalmente cangrejos introducidos que están expandiéndose en la región pueden constituir aún otro riesgo a la vegetación de humedales, invertebrados y a la herpetofauna. Los animales introducidos están amenazando a las ranas nativas las cuales ya enfrentaban la degradación de su habitat y la contaminación ambiental. El efecto predecible de la capacidad de penetración de los depredadores a lo largo de esta área es la extinción de los anuros nativos impactados a través de una falla metapoblacional. Más optimisticamente, sí nosotros podemos probar que los depredadores exóticos son los que ocacionan el decline, nosotros podemos removerlos- local o regionalmente- y restablecer fortalezas poblacionales para las especies nativas. Los depredadores exóticos pueden ser más tratables que problemas globales tal como la reducción del osono, el cambio climático y la contaminación atmosférica. Nosotros resumimos los resultados de un intento inicial del manejo de la rana toro y describimos el trabajo en curso diseñado para probar la recuperación de las ranas y serpientes nativas después de la remoción de la rana toro. Sí éstos esfuerzos son exitosos, remociones más extensivas serían justificadas.

22. Aspectos de la Historia de Vida y Ecología de la Torutuga del cieno de Sonora.

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Las tortugas del cieno de Sonora (*Kinosternon sonoriense*) fueron estudiadas desde 1990 hasta el presente en El Coronado Ranch al lado oeste de las Montañas Chiricahua. A lo largo de 1993, 368 tortugas fueron marcadas y se hicieron 669 recapturas. El máximo tamaño corporal de la tortugas (máximo tamaño del caparazón de los machos = 169 mm; hembras = 158 mm) en el arroyo West Turkey Creek y en los tanques de almacén adyacentes esatán entre los más grandes reportados en Arizona. El máximo peso corporal de los machos fué de 690 gramos y de las hembras fué de 640 gramos. El mínimo CL de las hembras reproductivas capturadas hasta la fecha es de 113 mm, sin embargo la hembra siguiente más pequeña midió aproximadamente 120 mm. en CL. Una regresión linear del tamaño de puesta, determinada a través de 124 radiografías de hembras grávidas, en CL (PC = 0.059 x - 0.673 CL) explican el 15% de la variación en CS. El tamaño de puesta promedio fué de 7.3 (mín, = 3, máx = 11) huevos. Las observaciones de hembras grávidas en el campo indican que la estación de anidación se extiende, al menos, desde junio hasta agosto. Datos preliminares indican que los recién nacidos no retrasan la emergencia del nido.

23. Lagartijas Unisexuales (Genero *Cnemidophorus) del Archipiélago Madreano: Un Recurso Biológico Natural.*

Charles J. Cole, American Museum of Natural History, Department of Herpetology, New York, NY; and, Herbert C. Dessauer, Biochemistry and Molecular Biology, Louisiana State University Medical Center, New Orleans.

Cerca de 20 especies de *Cnemidophorus* existen en la vecindad de las islas del cielo de suroeste de los Estados Unidos y el noroeste de México, en hábitats que van desde el bosque de encino hasta el desierto. Como vertebrados típicos, en general y muchas de estas lagartijas ocurren en poblaciones de un radio sexual de 50:50 y la reproducción depende del apareo y la fertilización interna. Sin embargo, la mitad de las especies del Archipiélago Madreano son especies unisexuales en las que solamente las hembras existen. Estos notables ver tebrados son recursos biológicos importantes para la investigación comparativa y multidiciplinaria sobre reproducción, genética, ecología, biología evolutiva y sistemática, integrando investigaciones de campo y de laboratorio. Los resultados incluyen lo siguiente: (1).- Las hembras de la especies unisexuales se reproducen independientemente por clonación partenogenética; (2).- Una diversidad de clones ocupa el área, incluyendo especies diploides y triploides; (3).- Las especies unisexuales originadas en ecotonos de hibridos F_1 entre especies bisexuales y varias combinaciones únicas de híbridos están involucradas; (4).- En cada ocasión el radio de la reproducción de esperma-dependiente a esperma-independiente ocurre en una sola generación; (5).- Estos animales tienen un potencial considerable para mejorar nuestro conocimiento de la biología reproductiva y otros fenomenos asociados para revelar la historia natural del Archipiélago Madreano y tierras adyacentes.

24. Murciélagos del Archipiélago Madreano: Conocimiento Actual; Direcciones Futuras.

Sarah L. Schmidt, Tucson, AZ.

Arizona tiene la segunda diversidad más alta de especies de murciélagos en los Estados Unidos, con 28 especies registradas. La mayoría de ellas existe en la región de las Islas en el Cielo. Dos son comedores de néctar y el resto son insectívoros. Requieren fuentes de agua, sitios adecuados de forrajeo y distintas perchas. Debido a que ellos vuelan, son nocturnos y frecuentemente no se ven, los murciélagos se encuentran entre los mamíferos menos estudiados y son frecuentemente ignorados en los inventarios de hábitats y en las evaluaciones ecológicas. Los avances en la tecnología y en la biología molecular han incrementado grandemente el potencial para estudiar la ecología de los murciélagos. A pesar de un resurgimiento reciente en la investigación sobre murciélagos, mucha información adicional es necesaria para mantener adecuadamente los recursos necesarios para la supervivencia de las especies de murciélagos. Los requerimientos de percheo, forrajeo e invernales para un número de éstas especies todavía se desconocen. Con particular énfasis en la especie en peligro federal *Leptonycteris curasaoe* (el murciélago de nariz larga de Lesser), éste artículo considera algunas importantes preguntas que permanecen sin contestar acerca de la ecología de las especies de murciélagos encontrados en las Islas en el Cielo y ofrecen sugerencias para la investigación futura. Mucho se ha dicho en la prensa popular en los años recientes acerca del mutualismo entre *Leptonyeteris* y algunas especies de cactus columnares y de agaves, sugiriendo que ciertos tipos de relaciones planta-murciélagos son obligadas ó mutuamente dependientes. Ciertos agaves demuestran características que sugieren que están adaptados para atraer a los murciélagos polinizadores. La investigación anterior postula un mutualismo altamente interdependiente y obligado entre *Leptonicteris* y *Agave palmeri* en los ecosistemas de montaña del sureste de Arizona. Se requiere más información para resolver ésta cuestión, remarcando la necesidad de información adicional sobre los requerimientos de polinización del agave sobre la dieta de *Leptonycteris*, y sobre los patrones de actividad de *Leptonycteris* en Arizona y México. Los recursos necesarios para los murciélagos, notablemente plantas alimenticias y sitios de percheo, pueden no estar lo suficientemente protegidos hasta que nosotros entendamos mejor las fuerzas que controlan las actividades estacionales de *Leptonycteris* en Arizona, y el grado de mutualismo entre los murciélagos y las plantas que ellos visitan, y el entrelazamiento de éstas relaciones en el complejo de ecosistemas del Archipiélago Madreano.

25. Las Relaciones Ecológicas del Perico de Pico Ancho con el Bosque de Pino del Sureste de Arizona.

Noel F.R. Snyder and Terry B. Johnson, Portal, AZ, and Susan E. Koenig, Arizona Game and Fish Dept., Phoenix.

El perico de pico ancho (*Rhynochopsitta pachyrhyncha*) una vez se distribuyó en todas las regiones montañosas del sureste de Arizona, llegando tan al norte como hasta el Mogollon Rim. Su desaparición al inicio del presente siglo fué aparentemente debido a que le disparaban ampliamente. Se desarrollaron liberaciones experimentales de ésta especie para regresarla a la región entre 1986 y 1993 y los estudios sobre las aves liberadas han revelado una fuerte dependencia sobre ciertas especies de coníferas tanto para alimentos como para anidación. La alta diversidad de especies de coníferas encontradas en ésta región parecen ser críticas para la supervivencia de éste perico, ya que la producción de conos (piñas) varía entre las especies, entre los años, geográficamente y entre las estaciones. La comida más importante de las aves liberadas han sido los conos (piñas) del pino de Chihuahua (*Pinus leiophilla*), pino ponderosa (*Pinus ponderosa*), y el pino de Arizona (*Pinus arizonica*), aunque los pericos también han sido observados comiendo del pino piñonero (*Pinus discolor*), pino Apache (*Pinus enegelmannii*), y el abeto de Douglas (*Pseudotsuga menziesii*). De todas éstas especies, el pino de Chihuahua parecer ser las más importante porque ésta especie produce cosechas de conos con una gran regularidad y las semillas se mantienen dentro de los conos en una base anual. La mayoría de las otras especies producen conos iregularmente y muchas ofrecen semillas solamente en períodos limitados del año. Parece probable que la extensión norteña de la distribución histórica de éste perico estuvo ampliamente ligada a la distribución del pino de Chihuahua.

26. El Uso de Ecuaciones Area/Especies para Estimar la Riqueza Potencial de especies de Murciélagos en Islas Montana Inadecuadamente Inventariadas

Ronnie Sidner and Russell Davis, Department of Ecology and Evolutionary Biology, University of Arizona, Tucson.

El inventario de Islas Montana para los murciélagos en el sureste de Arizona, usando redes así como otras técnicas más tradicionales comenzó hace casi 40 años. La información obtenida de éste inventario incrementó notablemente nuestro conocimiento y apreciación de la diversidad de vertebrados en ésta importante región biogeográfica de Norteamérica. Este estudio fué diseñado para determinar dónde un trabajo adicional de inventario de murciélagos puede aumentar significativamente nuestro presente conocimiento de la diversidad regional¾información que puede ser útil en decisiones respecto a la distribución de fondos para propósitos de inventarios. La riqueza específica de los murciélagos en montañas seleccionadas en el sureste de Arizona fué comparada con área de hábitats de bosque en cada una de éstas montañas. La ecuación resultante fué entonces comparada con ecuaciones similares generadas de curvas de especies-área que han sido reportadas para mamíferos que no vuelan y para aves en otras porciones del suroeste. Los datos resultantes de éstas ecuaciones fueron gráficadas y comparadas con la curva de regresión resultante del modelo de poder (log/log). Los datos resultantes apuntaron (aparentemente montañas anómalas) tanto hacia arriba y abajo de la linea de regresión cuando se examinaron. El muestreo inadecuado, la baja diversidad de hábitat, y el incremento en la distancia de la fuente (aislamiento) se muestran como los factores que contribuyen a la riqueza específica de ciertas montañas lo cual es menor a lo que podría predecirse de una sola área. Con murciélagos, la contribución a la riqueza específica de la intensidad de muestreo puede proporcionar una advertencia que puede ser importante en ciertas decisiones de manejo y conservación: la riqueza específica registrada no siempre es el resultado de procesos biológicos. Esté análisis también proporciona información que podra ser útil en decisiones concernientes al más exigente uso de presupuestos para inventarios de fauna,¾ permitirá que ésos sean dirigidos hacia las montañas donde la riqueza específica registrada es más probable que sea incrementada.

27. Diversidad e Importancia de las Abejas Nativas del Archipiélago Madreano en Arizona.

Stephen L. Buchmann. USDA-ARS, Carl Hayden Bee Research Center, Tucson, AZ.

Los insectos polinizadores, especialmente las abejas solitarias y sociales nativas, juegan importantes papeles ecológicos, frecuentemente clave, en ecosistemas naturales a través del mundo. No solamente polinizan plantas con flores cruzando sus gamentos, si no que contribuyen a la estabilidad ambiental de la biodiversidad al aerear los suelos, proporcionar alimento para otros predadores vertebrados e invertebrados, al utilizar recursos ricos en carbono y distribuír ampliamente sus heces ricas en nitrógeno, sus cuerpos y materiales de anidamiento en los ecosistemas. Al contrario de la mayoría de los organismos, su mayor riqueza específica no ocurre dentro de bosques tropicales pero sí en los desiertos áridos y hábitats de pastizales semiáridos y de sabana. Cerca de 3500 especies de abejas nativas tienen su hogar dentro de los Estados Unidos continentales. La región biogeográfica más rica para las abejas ocurre en el Desierto Sonorense de Arizona y Nuevo México junto con regiones desérticas en el Mediterráneo, especialmente en Israel. Este autor sugiere que las regiones desérticas alrededor de Tucson, Az. pueden tener cerca de 1500 especies de abejas nativas que anidan en el suelo o en ramas, las cuales hasta ahora no se han tomado en cuenta y se han menospreciado por sus relaciones ecológicas vitales. Este estudio selecciona un grupo de abejas grandes y fácilmente reconocibles, los abejorros del genero holártico *Bombus* y evalúa su biogeografía en las Islas en el Cielo de las montañas del sureste de Arizona. En las bajas elevaciones de Arizona, la fauna de abejorros está dominada por una especie de *B. sonorus*, pero unas cuantas otras especies existen en las cimas de montañas aisladas. Su distribución está documentada gráficamente y su importancia como polinizadores se discute. Aún más, un primer intento para usar el Sistema de Información Geográfica (GIS) que relaciona la producción hipotética de nectar y polen de diferentes asociaciones vegetales de Arizona, con las cantidades de polen requeridas por los abejorros y otras abejas nativas (por ejemplo, abejas Carpenter de los generos *Xylocopa*) fué removido por abejas exóticas no-nativas, incluyendo colonias de abeja melífera (*Apis mellifera*) domésticas y ferales.

28. Los Efectos de las Abejas Robadoras de Néctar, *Xylocopa californica*, sobre Plantas y Polinizadores.

Sarah C. Richardson. University of Arizona, Tucson.

Xylocopa californica roba a algunas especies de flores al abrir los lados de las flores para robar el néctar, presumiblemente sin polinizar las flores. Estudios ecológicos de los efectos de las abejas robadoras de néctar en plantas y polinizadores son pocos, considerando la gran abundancia de las abejas y la importancia de sus efectos sobre los mutualistas. La investigación fue conducida sobre *Chilopsis linearis* en fuentes del desierto en la base de las Montañas Chiricahua de mayo a junio de 1993 y 1994. Investigué las diferencias entre la longitud de los periodos de tiempo que las abejas polinizadoras pasaron visitando flores robadas y la proporción de flores no-robadas que las polinizadoras visitaron, comparándolo con el número disponible en las plantas. Las polinizadoras pasan menos tiempo en las flores robadas que en las no-robadas y no las visitan tan frecuentemente como sería esperable. De 228 flores marcadas en la estación de 1993, solamente 13 o sea 6% produjeron fruto. De ésas, 10 fueron robadas antes de que mduraran en frutos. El néctar fué producido en capullos en la última tarde antes de que abrieran, así las abejas robadoras ganaron el acceso al recurso, con anticipación, en la vida de la flor, a las abejas polinizadoras. Desde que las abejas polinizadoras deben buscar flores no-robadas y encontrar menos néctar en las flores robadas que en las no-robadas, el robo parece tener un efecto negativo sobre los polinizadores que visitan *C. linearis*. Sin embargo el robo puede no tener efecto sobre las plantas.

29. Filogenia y Biogeografía del Caracol de Tierra, *Sonorella* en el Archipiélago Madreano.

Robert D. McCord. Departmen of Ecology and Evolutionary Biology, University of Arizona, Tucson.

Más de 60 especies de caracol de tierra, géenero *Sonorella* han sido descritas para el Archipiélago Madreano y las regiones adyecentes. El ánalisi filogenético, usando PAUP y Macgleid fue hecho para esté genero, utilizando *Sonorelix* y *Tryonigens* como contraste. La construcción de un contexto filogenético de *Sonorella* permite una re-examinación de la biogeografía de *Sonorella* con sugerencias de posibles eventos de dispersión y vicarianza.

30. Comunidades de Helmintos de Poblaciones Aisladas de Montañas de la Lagartija Espinosa de Yarrow's *Sceloporus jarrovii* (Phrynosomatidae).

Stephen R. Goldberg, Department of Biology, Whittier College, Whittier, CA; Charles R. Bursey, Department of Biology, Pennsylvania State University, Shenango, Valley Campus, Sharon, PA; and, Robert L. Bezy, Natural History Museum of Los Angeles, Herpetology Section, Los Angeles, CA.

Las comunidades del helmintos de ocho poblaciones de montaña de *Sceloporus jarrovii* de Arizona (Montañas Chiricahua, Dragoon, Graham, Huachuca, Quinlan y Santa Rita) y Nuevo México (Montañas de las Animas y Peloncillo) fueron determinadas. Cada población contiene una comunidad única. *Spauligodon giganticus, Physaloptera retusa* y *Parapharyngodon scelopori* estuvieron presentes en todas las poblaciones de Arizona pero ausentes de las de Nuevo México. *Mesocestoides* sp. aparece en cuatro poblaciones de Arizona y una de Nuevo México. *Abbereviata terrapenis* fué encontrada en tres poblaciones orientales y la más sureña población: Chiricahua, Peloncillos, Animas y Huachuca. *Thubunaea intestinalis* aparece en las poblaciones de Chiricahua y Quinlan. *Strongyluris similis* fué encontrada solamente en la poblaciones de las Montañas Dragon. La similaridad de las poblaciones en composición de especies (coeficiente de Jaccard) carece de un patrón geográfico discernible. Sin embargo, cuando la abundancia de helmintos (índice de Morisita) fué considerada junto con las similaridades geográficas y de vegetación, las poblaciones caen dentro de tres grupos: (Quinlan, Santa Rita, Huachucas); (Dragon, Peloncillo); (Chiricahuas, Graham, Animas).

31. Hidrología y Manejo de Cuencas en el Archipiélago Madreano.

Malchus B. Baker Jr., Rocky Mountain Forest and Range Experiment Station, Flagstaff; Leonard F. DeBano, Rocky Mountain Forest and Range Experiment Station, c/o School of Renewable Natural Resources, University of Arizona, Tucson; and, Peter Ffolliott, School of Renewable Natural Resources, University of Arizona, Tucson.

Las interrelaciones entre los procesos hidrológicos, el complejo suelo-vegetación, y las prácticas de manejo de cuencas en el Archipiélago Madreano no han sido investigadas totalmente, con algunas notables excepciones, por ejemplo, las cuencas experimentales de Walnut Gukch en el sureste de Arizona. Una razón para esta deficiencia es la escasés de mediciones del flujo de tormentas, de la erosión del suelo y de la producción de sedimentos para caracterizar los ecosistemas representativos. Afortunadamente la información obtenida de estos ecosistemas, aún cuendo no están localizadas en el Archipiélago Madreano, pueden formar una base para acceder a los procesos hidrológicos en algunos campos. Este artículo presenta información climática y edafológica representativa del Archipiélago Madreano, examina importantes aspectos de manejo de cuencas y discute los procesos hidrológicos y sedimentarios comúnes a los ambientes de tierras áridas con caracteristicas similares al Archipiélago Madreano.

32. Zonas Riparias, No Son Montañas , No Son Desiertos.

Jack Whetstone, USDI BLM, San Pedro Riparian Natural Conservation Area, Sierra Vista, AZ.

La analogía se ha hecho en el sentido de que las Montañas Madreanas son como islas flotando en mares desérticos, altos puntos de diversidad rodeados por la monotonía relativa de los pastos y matorrales. Esto da la impresión desafortunadamente de que los valles pueden ser ignorados para protección e investigación. La diversidad en el suroeste está en correlación directa con el hábitat ripario. Ya que en las montañas o cuencas cási todas sus especies, de plantas o animales se encuentran en esas franjas de diversidad. El Río San Pedro fué una corriente permanente, un conjunto de pantanos rodeados por pastizales hasta los años 1980's. Las poblaciones inglesas de Thompson y Bisbee ocasionaron profundos efectos en el río y en su cuenca. El sobrepastoreo, la tala de madera para leña, la supresión de incendios y la erradicación de los castores se combinaron para cambiar la cuenca de pastizal a matorral y el río de perenne a intermitente. La adquisición de la parte superior de San Pedro y BLM y su designación como una área nacional de conservación, marcaron un nuevo comienzo para el río. Nuevas decisiones controversiales se hicieron eliminando algunos usos públicos tradicionales, el uso de ORV y de minería se terminaron y más importantemente, el pastoreo fue suspendido. La recuperación de la vegetación ha sido la clave en la historia existosa de la NCA. La regeneración de sauces y algodón y la producción de pastos anuales y matorrales han sido impresionantes. Con este incremento en la densidad vegetal ha regresado a la estabilidad en el almacén de escurrimientos, se ha reducido el gradiente de los arroyos y se han dado efectos benéficos en su flujo y el acontecimiento de incendios ha incrementado dramáticamente las poblaciones de vida silvestre. En los pocos años que el área nacional de conservación riparia de San Pedro ha existido, nosotros hemos visto un cambio de actividaddes agrícolas marginales hacia un turismo ecológico trayendo millones a la economía local. Para contrarrestar los efectos del crecimiento poblacional nosotros estamos trabajando activamente con las autoridades locales del condado del Estado y los mexicanos, para asegurar que el San Pedro permanezca como un río y no como el fondo de un valle donde una vez corrió un río.

33. El Programa de Investigación del Centro de Investigaciones en Cuencas del Suroeste.

Kenneth G. Renard and Leonard J. Lane, USDA-ARS, Southwest Watershed Research Center, Tucson, AZ.

El Centro de Investigaciones de Cuencas del Suroeste del Servicio de Investigaciones Agrícolas, USDA, consiste de un conjunto multidiciplinario de 10 científicos e ingenieros localizados en Tucson, Arizona. Este conjunto multidiciplinario opera la Cuenca Experimental del Walnut Gulch localizada en el sureste de Arizona. Las tierras semiáridas que representan a la cuenca están caracterizadas por una extrema variabilidad en precipitación, suelos, vegetación, infiltración, escurrimientos y erosión y en producción de sedimentos. Los resultados de investigaciones se presentan describiendo y resumiendo esta variabilidad espacial y temporal y el impacto de las decisiones de manejo en la alteración de los ciclos hidrológicos y de sedimentación. Los impactos potenciales del cambio global sobre los recursos naturales de tales tierras semiáridas se reportan también. Los resultados específicos incluyen las frecuencias para la cantidad de escurrimientos. Modelos de simulación analítica, tales como CREAMS, RUSLE, WEPP, y KINEROS, desarrollados usando datos de Walnut Gulch, se describen y están siendo usados para ilustrar el impacto del manejo de los ciclos hidrológicos en ambientes semiáridos. Finalmente, descubriemientos en los datos e investigaciones de la cuenca de Walnut Gulch están siendo utilizados para desarrollar nuevas tecnologías para el modelamiento y manejo de recursos naturales. Ejemplos específicos para control de zonas de impacto sobre calidad del agua se presentan.

34. Tabla de Producción Denso-Variable para el Encino de Emori: Aplicaciones en Cuencas en el Suroeste de los Estados Unidos.

Wm. Patrick Fowler, USDA Forest Service, Southern Forest Experiment Station Hot Springs, AR; and, Peter F. Ffolliott, School of Renewable Natural Resources, University of Arizona, Tucson.

Las tablas de producción denso-variables en las cuales la densidad en pié (en este caso, área basal) se usa como una variable independiente de la edad en pie y el índice del sitio para estimar el crecimiento y la producción, han sido desarrolladas para su aplicacione en bosques maderables de la misma edad en cuencas con bosques de encino del suroeste de Estados Unidos. Estas tablas de producción denso-variables estan representadas por un conjunto de ecuaciones para estimar la producción actual y futura, con la diferencia entre estas dos estimaciones de una producción de crecimiento neto para el período en consideración. Aproximaciones de la rotación de edades también pueden ser obtenidas.

35. Recursos Acuáticos de las Islas en el Cielo: Refugio y Hábitat para Especies Nativas, Amenazadas y Sensitivas.

John N. Rinne, Rocky Mountain Forest and Range Experiment Station, Flagstaff, AZ.

Debido a la precipitación pluvial producida orográficamente, las cadenas montañosas aisladas de la Provincia Montañosa de la Cuenca y del Sureste de Arizona reciben una mayor precipitación que las cuencas contiguas y que el suelo del desierto. Este fenómeno meteorológico provee agua extremadamente valiosa y hábitats riparios de arroyos para la fauna de esas Islas en el Cielo. Los peces nativos son beneficiarios importantes. Los arroyos de las altas elevaciones proporcionan refugio para un importante grupo de peces raros y nativos, muchos de los cuales tienen un estatus en las listas oficiales. Además el agua es transportada fuera de su sitio hacia las elevaciones bajas, arroyos y ríos desérticos. Por añadidura, los acuíferos se recargan y frecuentemente aparecen después como oasis desérticos, hábitats adicionales para peces nativos. Una discusión sobre la fauna de peces nativos y de los recursos acuáticos enfatisará la importancia de la fisiografía en la región para sustentar éstos valiosos recursos naturales.

36. Status del Pececillo de Gila, *Poeciliopsis occidentalis occidentalis* y Resultados del Monitoreo de la Comuinidad de Peces en el Cañon de Redrock, Bosque Nacional de Coronado Arizona, De 1979 al Presente.

Jerome A. Stefferud, USDA Forest Service, Tonto National Forest, Phoenix, AZ; and, Sally E. Stefferud, U.S. Fish and Wildlife Service, Phoenix, AZ.

El cañon de Redrock, un tributario intermitente al arroyo de Sonoita en el desagüe del Río Santa Cruz cerca de Patagonia, en uno de los ocho sitios en Arizona que soporta una población natural del Pececillo de Gila, *Poeciliopsis occidentalis occidentalis,* un pez amenazado. La comunidad de peces ha sido periódicamente monitoreada entre 1979 y 1993. En 1979 el nativo Pececillo de Gila y la Perca de Aleta Larga y *Agosia chrysogaster*, se encuentran a través del arroyo, y los peces Mosquito exóticos del oeste *Gambusia affinis* y la Lobina Bocona *Micropterus salmoides* en un tanque de almacenamiento en la cuenca superior. El Pez Mosco del oeste y la Lobina Bocona actualmente se encuentran establecidos aquí y los introducidos Peces Sol Verdes *Lepomis cyanellus* y el Pez Baranquias Azules *Lepomis macrochirus* también. Un sólo ejemplar del Chupador del Desierto *Catostomus* (*Pantosteus*) *Clarki* fue colectado en 1987. El Pececillo de Gila permacene presente a lo largo del Cañon de Redrock pero los peces Mosquito del oeste predominan en las aguas superiores, en tributarios y cerca de la boca. Se desconoce si éste patrón refleja una coexistencia o un desplazamiento gradual de las especies nativas. En muchos otros casos el Mosquito del oeste remplazó al Pececillo de Gila en pocos años. Los esfuerzos para la conservación de la biodiversidad acuática del Cañon de Redrock, incluyen cercas o vallas para excluír al ganado y a los vehículos motorizados, cambios en el manejo del ganado, estructuras para la estabilización de la cuenca y restricciones en la localización de un sendero recreativo. Se requerirán esfuerzos adicionales para la remoción de las especies introducidas, para continuar con una vigilancia de la comunidad de peces y para los mecanismos de retroalimentación para dirigir las actividades de manejo. Esta presentación usara el Cañon de Redrock para ilustrar como la invación de especies no nativas reducen la biodiversidad y que esfuerzos de manejo están siendo empleados para detener o revertir ésta tendencia.

37. Peces del Río Yaqui Relevantes para la Provincia Madreana: Colaboraciones Estados Unidos-México.

Francisco J. Abarca, Kirk L. Young, and Robert H. Bettaso, Arizona Game and Fish Department, Phoenix, AZ; and, Ivan Parra and Kevin Cobble, San Bernardino National Wildlife Refuge, Douglas, AZ.

La ictiofauna nativa del Sistema del Río Yaqui, Arizona, Estados Unidos, y Sonora y Chihuahua, México, incluye 36 especies, cuatro de las cuales no se han descrito. Aproximadamente 50% de la cuenca del Río Yaqui se localiza dentro de la Provincia Biogeográfica Madreana, donde 13 especies de peces nativos existen. Ocho de éstas "especies Madreanas" históricamente estuvieron distribuídas en Estados Unidos y en México. Las prácticas inadecuadas de uso de la tierra y del agua, así como la introducción de peces exóticos dieron como resultado la extinción de cuatro especies de peces históricamente encontrados en el ángulo sureste de Arizona. Esfuerzos binacionales para restablecer la fauna nativa de la Cuenca del Yaqui en Arizona han resultado en la reintroducción de la hermosa carpa plateada *Cyprinella formosa*, en el Refugio de la Vida Silvestre Nacional de San Bernardino y la adquisición de un pié de cría del bagre del Yaqui *Ictalurus pricei*, para ser utilizada en futuros intentos de reintroducción en Arizona. Las acciones de recuperación para las especies incluyen el desarrollo de un plan de recuperación para los peces de Río Yaqui en los Estados Unidos y un programa de manejo para evaluar el estatus de las poblaciones de peces de Sonora y Chihuahua. Estudios adicionales de la biológia y de la taxonomía de las especies no descritas que existen en la cuenca del Río Yaqui, así como la protección de hábitat y el monitoreo a largo plazo, se requieren urgentemente para preservar ésta ictiofauna única, de los efectos potencialmente negativos de los desarrollos económicos en curso, de los proyectos propuestos de recolección y tala de madera y de la introducción de especies exóticas.

38. Coservación y Manejo de Poblaciones Madreanas de la Rana Leopardo de Chiricahua.

Michael J. Sredl and Jeffrey M. Howland, Arizona Game and Fish Department, Phoenix.

El reciente declinamiento poblacional entre los ránidos nativos de Arizona ha sido el resultado de cambios ambientales, tanto naturales como impuestos por los humanos, combinados con limitaciones ecológicas y evolutivas. Nuestro conocimiento del estatus y distribución de las ranas leopardo de Chiricahua (*Rana chiricahuensis*), un candidato para listas federales, se está aproximando a un nivel de detalle que nos permite comenzar a desarrollar estrategias para su conservación y manejo. Los inventarios del Departamento de Caza y Pesca de Arizona y de otros han encontrado metapoblaciones discretas asociadas con las cadenas Montañosas Madreanas y en sistemas acuáticos permanentes de bajas elevaciones. Estas consisten típicamente de un pequeño grupo de subpoblaciones (10) distribuídas dentro de pocos kilómetros unas de otras en un simple desagüe o en un númeropequeño de desagües interconectados. Las escasas metapoblaciones remanentes en Arizona se encuentran muy separadas, con muy poco potencial para su expansión natural o su intercambio. Nuestros inventarios de campo y la investigación de la literatura, indican que la persistencia de poblaciones históricas ha sido mayor en sitios Madreanos (7 de 24 sitios) que a bajas elevaciones (1 de 9 sitios).

Las tasas de extinción de las subpoblaciones son naturalmente altas y tal vez elevadas artificialmente, y ahora sobrepasan las tasas de recolonización, las cuales se encuentran probablemente deprimidas debido al deterioro de los corredores de dispersión. Nosotros esperamos aumentar las metapoblaciones funcionales a través de la re-ubicación (dispersión facilitada) de ranas a sitios apropiados, no habitados dentro o alrededor de las metapoblaciones existentes. En algunos casos podemos crear metapoblaciones alrededor de sitios aislados por el mismo medio. La renovación o rehabilitación del hábitat y de los corredores de dispersión, serán importantes para el éxito a largo plazo de tal estrategia de conservación. La información se sigue colectando sobre nuevas líneas de investigación, de refinamiento y de las estrategias de manejo que deben seguirse. Recomendamos una investigación sobre la estructura genética de las poblaciones para un entendimiento más completo de la dinámica metapoblacional. Antes que metapoblaciones autosuficientes puedan ser restauradas en las montañas Madreanas debemos comprender los factores que influencían las tasas de extinción (demográfica, genética y de estocastidad ambiental) y la capacidad de recolonización (capacidad de dispersión: tolerancia fisiológica y ecológica).

39. Incendios y Vegetación en un Bosque de Encino Madreano, Montañas de Santa Catalina, Sureste de Arizona.

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La presencia de incendios y sus efectos en los bosques Madreanos de encinos han sido frecuentemente observados pero han sido pobremente estudiados, aún cuando el fuego puede jugar un papel significativo en la dinámica y la estructura de la vegetación. En ésta investigación nosotros examinamos los efectos y respuestas de la vegetación post-incendio siguiendo una quema en junio en un bosque de encino. Colectamos datos de la composición de plantas y biomasa en sitios quemados y no quemados en el norte, este y el sur, permitiendo diferentes niveles de comparación. Nuestros resultados indican cambios significativos en la composición de especies que causados por el fuego, con diferentes respuestas de las especies, las especies leñosas fueron reducidas con limitada recuperación, mientras que las especies herbaceas, las cuales fueron inicialmente reducidas, generalmente tienen una mayor cobertura en las áreas quemadas que en las áreas no quemadas, después de dos años y medio del incendio. La recuperación fué rápida en las pendientes del sur dominadas por herbaceas perenes y mas baja en las pendientes norte donde las especies leñosas y *Selaginella* fueron importantes antes del fuego. Las especies favorecidas por el fuego incluyen *Artemisia ludoviciana, Gnaphalium wrightii, Aristida orcuttiana, A. adscensionis, Bouteloua curtipendula* y *Eragrostis intermedia,* mientras que las especies intolerantes al fuego incluyen *Arctostaphylos pungens , Agave schottii, Haplopappus laricifolius, Trachypogon secundus* y *Selaginella rupincola.* Nuestra comparación sobre las dos principales especies de árboles muestra una buna recuperación despues del daño, indicando que *Quercus oblongifolia,* con la menor cantidad de muertes fué mas tolerante al fuego que *Q. emoryi,* aunque ambas especies sufren cerca del 15 % de mortalidad. La biomasa herbacea y de hojarasca (buenos combustibles) varían dos y medio años después del fuego entre 259 - 616 g/m^2 en los sitios no quemados y entre 243 - 365 g/m^2 en los sitios quemados. La rápida acumulación de buenos combustibles, particularmente las de orientación sur, permiten la existencia de intervalos cortos entre los incendios (1-2 años) aunque la acumulación puede estar influenciada por la precipitación. Estas observaciones proporcionan información básica acerca de la tolerancia y respuesta de las especies del bosque al fuego y sugiere que los incendios fueron un proceso importante para la formación y el mantenimiento de los bosques Madreanos de encinos en el pasado.

40. Historias de Incendios en las Montañas Pinaleno del Sureste de Arizona: Efectos del Clima y Perturbaciones Relacionadas al Hombre.

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Reconstruiremos el historial de incendios en dos sitios de los bosques mezclados de coníferas y en las Montañas Pinaleno del sureste de Arizon, a partir de 90 árboles de pino blanco (*Pinus strobiformis*) y pino ponderosa (*P. Ponderosa*), tanto vivos con cicatrices del fuego como muertos. Nosotros utilizamos técnicas dendroecológicas para fechar más de 500 cicatrices de fuego en su año exacto de formación, entonces comparamos éste historial de incendios con una reconstrucción dendroclimática cercana de sequía para investigar las interrelaciones fuego-clima. Durante el período precolonizador, antes de 1871, incendios superficiales de baja intensidad ocurrieron en promedio una vez cada 5 o 6 años, variando de un intervalo mínimo de un año (1773 y 1774) a un intervalo máximo de 19 años (1819 a 1838). Un intervalo inusualmente largo de 22 años ocurrió entre los incendios de 1871 y 1993. El cese de incendios episódicos después de 1893 puede ser atribuído a una combinación de perturbaciones relacionadas con las actividades humanas que incluyen el pastoreo, la tala y las actividades de supresión de incendios. La reconstrucción climática verifica que los incendios pasados ocurrieron probablemente más durante los años de sequía moderada a severa seguidos por años de lluvia por encima del promedio. La ausencia de incendios ecológicamente significantivos durante los últimos 100 años en las Montañas Pinaleno deben ser considerados cuando se desarrollen planes de manejo de incendios y de desarrollo de la tierra para esta área sensitiva ambiental y políticamente.

41. Historial de Incendios y Estructura en Pié de un Bosque de Pino-Encino Madreano no Cosechado.

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(1) El historial de incendios, la estructura del bosque (densidad, composición de especies, regeneración, combustibles del piso del bosque, cobertura herbácea, distribución espacial y edad), y el registro dendrocronológico en los anillos de los árboles fueron medidos en dos sitios pareados no cosechados de 70 hectáreas en la Sierra Madre Occidental del norte de Durango, México. Los intervalos promedio de incendio a largo plazo (I.P.F.) para todos los incendios en ambos sitios fueron similares, entre tres a cinco años, pero el fuego fué escencialmente excluído del sitio 1 después de 1945. Como resultado, el sitio 1 fue caracterizado por numerosos árboles relativamente pequeños (área basal = 23.4 m^2/ha, 2730 árboles s/ha) mientras que el sitio 2 tienen pocos árboles relativamente grandes (área basal = 37.2^2/ha 647/ha). La carga de combustibles podridos y la profundidad de la hojarasca fué también

mayor en el sitio 1. (2) A través de un ánalisis estadístico espacial, el efecto de incendios frecuentes sobre las distribuciones de los árboles puden ser cuantificadas: los árboles jóvenes se encuentran fuertemente agregados, mientras que los árboles expuestos a frecuentes incendios adoptan una distribución espacial uniforme. La distribución de los diámetros y de las edades de los pinos en ambos sitios indican que el establecimiento de árboles a ocurrido en pulsos siguiendo los incendios (3) La mayoría de los fuegos parecen ser de origen humano y existe evidencia histórica del uso intencional y accidental de los incendios por poblaciones indígenas y no indígenas en la Sierra Madre. Sin embargo, una correlación consistente se observó entre la ocurrencia promedio de incendios en ambos sitios y el índice estandarizado de anillos de los árboles: los incendios fueron más frecuentes en épocas de crecimiento reducido de los árboles. (4) La densa regeneración y la acumulación de combustible pesado en el sitio excluído de incendios probablemente mantiene un cambio que va del régimen original de incendios de baja intensidad a uno de alta intensidad, cuando un incendio a través del sitio remplazará todo, cuando la siguiente combinación adecuada de ignición y clima ocurra. Los manejadores deben considerar la historia de perturbaciones pasadas y sus efectos, en el diseño de estrategias de manejo basadas ecológicamente para bosques Madreanos.

42. Extructura en Pié del Bosque de las Montañas Animas y Sierra de los Ajos.

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Para evaluar la estructura en pié de el bosque de coníferas del sureste de los Estados Unidos y norte de México, las distribuciones por clase de edad -y tamaño- fueron determinadas para las comunidades dominadas por coníferas en las Montañas de las Animas, Nuevo México, USA, y Sierra de los Ajos, Sonora, México. La estructura en pié fue estudiada en tres comunidades de bosques en cada cadena montañosa: (1) Bosques de abeto de Douglas/encino de gambel se encontraron en orientaciónes norteñas por encima de los 2,200 metros, (2) Bosques del pino blanco del sureste -pino Chihuaheño y pino ponderosa- se encontraron en elevaciones intermedias (3) Bosque de pino piñonero, junípero y encino se encontraron en elevaciones bajas limitando con los pastizales. (4) Cuatro sitios representativos de cada comunidad en cada cadena montañosa fueron estudiados intensivamente durante los meses de verano de 1992 y 1993. Un lote permanente de 20 x 50 m. (0.1 ha) fue establecido en cada sitio, en los cuales el diámetro a la altura del pecho (DAP) de cada tallo de las plantas fué medido y la edad fué determinada por el análisis de anillos de dos árboles seleccionados al azar (20 árboles por sitio en total). Se utilizaron métodos dendrocronológicos standar para estimar las distribuciones de edades para cada comunidad boscosa. La frecuencia de las clases de edad se aproxima estrechamente a una distribución exponencialmente negativa para las comunidades boscosas de las Montañas de las Animas, Nuevo México. La estructura en pié aparentemente a sido influenciada por un régimen de incendios excepcional para los bosques semiáridos del sureste de los Estados Unidos, caracterizado por una mezcla de fuego superficial de baja intensidad y un fuego arrasador. Las distribuciones de clases de edad para las comunidades boscosas en la Sierra de los Ajos, Sonora, México, está en proceso, sin embargo resultados preeliminares para estás comunidades indican una gran influencia del fuego caracterizado por la presencia de lotes de bosques jóvenes y una mayor cantidad de crecimientos de anillos.

43. Regeneración Post-incendios en la Comunidad del Saguaro Gigante en Arizona.

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Los incendios en las comunidades altas del Desierto Sonorense en el Bosque Nacional Tonto en Arizona, se han incrementado en frecuencia y en extensión. Paisajes internacionalmente renombrados, compuestos del cactus saguaro gigante (*Carnigiea gigantea*) y la vegetación asociada han sido severamente degradadas por los incendios. Estos frágiles hábitats desérticos tienen una larga historia de uso humano lo cual ha sido agravado por el incremento de igniciones de incendios en áreas de un uso público alto. En los años de precipitaciones altas, ésas comunidades de tierras altas de cactus y matorrales frecuentemente desarrollan una contigua e inflamable cama de combustible compuesta de hierbas y pastos alrededor y debajo de las especies de cactus y matorrales. La mortalidad post-incendio es específicamente alta para la mayoria de los cactus incluyendo al saguaro gigante. La sobrevivencia a largo plazo del saguaro puede ser dependiente de la regeneración o restauramiento de las plantas de especies asociadas y reportadas como nodrizas. Los efectos temporales y espaciales del fuego en ésta comunidad no han sido delineados. Estudios posteriores a largo plazo son necesarios, sí las estrategias y técnicas de manejo para una restauración agresiva de las áreas degradadas por el fuego están siendo desarrolladas. Nosotros estamos actualmente conduciendo varios estudios sobre el efecto del fuego en ésta comunidad. En mayo de 1993 un pirómano provocó numerosos incendios en la vegetación del tipo saguro-matorral en el Desierto de la Mesa Ranger, Bosque Nacional Tonto. Durante enero de 1994, comenzamos una examen post-incendio en esas áreas quemadas para determinar el potencial, de las especies del matorral, para retoñar después del incendio. Saguaros rodeados de fuego y esqueletos carbonizados de arbustos cubrían las áreas quemadas. Los esqueletos de arbustos fueron examinados en busca de retoños basales o crecimiento nuevo de ramas. El retoño de las ramas de los matorrales fue evidente dentro de las islas de áreas parcialmente quemadas y a lo largo de los límites de los sitios quemados, el retoño basal fue observado en plantas que tienen aparentemente ramas superiores viables, ésto implica que algunas especies arbustivas en la asociación saguaro-arbusto estudiado tienen el potencial para regenerarse después de un incendio de primavera.

44. Un Centro Nacional de Agricultura Sustentable.

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El mundo está cada vez más preocupado acerca del deterioro de los recursos naturales causado ya sea por sistemas de alta tecnología o por sistemas de producción de subsistencia, los cuales llevan a la destrucción del suelo, la biota y la degradación ambiental general. Esta situación reducirá peligrosamente la producción de alimentos para las crecientes humanas cuyas necesidades también están creciendo. Es urgente implementar cambios drásticos en la tecnología de alimentos y en la producción de los mismos en México y en otras regiones del territorio de las Islas en el Cielo. El cambio debe empezar con la investigación de los procesos básicos los cuales puden ser usados para generar tecnología para su adaptación en granjas. Este esfuerzo se encuentra apenas iniciándose en el Centro Nacional de Agricultura Sustentable, en coordinación con el Centro de Investigación Regional del Instituto Nacional de Investigación Forestal y de Agricultura y Producción Animal (INIFAP) así como con otras organizaciones nacionales e internacionales. El Centro tiene un pequeño grupo de investigación altamente capacitado el cual desarrolla sus propios proyectos de investigación y coordina las actividades de investigación de redes nacionales distribuidas a través de México (300 Investigadores). Las funciones del Centro son: A) generar tecnologías para la producción sustentable B) establecer y mantener estandares institucionales en tecnologías de producción sustentable C) proporcionar entrenamiento técnico a todos los niveles, y de efectuar diagnósticos y proyectos especiales relacionados con la producción sustentable. Los siguientes proyectos están siendo desarrollados por el Centro: A) cultivos conservacionistas, B) otros sistemas agrícolas alternos (agricultura orgáanica, sistemas indígenas de producción etc.), C) posibilidades de mecanización para granjas pequeñas, D) manejo integrado de recursos (manejo de cuencas, cultivos alternos, etc.) y F) análisis del gasto energético usado en sistemas agrícolas. El centro sigue la estrategia de seleccionar problemas altamente prioritarios identificados en sistemas específicos para desarrollar la investigación no sólo en el problemas en sí, sí no para todo el sistema. Todos los componentes del sistema de producción son analisados, incluyendo factores ambientales, grado de evolución, insumos, productos (cantidad y calidad) así como parámetros socioeconómicos. El sistema es introducido al más viable de los seis proyectos arriba mencionados para resolver el problema, pero una vez que se encuentran en la estructura del Centro éste pasa a través de los otros cinco proyectos remanentes para alcanzar una solución integral, así cuando el sistema sale del Centro uno puede confiar en que los aspectos más importantes relacionados a la producción sustentable han sido cubiertos de acuerdo a nuestro nivel actual de conocimiento. Estrategias de éste tipo son muy complejas para ser desarrollados sitisfactoriamente por una sola institución. Sin embargo se requiere que INIFAP colabore eficientemente con la enseñanza clave, desarrollo, investigación e instituciones nacionales e internacionales. El Centro no duplica tecnologías sustentables generadas por el INIFAP ni ninguna otra en el país. El Centro está utilizando ésta aproximación de investigación integral para cubrir un vacío actual.

45. Impactos Ecológicos del Pastoreo de Ganado Sobre la Vegetación, Suelo y Vida Silvestre de Las Montañas de Sonora.

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La región montañosa del este de Sonora, conocida como "la Sierra" fue elegida para el asentamiento por los primeros colonizadores sobre las planicies costeras más extensas, planas y áridas, en razon de su más alta precipitación, arroyos y valles fértiles. La cría de ganado comenzó en la región, alrededor de 1670 y ha sido un importante factor económico, social, cultural y ecológico desde entonces. Con el tiempo y con el advenimiento de técnicas de irrigación para la agricultura, los centros de población humana se han trasladado hacia las costas. A pesar de los esfuerzos de las agencias Estatales y Federales, la mayor parte de las tierras altas subcomunicadas del este de Sonora no han mantenido el paso con el desarrollo que ocurre en el resto del Estado y son todavía economicamente marginales en comparación a cualquier actividad económica. La dependencia de la agricultura de subsistencia y de los ranchos, está comenzando a dar camino a otras actividades económicas y a la consideración de que uno de los más importantes recursos de está región es el agua, que capturada y almacenada en presas, grandes y pequeñas, y usadas en su mayor parte por las grandes ciudades por debajo de su crecimiento poblacional e incremento industrial y en la irrigación del desierto para producir grandes áreas de unos cuantos cultivos introducidos de alto valor económico y social. El manejo y el uso racional de todos estos recursos naturales de las montañas de Sonora, incluyendo la protección y conservación de alguna áreas únicas, ofrecen desafíos a legisladores, planeadores, manejadores y residentes de está relativamente poco estudiada región de Sonora.

46. Biodiversidad Versus Minería - Una Prioridad en el Cañon de la Cueva.

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Bajo la leyes federales actuales, la minería es considerada como un uso prioritario de las tierras federales, a no ser que las áreas sean específicamente retiradas de la minería por la acción administrativa de Agencias Federales o por el retiro formal por el Congreso. Esta dominancia de la minería sobre múltiples usos tradicionales tales como la vida silvestre, la recreación, la recolección de madera y el pastoreo, ha llevado en años recientes a difundir un llamado para la reforma de las leyes federales para permitir a las agencias Federales mayor discreción en el manejo de las tierras bajo su control. A fines de 1991, una propuesta para conducir actividades mineras exploratorias en tierras del Servicio Forestal en la Boca del Cañon de la Cueva en las Montañas Chiricagua lavantó un torrente de protestas entre los ciudadanos locales, biólogos y entusiastas de la vida silvestre a lo largo del país. Esta propuesta, que cubre una milla cuadrada de tierras que podrían ser sujetas a la pulverización por una mina a cielo abierto y lavado con cianuro para la extracción de oro, generó situaciones de conflictos con otros usos a largo plazo y valores de las tierras implicadas. En particular el Cañon de la Cueva tiene un renombre mundial por su biodiversidad exepcional y por la Estación de Investigación del Sureste del Museo Americano, la cual ha servido como centro de numerosos estudios biológicos terrestres. Mucho más de 1,000 artículos científicos basados en investigación en el Cañón de la Cueva han sido publicados en las décadas recientes. Las actividades de minería en gran extensión en el cañon podrían generar diversos impactos negativos sobre tales valores. Afortunadamente, la persuación ciudadana masiva tuvo éxito en convencer a la Coorporación Minera Newmont para abandonar voluntariamente su propuesta de minería para el Cañón y el Congresista Jim Kolbe obtuvo con éxito el ácta de protección para el arroyo de la Cueva en 1993, lo cual retira de la minería todas las tierras federales en la cuenca de la Cueva. El tema más amplio de la reforma total de leyes mineras permanece todavía sin resolver.

47. Comparación de los Métodos Para Evaluar la Diversidad Genética en Plantas: Aplicaciones en el Archipiélago Madreano.

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La información sobre niveles y patrones de variación genética es importante para los esfuerzos enfocados a la conservación de la biodiversidad. Acuerdos tales como sí dos grupos son genéticamente diferentes (por ejemplo sub-especies) y cuáles poblaciones deben ser conservadas, dependen de ésta información. La variación genética en plantas encontradas en el Archipielago Madreano, pueden ser evaluadas de varias de maneras, que van desde los estudios de jardinería común, en los cuales los rasgos morfológicos son medidos, hasta los marcadores genéticos moleculares recientemente desarrollados. Cada método de evaluación de la variación genética tiene ventajas y desventajas. Algunos investigadores preferieren marcadores moleculares genéticos debido a que pueden ser obtenidos resultados más rapidamente de un mayor numero de individuos; sin embargo, los resultados obtenidos de éstos estudios pueden no ser consistentes con los resultados obtenidos por los estudios de jardinería común. Estas diferencias resultan de los diferentes balances de las fuerzas evolutivas que han afectado los rasgos a ser medidos, con patrones de variación de marcadores moleculares genéticos generalmente son más fuertemente influenciados por la deriva genética y por el flujo de genes entre poblaciones y los rasgos morfológicos frecuentemente muestran un mayor efecto de la selección basada en los factores ambientales. Los estudios en una variedad de plantas intercruzadas han revelado muy diferentes patrones de variación genética para rasgos morfológicos y para marcadores moleculares genéticos, con los primeros generalmente muestran una mucho mayor diferenciación interpoblacional y fuertes asociaciones con factores ambientales. Dependiendo del rasgo examinado, uno puede obtener conclusiones diferentes respecto a importantes decisiones de conservación. Estudios utilizando ambas aproximaciones proporcionarán la mejor información en la cual basar éstas decisiones en el Archipiélago Madreano.

48. Obstáculos para Alcanzar Los Propósitos de Manejo de Tierras Federales: La Disyunción Entre La Planeación y la Presupuestación. Un Estudio de caso del Bosque Nacional del Coronado, Arizona.

Paul W. Hirt. Department of History, Washington State University, Pullman.

El manejo de tierras federales está gobernado por un elaborado proceso público de planeación que involucra evaluaciones detalladas de los impactos ambientales, sociales y económicos de las acciones propuestas y alternativas. Designado por el Congreso como un medio para mejorar el manejo de la tierra, éste "modelo regional" de toma de decisiones está basado en varias e interesantes, pero dudosas, suposiciones acerca del ambiente institucionasl dentro del cual los manejadores funcionan. Primero, se asume que un mejor conocimiento llevará automáticamente a mejorar la toma de decisiones; igualmente, se asume que un mayor público involucrado en la planeación producirá una mayor aceptación pública de las decisiones. Nada de esto es necesariamente cierto. Se asume también que los planes de manejo, llegan racionalmente para su consideración a un consejo experto, que, en realidad, los llevará a cabo. Nuevamente nosotros sabemos por experiencia que éste no es frecuentemente el caso. A lo largo de todo el país, los planes nacionales de manejo forestal no están siendo efectivamente implementados. Las razones para ello son varias: (1) Muchos planes de manejo no son tan "racionales" como parecen superficialmente, por ejemplo, diferentes elementos del plan entran en conflicto unos con otros, información crucial puede faltar o ser inadecuada, suposiciones acerca de la tecnología económica, aceptabilidad social, respuesta ambiental, potenciales de mitigación pueden ser insostenibles. (2) Tanto los planes como las acciones subsecuentes de manejo pueden ser sensibles a la dirección que tome una política cambiante y a la producción de blancos anuales por los altos niveles de la burocracia federal. (3) Las intenciones de manejo llegan a ser acciones solamente cuando la agencia puede actuar a través de sus recursos monetarios y de personal, y **todavía una gran, y en su mayor parte no examinada discusión existe entre la planeación de los bosques nacionales y el financiamiento del Servicio Forestal.** Este artículo tocará todos estos obstáculos para implementar planes de manejo, pero se enfocará especialmente sobre el último elemento, usando el Bosque Nacional de Coronado como un caso de estudio. El autor sostiene que a los manejadores y los planeadores del bosque les falta tomar en cuenta adecuadamenten las realidades fiscales cuando escriben los planes forestales, volviendo así muchos objetivos de manejo solo un poco más que pensamientos alentadores. El autor además argumenta que las políticas federales de financiamiento son erráticas, no balanceadas y altamente desconectadas del proceso de planeación, interpretando así muchas de las buenas intenciones de los planes de manejo. La única consistencia en las políticas de financiamiento parece ser una tendencia del Congreso a apoyar generosamente el desarrollo del programa de recursos mientras escatima en los programas asociados de rehabilitación de recursos necesarios para alcanzar el desarrollo sustentable y la protección ecológica. Entonces, reformas clave que deberían ser desarrolladas por los manejadores de la tierra y los ecológistas son para incrementar la *factibilidad* de los planes forestales y el trabajo de los grandes compromisos político/fiscales para implementar *todos* los elementos interconectados de estos planes. Una manera de lograr esto puede ser el hacer que los componentes de mitigación ambiental y de rehabilitación en los planes de los bosques sean prerequisitos explícitos para continuar con las actividades asociadas al desarrollo.

49. Prácticas de Manejo en Beneficio del Pavo de Gould en las Montañas Peloncillo, Nuevo México.

Sanford D. Schemnitz and Mark L. Zornes. Department of Fisheries and Wildife Studies, New México State University, Las Cruces.

Las prácticas de manejo para incrementar el hábitat del pavo de Gould se discutirán. Las áreas de alimentación deben ser mantenidas con un mínimo del 50 % de árboles productores de mástiles. Los niveles de existencias de ganado deben ser ajustados para permitir un máximo de la utilización del 35% de la vegetación herbácea. El hábitat de crianza de verano debe incluír claros que contengan plantas herbáceas de no menos de 30 cm. de altura, después del pastoreo. La biomasa herbácea ideal debe ser de 400-600 kgs. por hectárea. La distancia a los sitios de cobertura de bosque o arbustos deben ser menores de 100 metros. Los claros creados por manejo no deben exeder de 150 a 200 m en amplitud y deben ser de formas irregulares. Todo el pastoreo de ganado dentro de los hábitat claves de crianza deben ser diferido hasta el primero de septiembre. Los claros no deben ser menores que el 15% del hábitat del pavo y deben de estar bien distribuidos. El cierre temporal o permanente de caminos a través de los hábitats de crianza se recomienda. La poda de ramas muy juntas de árboles con gruesos ramajes y el clareo de la vegetación de sotobosques ayudará a incrementar el uso de sitios de percheo. Los conjuntos de pino de Chihuahua pueden ser protegidos para sitios de percheo presentes y futuros. No se deben construir nuevos caminos a través de los sitios de percheo. Los sitios con agua pueden ser mejorados para los pollos proporcionando rampas de entrada y de salida. Sitios adicionales con agua necesitan ser contruidos en lugares de los cañones donde puedan ser construídas represas con rocas. Las poblaciones necesitan controlarse. El reforzamiento de las reglas y regulaciones existentes debe incrementarse, particularmente en relación a la cosecha ilegal de leña.

50. Manejo y Coservación de la Islas en el Cielo más Importantes en Baja California sur.

Alfredo Ortega-Rubio, Centro de Investigaciones Biológicas del Noroeste, La Paz, B.C.S. México.

Durante más de ocho años las autoridades e investigadores del Centro de Investigaciones Biológicas promovieron el decreto formal para la protección de las Islas en el Cielo más importantes de Baja California Sur: La Sierra de la Laguna. A pesar de que nuestros esfuerzos tuvieron el apoyo de Agencias Nacionales e Internacionales, así como de Universidades tales como el World Wildlife Fund y la Universidad de Arizona, hasta la fecha no existe una protección oficial para la zona. Para garantizar la protección de los recursos naturales de la zona y para apoyar a las comunidades de habitantes locales nuestro Centro de Investigaciones ha desarrollado intensos esfuerzos en la búsqueda de alternativas específicas para el uso óptimo de los recursos de la zona. Las principales características de ésta zona son descritas en este trabajo, así como la estrategia seguida con el objetivo de proteger sus recursos naturales.

51. Quema Prescrita como una Herramienta de Trabajo para los Humedales de las Islas en el Cielo con Referencia al Manejo de la Orquídea en Peligro *Spiranthes delitescens.*

Mark Fishbein, Department of Ecology and Evolutionary Biology, University of Arizona, Tucson; Dave Gorr, The Nature Conservancy, Arizona Field Office, Tucson; and, Donya Meggs, Tucson, AZ.

Las ciénegas de las Colinas Canelo en el sureste de Arizona son un raro humedal de elevación media que es uno de los cuatro hábitats conocidos para la orquídea en peligro *Spiranthes delitescens.* Este humedal, una reserva de Nature Conservancy, es un raro pantano perpetuamente húmedo en un valle entre las cordilleras de las Islas en el Cielo. Una amenaza potencial para la *S. delitescens* de éste sitio, es la acumulación de vegetación seca la cual puede estar inhibiendo la emergencia y la reproducción sexual de ésta especie. De

1990 a 1993 investigamos el potencial de utilizar quemas prescritas como una herramienta de manejo para remover la vegetación seca en este sitio. Tres tratamientos de quema, variando solamente en frecuencia fueron aplicados al azar en nueve lotes experimentales. La altura de la vegetación y la profundidad de la materia seca, la cobertura de cada especie y la diversidad de especies no graminoides (por ejemplo, otras diferentes de Cyperanceae, Juncaceae, y Poaceae) fueron medidas anualmente en cada cuadrante. La materia seca acumulada fué efectivamente removida por la quema, pero regresa a los niveles de antes de la quema después de un año. La altura de la vegetación no fue significativamente afectada por la quema. Los tratamientos también tienen efectos menores sobre la cobertura y densidad de las especies de plantas. Dos especies de juncos (*Juncus*) decrecieron significativamente su cobertura en respuesta a la quema. La juncacea *Scirpus americanus*, sin embargo, fué favorecida significativamente por la quema. *Eleocharis rostellata* una juncacea, y los pastos *Muhlenbergia utilis* y el introducido *Poa prantensis* decrecieron significativamente en cobertura en el tiempo, independientemente del tratamiento de quema. El botón de oro *Ranunculus macranthus* se incrementó significativamente en cobertura con el tiempo independientemente del tratamiento de quema. La densidad de la cola de caballo *Equisetum laevigatum* y *R. macranthus* respondieron positivamente y significativamente al tratamiento de quema. En 1993, existió un incremento dramático en el número de *S. delitescens* que floreció en los sitios, sin embargo, éste incremento no se puede atribuir a los tratamientos de quema. Estos resultados sugieren que el efecto de la quema prescrita en la vegetación de la ciénega son sutiles aunque detectables y que la quema por sí misma no es probablemente una técnica de manejo satisfactoria para *S. delitescens* en este sitio. Los efectos nagativos potenciales de la quema, tales como la promoción de especies exóticas debieron tambíen ser considerados.

52. Un Acuerdo de Conservación para Caracol de Tierra del Cañon Húmedo, Condado de Graham, Arizona.

Jerome Stefferud, USDA Forest Service, Tonto National Forest, Phoenix, AZ; and, Debra Bills, U.S. Fish and Wildlife Service, Phoenix, AZ.

El caracol de tierra del Cañon Húmedo *Sonorella macrophallus* es un caracol de tierra endémico altamente localizado, cuyo rango de distribución total esta aparentemente restringido a las laderas en una milla del Cañon Húmedo a las Montañas Pinaleno, Condado de Graham, Arizona. Esta especie parece requerir humedad y posiblemente un hábitat de elevación más baja que otros caracoles en este sitio montañoso. El Servicio de Pesca y Vida Silvestre de U.S. (USFWS) ha colocado a ésta especie en la categoría 1 de su lista de candidatos, esto es, taxa, para el cual el USFWS tiene suficiente información sobre su vulnerabilidad y amenaza para apoyar una propuesta para enlistarlo como una especie amenazada o en peligro. Para depurar el listado, el USFWS y el USDA (USFS) se encuentran desarrollando un convenio de conservación que enfatizan los métodos para remover las amenazas y para mantener la estabilidad de especie y de su ecosistema. Esta presentación discutirá el uso de acuerdos de conservación en la preservación y el manejo de especies silvestres en decline y no listadas. Los requerimientos de los acuerdos de conservación seran discutidos así como sus defectos y conveniencias.

53. Un Reporte Inicial Sobre la Formación del Grupo Fronterizo Malpai y su Trabajo Conjunto con Agencias Públicas de Manejo de Tierras.

Bill McDonald. 1553 10th Street, Douglas, AZ.

En marzo de 1993 un grupo de rancheros vecinos del ángulo sureste de Arizona y del ángulo sureste de Nuevo México se reunieron en el Rancho Malpai para discutir sus intereses compartidos para desarrollar un plan para coordinar los incendios naturales en el paisaje. De ésta reunion inicial, un grupo de trabajo de propietarios de tierras en el Condado de Hidalgo, Nuevo México y del Condado de Cochise, Arizona se ha unido en el Grupo Fronterizo Malpai Inc. para perseguir un propósito común. " Nuestro propósito es restaurar y mantener los procesos naturales que forman y protegen un paisaje sano, no fragmentado, para soportar una comunidad diversa y floreciente de vida humana, vegetal y animal en nuestra región de tierras fronterizas. Juntos nosotros lo lograremos trabajando para promover el trabajo redituable de los ranchos y otros estilos de vida tradicionales los cuales sustentarán el espacio abierto de nuestra tierra para las generaciones que vienen". La cooperación activa ha comenzado entre el Grupo Fronterizo de Malpai y el Servicio Forestal del Bosque Nacional Coronado USDA, la Oficina de Manejo de Tierras de los Distritos de Safford y Las Cruces USDI, La Fundación Animas, el Departamento de Tierras del Estado de Arizona, el Departamento de Tierras del Estado de Nuevo México, el Servicio de Conservación de Suelos de Arizona y Nuevo México, el Laboratorio del Desierto de la Universidad de Arizona, el Distrito Hidalgo de Conservación de Suelos y Agua, el Distrito de Conservacíon de Recursos Natuarales Whitewater Draw y Conservación de la Naturaleza.

54. Islas en el Cielo: Melancolía o Gloria.

Ervin H. Zube. School of Renewable Natural Resources, University of Arizona, Tucson.

Una encuesta en 1982 acerca de las actitudes y percepciones de los residentes de Arizona hacia el estado de los recursos naturales, sin sorpresa, arrojó evidencisa convincentes que los dos tipos de paisaje con más alto valor en el Estado fueron las montañas y las áreas riparias. Incluídas en la categoría de montañas, implícitamente estuvieron las Islas en el Cielo "de la región del Desierto de Sonora". Este artículo analiza la cuestión de los valores atribuídos a los paisajes de montaña, cómo han evolucionado históricamente y qué factores han influenciado ésta evolución. Tal como el título de éste artículo sugiere, las montañas han sido algunas veces preservadas del modo menos favorable. Es más, los valores han sido conflictivos. Entre los valores explorados están aquellos referentes al escenario, recreación, vida silvestre, cosecha de madera y protección de cuencas. Percepciones y valores de melancolía y gloria están ilustrados con los ejemplos históricos y contemporáneos de diversos sitios geográficos pero con especial énfasis en las Islas del Cielo del sureste de Arizona.

55. De Casas Grandes A Casa Grande: Adaptaciones Prehistóricas en las Tierras Altas del Sureste de Arizona y Norte de México.

Patricia M. Spoerl, Coronado National Forest, Tucson; and, John C. Ravesloot, Gila River Indian Community and Arizona State University, Tempe.

Las culturas, pasadas y presentes, como los ecosistemas son entidades dinámicas y sus relaciones entre ellas deben ser cuidadosamente consideradas. Las relaciones entre la gente y el ambiente natural han sido un tópico de investigación arqueológica por muchos años. Datos florísticos, faunísticos y climáticos recuperados de sitios arqueológicos, pueden ser usados para reconstruir aspectos importantes de ecosistemas pasados y para determinar como han cambiado a través del tiempo. La imagen que emerge es una interacción entre un ambiente constantemente cambiante y un sistema humano constantemente cambiante también. Este artículo resume nuestro reciente conocimiento de la prehistoria de las Islas en el Cielo y discute las estrategias para obtener una mejor comprensión de las relaciones pasadas entre la gente y su ambiente en el suroeste de los Estados Unidos y el noroeste de México.

56. La Etnoecología del Area de Lone Mountain/San Rafael, Y Este de Arizona: Una Visión Histórica de 1540 al Presente.

Thomas E. Sheridan and Diana Hadley, Arizona State Museum, University of Arizona, Tucson.

Este artículo presentará una visión de los resultados de la investigación conducida por el Coronado National Forest en el las áreas del proyecto de ecosistemas de Lone Mountain/San Rafael. El propósito del proyecto de investigación es la historia del uso de la tierra y del cambio en ecosistema dentro del área del proyecto. La metodología de investigación incluye archivos, examen de fotografías históricas del área y entrevistas orales extensivas con residentes permanentes del área de estudio. La visión presentada en la conferencia sera ilustrada con diapositivas de fotografías históricas y mapas históricos los cuales ofrecerán indicios del uso de la tierra y de los cambios de los ecosistemas que resultaron de usos específicos. El manuscrito incluirá una breve descripción de la ocupación histórica humana por los grupos étnicos principales del área (Americanos nativos, Españoles, Mexicanos y Anglo-americanos) con un resúmen del patrón de asentamientos de cada grupo, actividades de uso del suelo, percepciones de los ecosistemas locales y posibles impactos ambientales. El artículo se enfocará en evaluar los impactos comparativos por los grupos étnicos del área de acuerdo a las actividades específicas de subsistencia y economía a las cuales se dedicaron cada grupo. Concluirá con un análisis general de los cambios de la vegetación y del porcentaje dentro de componentes específicos del ecosistema del área del proyecto incluyendo planicies de pastizales, bosques de encinos, hábitat ripario y bosque de coníferas.

57. Ecoturismo en el Archipiélago Madreano.

David A. King and Brian Czech. School of Renewable Natural Resources, University of Arizona, Tucson.

Este artículo proporciona un enfoque crítico del ecoturismo en relación a los sistemas de biodiversidad y sistemas sociales humanos en la región del Archipiélago Madreano. La literatura en general sobre ecoturismo, se revisará para identificar la naturaleza y el carácter de los impactos positivos y negativos del ecoturismo sobre la bidiversidad y los sistemas sociales. Entonces el ecoturismo como actualmente existe en la región, será discutido en relación a los sistemas de biodiversidad y sistemas sociales de la región. Basado en éstas revisiones generales y regionales, escenarios futuros posibles que surgieran de ésta situación actual serán identificados. Finalmente, se sugerirán políticas para dirigir estos futuros escenarios.

58. Recolección de Madera para Leña en las Islas del Cielo Del Sureste de Arizona.

Duane A. Bennett, Sierra Vista Ranger District, Coronado National Forest, Hereford, AZ.

La recolección de madera para leña ha ocurrido dentro y alrededor de las Islas en el Cielo de Montaña del sureste de Arizona durante siglos. Los americanos nativos utilizaron los bosques como una fuente de combustible para cocinar y para calentarse. Los exploradores Españoles, Mexicanos y los colonizadores Americanos posteriormente expandieron la utilización para incluir usos tales como corte de madera para soporte en las minas, producción de carbón y producción de cercas. La utilización de los bosques tuvo un impacto mínimo sobre los recursos forestales hasta el auge de la minería local las cuales tuvieron lugar a fines del siglo IXX y más recientemente duranante la recolección de madera para combustible a fines del siglo XX. Durante la "crisis energética" de los años de 1970 la gente cambió de la exclusiva dependencia de fuentes convencionales para calentarse y cocinar, tales como las eléctricas y de gas hacia el consumo de madera como una forma de evitar los costos de energía. Este artículo remarca la historia de las ventas permitidas de madera para leña, tanto para uso personal como comercial, en el Bosque Nacional del Coronado lo cual es usado como un indicador de la demenda cambiante para el uso de leña en sureste de Arizona desde principio de los años setenta hasta 1993. Se presentará también una versión de la respuesta de los manejadores de recursos a los cambios en la demanda de leña y su impacto sobre los bosques en las Islas en el Cielo.

59. Diseño de Protección para mantener la Biodiversidad en la Región de las Islas en el Cielo.

Dale S. Turner, Sky Island Alliance, Tucson, AZ; Susan Brandes, Sky Island Alliance, Tucson; Mark Fishbein, Department of Ecology & Evolutionary Biology, University of Arizona, Tucson; and, Paul W. Hirt, Department of History, Washington State University, Pullman.

La región de islas en el cielo de Arizona, Nuevo México, Chihuahua y Sonora se distingue por tener una diversidad de especies de las más altas en la zona templada de Norteamérica, pero el manejo de las tierras en la región nunca ha reflejado este valor único. La jurisdicción está ampliamente dispersa en varias agencias federales, estatales y privadas. Ha habido muy poca coordinación de esfuerzos de manejo y la más cercana aproximación a una filosofía común de manejo ha sido la maximinización de la utilización. Nosotros proponemos un modelo alterno, que involucra la cooperación interagencias e internacional y basada en la conservación de la biodiversidad nativa, como el más alto valor a ser considerado en las decisiones de uso del suelo. Utilizando los principios desarrollados por el Proyecto de Recuperación de Tierras Silvestres de Norteamérica (North American Wilderness Recovery Project), nosotros proponemos un sistema de reservas núcleo rodeadas por áreas de amortiguamiento y ligadas por corredores de movimiento. Nosotros sugerimos um proceso para establecer medidas básicas de biodiversidad, así como el monitoreo asociado y programas de restauración y otros de programas de manejo.

60. Planeación de Manejo de Ecosistemas en el Servicio de Bosques, Región Suroeste.

Art Briggs, USDA Forest Service, Southwestern Region, Albuquerque, NM.

Esta presentación discute las nuevas políticas de manejo de ecosistemas del Servicio de Bosques, la cual está siendo implementada a través del Plan Nacional de Manejo de Bosques y su revisión. Esta aproximación es a gran escala, una estrategia inter-regional que está siendo desarrollada cooperativamente por las cuatro regiones del Servicio de Bosques Rocky Mountain, la Estación Experimental de Rocky Mountain y la Estación de Investigaciones Inter-montaña. Esta aproximación incorpora políticas de manejo en sub-bosques y niveles de planeación de proyectos a través de un proceso integrado de manejo de recursos.

61. Un Sistema de Reserva para la Región de Islas en el Cielo del Río Gila de Arizona y Nuevo México: Algunas Sugerencias Preeliminares.

Tony Povilitis, Life Net, Glorieta, NM.

Las Bio-regiones están siendo un foco importante en la biología de la conservación. La región de Gila en el Río Gila (GSR), localizada en la unión de cuatro provincias biogeográficas mayores, es casi la más diversa y compleja en Norteamérica. La diversidad de especies para los vertebrados del Oeste de los Estados Unidos alcanza un pico en la GSR, mientras que para otros taxa parece excepcionalmente alta. Desafortunadamente la diversidad biológica de la región es amenazada por el rápido crecimiento poblacional (19% de incremento sobre la década pasada), el incremento de la urbanización, y otros usos intensivos de la tierra. treinta y seis especies nativas de la GSR se encuentra en las listas federales como amenazadas o en peligro. Aproximadamente 110 taxas adicionales son candidatos federales (C-1) o NHP clasificadas globalmente (G1-3). Aún, la GSR es una de las regiones menos impactadas del continente con una densidad de solamente cuatro personas por kilómetro cuadrado y por encima del 75% de su tierra base es propiedad pública. Este artículo presenta los resultados de una aplicación preeliminar de los principios para el diseño de reserva para la GSR. Siete potenciales "Areas núcleo ecológicas" fueron seleccionadas basadas en la cobertura de la comunidad biótica y de la zona ecotonal, la presencia de especies amenazadas y los comparativamente niveles bajos de usos humanos. Veintitrés corredores potenciales que ligan esas áreas núcleo fueron también identificados, con 6 categorías como los más prometedores usando criterios biológicos y de paisaje. El "Sistema de Reserva" aparece adecuado para cubrir las necesidades espaciales y de hábitat de varias especies indicadoras, incluyendo el búho manchado mexicano, el jaguar y el borrego cimarrón del desierto. La factibilidad de establecer para la GSR un sistema de reserva integral tal cual es descrito en este artículo es examinado a la luz de los desarrollos actuales y de desarrollo sustentable en Norteamérica.

62. Planeación de Ecosistemas en las Cuencas Superiores de los Ríos San Pedro y Santa Cruz del Bosque Nacional de Coronado

Jeanne M. Wade and Paul T Deecken, Sierra Vista Ranger District, Coronado National Forest, Hereford, AZ; and, Jennifer Ruyle, Santa Catalina Ranger District, Tucson, AZ.

El manejo de ecosistemas es una filosofía para considerar todos los elementos como un total cuando se planea para el futuro de un área. En un proyecto demostrativo en el Bosque Nacional de Coronado, en la porción superior de los Ríos Santa Cruz y San Pedro, esos factores físicos, biológicos y sociales han sido usados para compatibilizar las demandas de la gente con la capacidad de la tierra. Se presentan los progresos de los esfuerzos cooperativos del proyecto y los resuménes de investigación en el área.

63. Oportunidades de Conservación en las Fronteras: La Perspectiva Arizona-Sonora.

Francisco J. Abarca, R. Lee, and J.C. deVos, Jr. Arizona Game and Fish Department, Phoenix.

Las tierras fronterizas Arizona-Sonora se encuentran localizadas dentro del Desierto Sonorense, lo que proporciona una gran oportunidad para el manejo y la investigación de los recursos naturales compartidos. Esta área está caracterizada por nueve áreas protegidas, incluyendo refugios silvestres y Reservas de la Biósfera. Aproximadamente 75% de las especies enlistadas, como amenazadas, en peligro o en candidatura en Arizona, también existen en Sonora. Parte de los Ríos Colorado, Sonoita, Cconcepción, Santa Cruz, San Pedro y Yaqui - que contienen muchas de éstas especies -se encuentran también compartidas entre estos dos Estados fronterizos. Los desarrollos económicos propuestos a lo largo de la frontera representan un desafío para proteger y manejar la flora y fauna encontrada en esta área. El Departamento de Caza y Pesca de Arizona, mantiene esfuerzos comúnes con varios grupos públicos y privados, y agencias a ambos lados de la frontera, para asegurar la permanencia de especies amenazadas y en peligro, así como de sus hábitats. Programas de conservación para el borrego de Sonora (*Antilocapra americana sonoriense*), el pavo (*Meleagris gallopava mexicana*), la codornís enmascarada (*Colinus virginianus ridgwayi*), la tortuga del desierto (*Gopherus agassizii*), peces nativos (*Cyprinodon macularius, poeciliopsis occidentalis, Ictalurus pricei, Cyprinella fornmosa, Gila ditaenia, Gila intermedia)*, el búho manchado Mexicano (*Strix occidentalis lucida*), el lobo Mexicano (*Canis lupus baileyi*), el perico de cola tupida (*Rhynchopsitta pachyrhyncha*), el perico de frente marrón (*Rhynchopsitta terrisi*), y aves que anidan en Sonora, se están actualmente llevando a cabo. Estos esfuerzos incluyen actividades de evaluación y monitoreo, así como reintroducciones dentro de su rango histórico. Un elemento clave de varios proyectos ha sido el desarrollo de planes de manejo que responde a las necesidades de conservación para estas especies.

64. La Organización del Centro de Investigaciones Biológicas y el Programa de Investigación.

Alfredo Ortega-Rubio, Centro de Investigaciones Biológicas del noroeste, San Juan de la Costa, Baja California Sur, México.

La organización y el programa de investigación del Centro de Investigaciones Biológicas de Noroeste (CIB), con sede en la Paz, Baja California Sur, se presenta. El CIB tiene responsabilidades para la investigación en los ecosistemas terrestres y marinos del Golfo de California y de los estados de México que rodean al Mar de Cortés. Esta presentación en video (en español) enfatiza algunos de estos esfuerzos de investigación.

65. Investigación en la Frontera y Conservación: Donde Está Pasando ?

Leonard F. DeBano, USDA-FS, Rocky Mountain Forest and Range Experiment Station, c/o School of Renewable Natural Resources, University of Arizona, Tucson; Silvia Manzanilla-Naim, Centro de Ecología, Ciudad Universitaria, UNAM, México, D.F.; and, Roy R. Pollisco and Peter F. Ffolliott, School of Renewable Natural Reources, University of Arizona, Tucson.

Existe una inmensa cantidad de actividades relacionadas a la investigación y conservación que ocurre en la región del Archipiélago Madreano del suroeste de los Estados Unidos y del noroeste de México. Muchas de éstas actividades están concentradas en sitios específicamente dedicados a la investigación y conservación. Sin embargo, la información sobre estas actividades generalmente no está disponible, no ha sido documentada en documentos resumidos o en bases de datos. La presentación de éste poster es un intento para empezar a reunir la información sobre el sitio y la descripción general de la investigación y otras actividades relacionadas a la conservación en sitios específicos en ambos países con el propósito de una colaboración futura. Esto catalogaría específicamente la información sobre localización, puntos de contacto, actividades y otros atributos generales de las actividades en una amplia gama de sitios de investigación y conservación. El material presentado no es un intento de incluir todo, pero en lugar de ello constituirá el punto de partida para desarrollar una base integral de datos que describan éstas actividades a través del Archipiélago Madreano. También proporcionará el foro y la oportunidad para los participantes de la conferencia para agregar información sobre las actividades no incluídas en la base de datos presente.

66. Las Interacciones Suelo-Clima-Vegetación en la Sierra de La Laguna, Componente del Elemento de Bosques Madreanos.

Yolanda Maya Delgado, Centro de Investigaciones Biológicas del Noroeste, La Paz, B.C.S., México.

Grandes diferencias en la topografía, vegetación y clima se presentan, a pesar de una muy uniforme geología, en un área relativamente pequeña de la Sierra de La Laguna. En razón de éstas características éste sitio parece ser un buen ejemplo para apreciar el papel que estos factores juegan durante los procesos de formación del suelo. El clima varía, dependiendo de la altitud, desde cálido semiárido en las partes más bajas hasta los 100 m, a los templados húmedos en las planicies más altas formadas por la unión de varios sitios. Esta graduación en clima es responsable de los diferentes tipos de vegetación establecidos también en un patrón altitudinal: matorral xerófilo en las planicies más bajas desde los 300 metros a los 750 metros, bosque de encino hasta los 1 200 metros y bosque de encino-pino hasta los 1 650 metros. Además de una pequeña área de pastizales. Siete perfiles del suelo representativos de estas condiciones fueron descritos y las muestras analizadas en el laboratorio. Las diferencias en las características edafológicas tales como color, pH y porcentaje de materia orgánica son evidentes debido a las relaciones estrechas entre la clase de vegetación y la contribución de la hojarasca, aunado a las diferentes condiciones prevalecientes durante los procesos de desomposición. Por otra parte la topografía es la principal responsable de las diferencias en las características tales como la profundidad y grado de madurez del suelo.

67. Emergencia de Insectos Acuáticos Durante Marzo y Abril de 1993 de los Arroyos en el Monumento Nacional Chiricahua.

E. C. Masteller, Penn State University at Erie, The Behrend College, Division of Science, Erie, PA.

Dos trampas de emergencia, que cubrían aproximadamente cuatro metros cuadrados de superficie del agua, fueron colocadas sobre el Arroyo Bonita y sobre el Arroyo Cola Blanca del Este en el Monumento Nacional Chiricahua durante la época cuando el flujo superficial de agua estuvo presente. Veinte colectas fueron hechas periódicamente entre el 19 de marzo y el 15 de abril de 1993. De éstas muestras, 20 taxas han sido identificadas dentro de 800 especímenes colectados. Los grupos más abundantes fueron las móscas (*Chirinomidae, Diptera*) y los mosquitos (*Capniidae, Plecoptera*). Más de 75 mosquitos emergieron perteneciendo a dos especies; *Mesocapnia arizonensis* y *Capnia californica*. Veinticinco mosquitos de mayo (*Baetidae, Ephemeroptera*) emergen durante éste período con la muy común especies Norteaméricana *Baetis tricaudatus* presente así como la especie muy poco común *Fallceon quilleri*. Moscas negras y maduras (*Simuliidae, Diptera*) fueron observadas en los arroyos en grandes números pero fueron colectadas infrecuentemente en las trampas de emergencia. *Prosimulium imposter* fue la mosca negra más común presente. Investigaciones futuras deben dirigirse para determinar como estos insectos enfrentan los períodos de larga sequía cuando no existe agua superficial presente. Puede ser que el flujo subsuperficial mantenga a estos insectos.

68. Alternativas de Restauración para las Islas en el Cielo: Casos de Estudio de Guatemala.

R. Phillips and J.G. Mexal, Forestation Center for the Americas, New México State University, Las Cruces; and, R. Beltranena, Agrobosques, Guatemala City, Guatemala.

Guatemala es el país más poblado de América Central y tiene una de la más altas tasas de crecimiento poblacional en América Latina. Mucha de ésta población depende del bosque para satisfacer sus necesideades de leña. La leña representa 65% del consumo de energía de Guatemala. Sin embargo, el desmonte de la tierra para cambiar hacia agricultura, la tala de madera y la producción de ganado han dado como resultado la escasez de leña. Un alto porcentaje del presupuesto e ingresos se dedican a la colecta de leña. Desde 1960, más del 48% de los bosques se han perdido. Sin prácticas de manejo y alternativas a las prácticas actuales, menos del 2% de los bosques originales permanecerán para el año de 2010. El gobierno de Guatemala ha establecido una limitada pero exitosa asociación con el sector privado para reforestar muchas áreas. Este programa no solamente ha reforestado exitosamente miles de hectáreas, sino que también ha proporcionado una alternativa viable para la continuar con la cosecha del bosque nativo. Además, el Programa de Incentivos fiscales (IF) ha generado empleo en la sociedad rural, predominantemente agraria. El programa IF otorga reducciones en los impuestos en cinco años para cubrir el primer año del costo de establecimiento y los siguientes cuatro años de los costos de manejo de la plantación. El programa actualmente financía no más de cinco mil hectáaeas por año. Este nivel de financiamiento es demasiado pequeño para reforestar totalmente las áreas aclaradas para ganadería y para agricultura. Sin embargo, el modelo es muy promisorio. El programa IF de Guatemala puede ser un modelo para el manejo de las Islas en el Cielo. Estos programas de reforestación exitosa son: a) restaurar sitios deforestados para hacer bosques productivos, b) proporcionar empleo para poblaciones rurales, y c) crear alternativas para continuar la tala contínua de bosques nativos. Tres casos de estudios serán examinados los cuales representan diferentes ecosistemas variando desde ecosistemas semiáridos hasta tropicales húmedos usando especies de árboles nativas y exóticas y produciendo múltiples productos de madera. Los beneficios ambientales, sociales y económicos de estos programas serán discutidos en el contexto de la aplicación de estos principios a las Islas en el Cielo.

69. Condiciones en la Interface de los Bosques de Pino Piñonero-Junípero y de Encino.

Roy R. Pollisco and Peter F.Ffolliott, School of Renewable Natural Resources, University of Arizona, Tucson; and, Gerald J. Gottfried, USDA-FS, Rocky Mountain Forest and Range Experiment Station, Flagstaff, AZ.

Los estudios de investigación pasados y presentes se han enfocado primariamente en los bosques de encino y de pino piñonero-junípero, pero existe una falta de información acerca del área de traslapamiento entre ellos. Este estudio ofrece nueva información acerca de las condiciones ecológicas del área de traslape y como se relacionan con ambos bosques, el de encino y el de pino piñonero-junípero. Existen diferencias significativas entre las áreas de traslape entre el encino y el pino piñonero (estratos) en los tres sitios de estudio: Valle de San Rafael (cerca de Sierra Vista), las Colinas Canelo (cerca de Samarita) y el Arroyo de la Cueva (en las pendientes orientales de las Montañas Santa Rita). Las variables encontradas que difieren incluyen el número de árboles, el área basal de los árboles, el volúmen de los árboles, la irradiación solar estimada, los fragmentos gruesos de suelo y, el pH del suelo. La regeneración de árboles fué descrita en relación a las variables estrato, dosel y fisiografía. Se concluye que los pinos piñoneros-juníperos, poseen caracteristicas únicas que contribuyen a la complejidad de los bosques de encino y que las estratégias futuras de manejo de la tierra deben ser formuladas para acomodar la contribucion única de los estratos. Equipados con ésta información presentada por éste estudio, los manejadores de la tierra, ecologistas y los políticos deben ser capaces de mejorar nuestras actuales estratégias de manejo de tierras de los bosques de pino para obtener múltiples beneficios óptimos tanto para el hombre como para la naturaleza en una base sustentable.

70. Tierra en el Balance.

Goerge B. Ruyle, School of Renewable Natural Resources, University of Arizona, Tucson; and, Lynn Ketchem, Oregon State University Corvallis, OR.

El distrito de Sierra Vista del Bosque Nacional de Coronado, localizado en el sureste de Arizona, ha iniciado un proyecto demostrativo de manejo de ecosistemas. El Area Ecosistema de Manejo Montaña Sola/Cañon de Redrock cubre un área de 130,000 acres desde la cresta de las Montañas Huachuca en el norte hasta la frontera de México y del Paso de Moctezuma en el este hasta las Montañas Patagonia en el oeste. Esta área tienen varias comunidades vegetales únicas incluyendo bosques Madreanos de encino y planicies de pastizales. Existe una cantidad de plantas raras y de especies animales que habitan el área. El nacimiento de dos ríos importantes, el San Pedro y el Santa Cruz se encuentran dentro de los límites del área de manejo. Asimismo el área rodea una de las más grandes parcelas de tierra de propiedad privada en Arizona así como una cantidad de pequeños propietarios privados. El estilo de vida rural de los residentes de éstas tierras, definido principalmente por la producción de ganado, ha sido el principal factor contribuyente al mantenimiento de espacios abiertos y de la apariencia sin desarrollo del paisaje. Tomando una aproximación ecológica del manejo de éste ecosistema, el Servicio Forestal reconoce que es complejo y dinámico y que la gente depende de sus valores y usos. Con el objeto de articular lo que el manejo de ecosistemas es y lo que significa para la comunidad local y para otras gentes interesadas, un video intitulado "Tierra en balance" fué producido por la Universidad de Arizona, Escuela de Recursos Renovables y el Distrito de Manejo de Sierra Vista. El propósito principal del video es el de introducir el concepto de manejo de ecosistemas a la gente en las comunidades involucradas, con el manejo de ecosistemas de la Montaña Sola y del Cañon de Redrock como un ejemplo específico. El video incluye entrevistas con varias gentes de la comunidad local, de la Universidad de Arizona, de Nature Conservancy y de la Comisión de Planeamiento y Zonificación del Condado, del Distrito de Conservación de Recursos Naturales del Condado y del Servicio Forestal. Una guía para el observador acompaña al video, el cúal funciona como un prontuario para la gente que ve el video, y que se enviará sólo por correo para alcanzar una audiencia más grande.

71. Banco de semillas y Claros formados por la Caída de árboles en un bosque templado Mexicano.

Carmen Mercado y Laura Arriaga-Cabrera, División de Biología Terrestre, Centro de Investigaciones Biológicas del Noroeste, La Paz, Baja California Sur, México.

La porción sur de la península de Baja California contiene un bosque de encino-pino restringido a las partes altas de la cadena montañosa conocida localmente como la Sierra de La Laguna, la cual representa el límite suroeste del componente Sierra de la Laguna del elemento forestal Sierra Madrean, formando parte de la flora Madro-terciaria. Este bosque presenta claros en el dosel creados por tres principales tipos de muerte: árboles muertos en pie, árboles rotos y árboles desenraizados. Se seleccionaron siete sitios dentro del bosque, con el objeto de estudiar el tamaño del banco de semillas y la composición florística; dos claros formados por cada tipo de muerte y un cuadrante representativo del bosque maduro. Durante 1991, se obtuvieron al azar muestras del suelo, se llevaron al laboratorio y se extendieron en charolas, humedeciendo el suelo periódicamente. Diariamente se registró la emergencia de plántulas hasta no observar más germinación. Adicionalmente, se realizaron análisis fisicoquímicos del suelo. Los resultados muestran que el banco de semillas está constituído por 21 especies pertenecientes a 14 familias, de las cuales solamente cinco constituyen el banco de semillas persistente, mientras que el resto son parte del banco de semillas transitorio. Las principales especies de este bosque *Quercus devia* y *Pinus lagunae* no estuvieron representadas en el banco. los claros creados por los árboles desarraigados y el bosque maduro presentan los valores más altos de riqueza específica y emergencia de plántulas. La tasa de germinación fue más alta en las muestras obtenidas durante la estación de lluvias. Las característica fisicoquímicas del suelo no mostraron ningún patrón, y no presentaron relación con el tipo de muerte.

72. El Drenaje del Cañon Copper en el Bosque Nacional del Coronado: Un Panorama de Biodiversidad.

Bill Van Pelt, Arizona Game and Fish Department, Phoenix.

El Programa de No Caería y de Vida Silvestre en Peligro del Departamento de Caza y Pesca de Arizona, ha estado monitoreando el drenaje del Cañon Copper en busca de la musaraña de Arizona (*Sorex arizonae*) usando una serie de trampas a lo largo de los cauces de agua. En adición, equipos de cámaras de sensor remoto han sido utilizadas para determinar el uso del cañon por otras especies de mamíferos. Las trampas fueron instaladas el 27 de mayo y recogidas el 17 de noviembre de 1993. Como resultado, las musarañas de Arizona fueron registradas por vez primera en el Cañon Copper. Otras observaciones notables de vida silvestre en este sitio incluyen un par nidante del búho moteado

Mexicano y una posible salamandra tigre de Huachuca (*Ambystoma tigrinum stebbinsi*). El equipo de cámara de sensor remoto fué instalado el 28 de septiembre de 1993 y se encuentra en uso todavía. Los monitoreos han mostrado 15 especies de mamíferos presentes en el drenaje del cañon. Una limitada cantidad de tiempo es necesaria para el empleo de éstas técnicas de monitoreo. La serie de trampas puede ser utilizada para monitoreaer poblaciones de pequeños mamíferos investigando su diversidad, densidad y uso de hábitat. El equipo de cámaras de sensor remoto puede ser utilizado para documentar especies de mamíferos grandes difíciles de trampear y de observar, de corredores de viaje y de uso de hábitat.

73. Simulaciones de Cambios en la Estructura de los Bosques en el Archipiélago Madreano

Peter F. Ffolliott and Phillip Guertin, School of Renewable Natural Resources, University of Arizona, Tucson.

Un modelo de simulación está disponible para estimar los cambios en la estructura de los bosques de encino y pino piñonero-junipero en la región del Archipiélago Madreano. Las estimaciones de los cambios en la estructura pueden ser generadas para representar las condiciones anticipadas para algún punto en el futuro bajo las prácticas de manejo actuales, o después de la implementación de algunas prácticas de manejo propuestas. La simulación de cambios en la estructura, cuando se acoplan con aplicaciones de sistemas de ecuaciones, son una ayuda para estimar los efectos anticipados de prácticas de manejo propuestas para la producción de leña y ganado, recursos de vida silvestre, protección de cuencas y oportunidades recreacionales. Las soluciones de los sistemas de ecuaciones representan las proporciones de lo encontrado que debe ser inventariado para especificar niveles basales de áreas.

74. Los Efectos de la Historia del Pastoreo Sobre las Comunidades de Insectos de un Pastizal Semiárido.

Sandra J. DeBano, Department of Entomology, University of Kentucky, Lexington.

Las comunidades de insectos son un componente esencial de los ecosistemas, con miembros que llenan papeles importantes en la polinización, en las redes alimenticias y en los ciclos de nutrientes, así, el manejo efectivo y la conservación de los pastizales Apacherianos, depende de la comprensión básica de cómo, los usos del recurso, tales como el pastoreo por ganado, afectan las comunidades de insectos. Sin embargo, la mayoría de los estudios sobre los efectos del pastoreo han dejado a un lado a los insectos y se han enfocado primariamente sobre plantas y vertebrados. En un esfuerzo para incrementar nuestro conocimiento de los efectos del pastoreo sobre los insectos, un estudio comparativo de los pastizales Apacherinos con diferentes historias de pastoreo fué desarrollado. El estudio se desarrolló en el Rancho de Investigación de Audubon Appleton-Wittel, el cual no ha sido pastoreado por más de 25 años y en ranchos que lo rodean con ganadería activa. Las comunidades de insectos fueron muestreados con trampas y con redes de golpe dos veces por semana en el verano de 1993 y de 1994, en ocho sitios del rancho experimental y ocho sitios comparables en los ranchos de ganado circunvecinos. Los resultados de éstos censos serán presentados y discutidos.

75. Requerimiento de Agua y el Uso potencial del Frijol Gandul en Sistemas Agroforestales Apropiados para el Manejo de Islas en el Cielo.

Enrique Troyo-Dieguez and Federico Salinas-Zavala, Centro de Investigaciones Biológicas del Noroeste, La Paz,BCS., México.

Un modelo biofísico basado en las interacciones planta-agua-clima se propone para establecer los efectos de la Radiación Fotosintéticamente Activa (PAR) como una fracción de la radiación solar total, sobre los procesos de demanda de agua de un cultivo. Se muestra que una relación existe entre la PAR, la temperatura de la hoja y la transpiración de ecotipos regionales del frijol Gandul (*Cajanus Cajan* (L.) Millsp), un cultivo bianual representativo de la familia de leguminosas, el cual fue introducido a Baja California Sur, México desde Asia, a la mediados de este siglo. Este ecotipo fué encontrado en el área de influencia de la Sierra de la Laguna, B.C.S.. Las interrelaciones propuestas se encuentran apoyadas por mediciones de la hoja y temperaturas ambientales y la PAR, de la cual los procesos de transpiración son dependientes. Dados los datos disponibles en temperaturas ambientales y radiación solar teorica en el país, se concluye que éste procedimiento es útil para establecer el nivel esperado de traspiración de frijol Gandul, así como sus requerimientos de agua mínimos en áreas marginales. La morfología observada y las características fenotípicas sugieren la utilidad del frijol Gandul en ecosistemas de Islas en el Cielo: la producción de frijoles fué de casi 6 toneladas por hectárea por año. Los resultados nos permiten diseñas sistemas agroforestales apropiados en los poblados de la Sierra de Laguna y de Islas en el Cielo similares; estos sistemas pueden incluir especies hortícolas de sotobosques y frijol Gandul como un componente con bajos insumos.

76. El Bosque Tropical Caducifolia de la Sierra de la Laguna: Un análisis fitogeográfico.

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Sobre las laderas de la Sierra de la Laguna se desarrolla el único bosque tropical caducifolio de la Península de Baja California. Esta vegetación se encuentra aislada de comunidades similares por el Golfo de California, de modo que puede ser considerada como una isla biológica. En el bosque tropical caducifolio de la Sierra de la Laguna existen miembros de dos componentes de la Flora Madro-Terciaria: las especies del componente del Cabo coexisten con especies propias de comunidades boscosas del componente Sierra de la Laguna.Entre todos los tipos de vegetación que se desarrollan en México, el bosque tropical caducifolio es uno de los más característicos del país. Esta vegetación representa la transición entre el tropico seco y las comunidades desérticas. El bosque tropical caducifolio se distribuye a lo largo de la costa del Pacífico y cubre aproximadamente 10% del territorio mexicano.

El aislamiento geográfico y ecológico de la comunidad de la Región del Cabo plantea preguntas interesantes acerca de la distribución actual de su flora y sus implicaciones biogeográficas. En este trabajo se analizan las afinidades geográficas de la flora del bosque tropical caducifolio de la Sierra de la Laguna, y se comparan los índices de similitud florística con el Desierto Sonorense y con varias floras del macizo continenetal mexicano. Para alcanzar estos objetivos se obtuvo la composición florística de la comunidad, resultado obtenido de un intenso trabajo de campo. Actualmente se han determinado 558 especies y 326 géneros en esta comunidad que cubre aproximadamente 19,000 millas cuadradas. Estimamos que este listado florístico comprende aproximadamente el 90% de la composición florística total y se ha calculado un endemismo a nivel específico del 9%. Resultados preliminares muestran que esta flora, a nivel genérico, tiene afinidades pantropicales y neotropicales. A nivel específico encontramos que casi 55% de ellas estan restringidas a México y a las áreas vecinas. Comparando esta flora con otras disponibles para el macizo continental, y usando tres índices de similitud, se encontró que existe una mayor similitud con el Desierto Sonorense, seguido por Sinaloa, Río Mayo, Chamela y finalmente Chiapas.

77. Demografía de Organismos de Larga Vida: Implicaciones para La Conservación y el Manejo.

J.D.Congdon, Savannah River Ecology Laboratory, Aiken, SC; R.C. van Loben Sels, Red Mountain High School, Mesa, AZ; and, A. E. Dunham, University of Pennsylvania, Philadelphia.

Los estudios demográficos de la tortuga de Blanding (*Emydoidea blandingii*) y las tortugas mordedoras (*Chelydra serpentina*) desarrolladas durante los pasados veinte años han generado suficientes datos demográficos para examinar el como las caracteristicas de las historias de vida pueden restringir las respuestas poblacionales de organismos de larga vida. Ambas tortugas exiben una madurez sexual retrasada (de once a veinte años) y una alta supervivencia de adultos (96%). La supervivencia en el nido de ambas especies fué variable en un rango de 0.0 a 63% anualmente. El reclutamiento de juveniles y adultos de ambas especies fue suficiente para reponer a los individuos estimados muertos durante el estudio. Las tablas de vida para las poblaciones resultaron en tiempos generacionales myores de treinta años y requirieron de una supervivencia anual de juveniles del 72% de entre 1 año a la madurez sexual para mantener las poblaciones estables. La estabilidad poblacional fue más sensitiva a los cambios en la supervivencia de adultos y juveniles y menos sensitiva a los cambios en edad a la madurez sexual, a la supervivencia en los nidos y a la fecundidad. Los resultados del presente estudio indican que los rasgos de las historias de vida de los organismos de larga vida consisten de rasgos coevolutivos que resultan en severas limitaciones para la habilidad de las poblaciones para responder a las perturbaciones crónicas. Los programas exitosos de manejo y conservación para los organismos de larga vida serán aquellos que reconozcan que la protección de todos los estadíos de vida es necesaria. Los programas para la protección o mejoramiento sóloamente de los sitios de anidamiento pueden ser menos adecuados para salvar a los organismos de larga vida, tales como las tortugas de agua dulce y marina y algunas tortugas terrestres.

78. Estudio dendroclimatológico en la Sierra de la Laguna, B.C.S. México.

Sara Díaz-Castro, Laura Arriaga-Cabrera, Daniel LLuch-Cota, and Cesar Salinas-Zavala, Centro de Investigaciones Biológicas del Noroeste, San Juan de la Costa, B.C.S., México.

En la Sierra de la Laguna, se desarrolla el único bosque de pino-encino del Estado de Baja California Sur, cuyo rango de distribución altitudinal varía entre los 1,800 y 2,000 m.s.n.m. Este bosque representa la porción suroeste de la flora mado-terciaria donde la especie de conífera que constituye al bosque, es una especie endémica *Pinus lagunae*. Como la mayoría de los pinos, se trata de una especie longeva que en sus anillos de crecimiento puede registrar fluctuaciones climáticas. El principal objetivo de este trabajo es analizar la información climática disponible para la Sierra así como las series de las medidas de los anillos de crecimiento del pino, por medio de técnicas dendroclilatológicas. Para ello, se fecharon las muestras de 80 pinos seleccionados, se midieron y estandarizaron con el objeto de obtener una dendrocronología maestra. La serie climática regional se basó en los datos registrados para las nueve estaciones meteorológicas más cercanas al bosque, cuya distribución se encuentra en las partes medias y bajas de la Sierra. Subsecuentemente ambas series fueron correlacionadas, obteniéndose una correlación significativa ($r=0.52$; 45 d.f.; p.05). Este resultado indica que *Pinus lagunae* si esa sensible a cambios climáticos. La dendrocronología maestra se comparó con otros estudios dendrocronológicos del suroeste de Estados Unidos con flora madro-terciaria. Consideramos que análisis posteriores deberán incluir la calibración y verificación de las series, con el objeto de obtener un modelo preciso, basado en la reconstrución climática a partir de la información dendrocronológica, para hacer prediciones de las variaciones climáticas futuras.

79. Investigación sobre Percepeción Remota y Sistemas de Información Geógrafica en el Sureste de Arizona.

D. Phillip Guertin, Lee. A. Graham, George L. Ball, Craig Wissler, and Randy H. Gimblett, Advanced Resource Technology Program, School of Renewable Natural Resources, University of Arizona, Tucson; and, Michael R. Kunzmann, National Biological Survey, University of Arizona, Tucson.

El Programa de Tecnología de Recursos Avanzados de la Escuela de Recursos Naturales Renovables, de la Universidad de Arizona, ha hecho una extensa investigación sobre el uso de la percepción remota y los sistemas de información geográfica para los recursos naturales y problemas ecológicos. Esta investigación incluye el desarrollo técnicas de mapeo para áreas riparias y de vegetación, desarrollo de aplicaciones de manejo de cordilleras, desarrollo del manejo de fuego como herramienta, y la investigacioñ del uso de los sistemas de información geográfica para el manejo de ecosistemas. Este poster presentará un resumen del trabajo que ha sido completado en las islas de montañas del sureste de Arizona.

80. Lagartijas de la Sierra de la Laguna, Baja California Sur, México.

Patricia Galina-Tessaro, Sergio Alvarez-Cardenas, and Alfredo Ortega-Rubio, Centro de Investigaciones Biológicas del Noroeste, San Juan de la Costa, Baja California Sur, México; and, Alberto González-Romero, Instituto de Ecología. Antigua carr. a Coatepec, Xalapa, Veracruz, México.

Debido a tan importantes aspectos, tales como su historia geológica particular, su aislamiento biológico y geográfico, su composición florística y la cantidad de endemismos, la Sierra de la Laguna en la Región del Caba, Baja California Sur, México, es un lugar sobresaliente para el estudio de anfibios y reptiles. La herpetofauna de ésta región es considerada por Savage (1960) como uno de los elementos de la herpetofauna de la Sierra Madreana. En éste trabajo nosotros analizamos la distribución espacial de las lagartijas de la Sierra de la Laguna. Durante tres años recorrimos el sitio de estudio en diferentes estaciones con el objeto de obtener los siguientes registros de cada lagartija observada: especie, clase de vegetación en la que se encontraba, altitud sobre el nivel del mar y clase de sustrato utilizado por la lagartija. Dieciocho especies fueron registradas a lo largo de un gradiante altitudinal desde el nivel del mar hasta 2,200 metros. Muchas de ellas son endémicas a nivel específico. La subcomunidad de lagartijas está subdividida espacialmente a nivel de la vegetación en diferentes subconjuntos de sólo 4 o 5 especies, las cuales se separan ecológicamente por la utilización diferencial del microhábitat así como por estrategias de forrajeo complementarias o por preferencias alimentarias. Las influencias posibles que pueden existir entre la especialización espacial observada y la competencia interespecífica es analizada y discutida. La importancia de las lagartijas de la Sierra de la Laguna de manera particular y las de la Región del Cabo de manera general como un apoyo a las teorías biogeográficas y para la conservación y manejo de estos ecosistemas y también se discuten.

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