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Fire Effects in Southwestern Forests

Proceedings of the Second La Mesa Fire Symposium

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Abstract: In 1977, the La Mesa Fire burned across 15,444 acres of ponderosa pine forests on the adjoining lands of Bandelier National Monument, the Santa Fe National Forest, and Los Alamos National Laboratory. Following this event, several fire effects studies were initiated. The 16 papers herein document longer-term knowledge gained about the ecological effects of the fire and about Southwestern fire ecology in general. The presentations are also designed to give resource managers practical information for managing fire in local landscapes. Studies presented range from fire histories and avifauna to geomorphology and arthropods.

Keywords: fire history, fire management, flood history, elk, arthropods, fungi

Compiler's note: Final drafts of manuscript copy were received in June 1996. To avoid further delay in delivering the proceedings to readers, many manuscripts did not undergo full editing. 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.

Fire Effects in Southwestern Forests

Proceedings of the Second La Mesa Fire Symposium

Los Alamos, New Mexico
March 29–31, 1994

Technical Editor

Craig D. Allen, Research Ecologist
USDI National Biological Service
Los Alamos, New Mexico

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Overview of La Mesa Studies

Craig D. Allen¹

This 1994 Symposium on the La Mesa Fire reflects the efforts of the presenters and organizers to share some of the knowledge gained since 1977 about the ecological effects of the La Mesa Fire in particular, and Southwestern fire ecology in general. We are glad you came. We hope that you come away from this symposium with: 1) a greater understanding and appreciation for the varied and vital ecological role fire plays in many Southwestern ecosystems; and 2) some practical and useful information to help you manage fire in your local landscapes.

BACKGROUND CREDITS

The information presented at this symposium is built upon a foundation created by many people. In 1977 former National Park Service (NPS) regional scientist Ro Wauer recognized the research potential of the La Mesa Fire, and had the vision to immediately initiate and support many of the post-fire studies. Today's moderator, Terry Foxx of Los Alamos National Laboratory (LANL), conducted several post-fire studies and compiled the proceedings of the first La Mesa Fire Symposium (Foxx 1984-a). It is also appropriate to recognize emeritus professor Loren Potter of the University of New Mexico, in attendance today, for the many contributions to ecological research he made to Bandelier during the 1970's and 1980's, including La Mesa Fire research.

Three years ago Ro's successor as regional scientist, Dr. Milford Fletcher, suggested that it was time to revisit the topic of the La Mesa Fire and see how things had changed. He initiated financial support for many of the studies which will be reported on here. When the current regional scientist, Dr. Sam Kunkle, took over 2 years ago he continued to support these research activities as well as this symposium itself, despite very tight regional budgets. Bandelier National Monument's fire management officer (FMO), John Lissoway, and the NPS regional FMO, Cliff Chetwin, have also supported portions of this work. We appreciate the words of welcome Mary Bradford squeezed in today amidst

the press of her duties as NPS deputy regional director in this time of NPS restructuring.

For the past several years the Santa Fe National Forest has supported cooperative landscape ecology studies in the Jemez Mountains, including some of the work to be presented here. Jerry Elson has been instrumental in supporting this cooperative work. The support of numerous people on all four US Forest Service ranger districts in the Jemez Mountains (Española, Jemez, Cuba, and Coyote) was necessary to accomplish the fire history studies. One study (Wolters—This Volume) was conducted in collaboration with the US Forest Service Rocky Mountain Forest and Range Experiment Station in Albuquerque.

I thank the Los Alamos Ski Club for allowing us to conduct fire history research on Pajarito Mountain.

Both the University of New Mexico and the University of Arizona have helped support various studies through matching contributions as part of cooperative agreements to conduct research activities. These contributions and negotiated low overhead rates were critical in allowing the necessary followup research to be conducted given the limited funding available to us.

Los Alamos National Laboratory has been instrumental in supporting La Mesa Fire studies through the contribution of time by Terry Foxx and her associates to work on the various vegetation plots which Terry had established between 1976 and 1978 at BAND. In addition, LANL has provided essential financial support for putting on this symposium. Pat Martinez and Marion Hutton of LANL's protocol office have been most helpful in arranging the logistics of this symposium.

Terry Foxx, Milford Fletcher, John Lissoway, and I have served as the organizing committee for this symposium. I have enjoyed and benefited from the counsel of my elders in this group.

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Finally, I am pleased to recognize the assistance provided by many members of Bandelier National Monument's staff in recent years. Certainly recent park management, notably superintendent Roy Weaver and chief of resources management Charisse Sydoriak, have encouraged and supported our efforts to study La Mesa Fire effects. Without John Lissoway's vital support several years ago the current ecological research program at Bandelier would not have developed. The fire crew at Bandelier has helped our work numerous times, especially David Garcia, Merry Beyler, and Chris Chiverton. Members of the administrative group, notably Tammy Gallegos and Eiko Adkisson, have supported the variety of contracting and procurement activities necessary to conduct all this work. Kee Elsie, Manuel DeVargas, and Moon Almanzar have provided essential horse-packing support when needed. Carlos Gonzales and Moon are clearing the fresh snow from Ponderosa Campground's parking area now so that the field trip can proceed this afternoon. A number of seasonal resource management employees and volunteers have worked with various researchers and helped collect data, notably John Hogan, Kay Beeley, Geneva Chong, and Doug Thayer. Really, almost everyone at Bandelier has helped facilitate portions of this work at one time or another. However, I wish to especially recognize Kay Beeley for her extraordinary and varied support efforts, from conducting and overseeing fieldwork to data analysis and creating graphics to handling the bulk of the registration and mailing work for the symposium. Kay has kept me and symposium planning activities on track. Thank you, Kay.

EARLIER LA MESA FIRE STUDIES

The first La Mesa Fire Symposium took place October 6-7, 1981, here in Los Alamos. The symposium proceedings (Foxy 1984-a), now out of print, present much of the earlier work. Table 1 outlines the earlier studies, which are summarized below.

Foxy's introductory chapter (1984-b) presents background information on the landforms and climate of this area, as well as a detailed description of the La Mesa Fire itself.

Wauer and Johnson (1984) studied "La Mesa Fire Effects on Avifauna" by following changes in breeding bird communities along four transects established before the fire by Wauer. The mile-long transects are arrayed across an elevational gradient, with one each on Frijoles, Burnt, Escobas, and

Table 1. La Mesa Fire studies. Names of participants in the 1981 symposium are in italics, while those involved in both 1981 and 1994 symposiums are bolded. "Year(s)" indicates the 19__ year(s) that fieldwork was conducted.

Topic	Investigator(s)	Year(s)
Birds	Wauer, Johnson	77,78,79,81,83,91
Erosion	W.White	77,78,79,80,92,93
Vegetation succession	Foxy, Potter	76,77,78,85,93
Grass/tree competition	<i>Barnes</i>	80
Elk	<i>White</i>	77-91
	<i>Sivinski, Conley</i>	77-79
	<i>Weber</i>	79,80
	<i>Rowland</i>	80
	<i>Wolters</i>	92-94
Nitrogen cycle	<i>Allen</i>	90-95
	<i>Freeman</i>	78
Cryptogams	<i>C.White</i>	92,93
	<i>Loftin, C.White</i>	93
Fungi	<i>Jarmie, Rogers</i>	92-94
Arthropods	<i>Pippin, Nichols</i>	77,78
	<i>Lightfoot</i>	93
Fire history	<i>Potter, Foxy</i>	76-78
	<i>Touchan, Allen,</i>	
	<i>Swetnam</i>	91-93
Archeological sites	<i>Traylor et al.</i>	77,78
Water Quality	<i>Purtymun</i>	77,78
Floods	<i>McCord</i>	90-93
Small mammals	<i>Guthrie</i>	77-79
Tree clearing	<i>Moeur, Guthrie</i>	79

Apache Mesas. These transects provided a spatial framework around which many of the other studies were conducted, as all but the Frijoles transect were burned by the La Mesa Fire. Wauer and Johnson (1984) provided detailed documentation of post-fire changes in the avifauna which are now best summarized in the followup work by Johnson and Wauer (This Volume). As they state (This Volume):

Species diversity increased after the fire, but breeding populations generally declined for several years before increasing above prefire levels. This temporary population decline was more pronounced and lasted longer on the more severely burned transects... Even an uncontrolled crown fire such as the La Mesa Fire can increase the diversity and population of breeding birds.

White and Wells (1984) studied the "Geomorphic Effects of La Mesa Fire" in six small watersheds on Burnt and Apache Mesas—this work also comprised W. White's 1981 master's thesis work. They show that water runoff in the Frijoles watershed

became "flashier" after the fire due to the loss of vegetation and litter ground cover. They determined that the amount of post-fire erosion depended upon upslope catchment area, slope steepness and shape, amount of vegetation regrowth, and most importantly, the degree to which impermeable ash layers developed. They found that the higher elevation sites on Apache Mesa had largely stabilized within two years due to the rapid recovery of vegetation cover. William White (This Volume) follows the recovery of these watersheds into the 1990's.

Foxx and Potter (1984) reviewed "Fire Ecology at Bandelier National Monument." Their fire scar analyses at that time indicated a mean fire interval of 15.1 years for the Escobas Mesa area, with a major decline in fire frequency after 1893. Subsequently, more extensive fire scar sampling (Allen 1989; Touchan et al.—This Volume) suggests pre-1900 fire return intervals of about 7 years for the La Mesa Fire area. Foxx and Potter's compilation and analysis of the historic fire record at Bandelier shows that 86% of the fires were lightning caused, with two-thirds of fires occurring in the May-July period and 87% between May and August. They found that intensity of tree damage from the La Mesa Fire was related to the time since the last previous fire. Foxx (This Volume) follows up on some of these initial findings. They conducted several related studies, including Foxx and Potter (1978), Potter and Foxx (1986), Foxx (1983), and Potter et al. (1982).

Potter and Foxx (1984) also presented their findings on "Post-Fire Recovery and Mortality of the Ponderosa Pine Forest After the La Mesa Fire". Their map of post-fire foliar damage classes remains the best assessment of La Mesa Fire burn intensities. They marked and followed 897 trees in 9 plots. All 504 trees lacking any green needles immediately after the fire were dead, while of the 393 trees which still had green needles after the fire, 357 (91%) remained alive after two growing seasons. They found 80% survival of even those trees with more than 50% singed needles. Up to 7100 shrub sprouts/acre were observed, mostly *Robinia neomexicana* and *Quercus gambelli*. They document the increased establishment of aerially seeded grasses where native grass density was lowest, also finding that ponderosa pine needlefall enhanced germination but diminished the vigor of seeded grasses.

Barnes (1984) treated the "Water Relations of the Dominant Grasses on La Mesa Burn." She demonstrated that the seeded grasses sheep fescue

(*Festuca ovina*) and slender wheatgrass (*Agropyron trachycaulum*) compete more intensely with ponderosa pine seedlings for water than the most common native grass, mountain muhly (*Muhlenbergia montana*). This greater competition is attributed to both the spring-growth phenology and shallow, mat-like rooting habits of these seeded grasses.

Freeman (1984) considered "The Effect of La Mesa Fire on Total Soil Nitrogen in Bandelier National Monument, New Mexico." He estimated that the La Mesa Fire caused losses of 45-65% of the total soil nitrogen.

Traylor (1984) studied the "Effects of La Mesa Fire on Bandelier's Cultural Resources," later published in greater detail as Traylor et al. (1990). The insistence upon the participation of archeologists in the firefighting efforts of the La Mesa Fire was a first for a major fire suppression effort, and it won the park superintendent a Department of Interior award. Nonetheless, Traylor et al.'s classic work documents how fire suppression activities damage archeological sites, even when archeologists are working together with fire crews to try to avoid site impacts. They found that 44 of the 100 archeological sites they studied after the fire had been damaged by fire suppression-related activities, especially the construction and rehabilitation of bulldozer-constructed firelines. Damage to cultural sites from the fire itself ranged from light to severe, depending upon the intensity, duration, and penetration of heat, which was largely a function of the amount of fuel present on a site. Documented examples of fire damage included spalling of tuff building blocks, carbonized or oxidized ceramics, heat alteration of obsidian, and the destruction of on-site pollen.

Purtymun (1984) assessed changes in the "Chemical Quality of Surface Water in Bandelier National Monument" caused by the La Mesa Fire in Frijoles, Alamo, and Capulin Creeks. He found that the fire induced increases in calcium, chloride, bicarbonate, and total dissolved solids, with declines to roughly pre-fire levels within 20 months post-fire.

Pippin and Pippin (1984) present an inventory report on the "Aquatic Invertebrates from Capulin Creek, Bandelier National Monument." They found 65 taxa, compared to 107 taxa found in the more voluminous Frijoles Creek. This report was apparently inadvertently published in the symposium proceedings instead of the Pippin and Nichols (This Volume) work on "Observations of Arthropod Populations Following the Bandelier

National Monument Fire of 1977," which was presented at the 1981 symposium.

Guthrie (1984) studied the "Effects of Fire on Small Mammals within Bandelier National Monument." The fire directly killed many arboreal squirrels (*Sciurus* and *Tamiasciurus* spp.) and chipmunks (*Eutamias* spp.), as well as some mice (*Peromyscus* spp.), although most burrowing mammals survived. Taxa which decreased after the fire included pinyon mice (*Peromyscus truei*) and red squirrels (*Tamiasciurus hudsonicus*). Deer mice (*Peromyscus maniculatus*) increased in all burned areas, along with voles (*Microtus* spp.) in grassy habitats and chipmunks in ponderosa pine and mixed conifer forests. Guthrie also documented winter-caused reductions of 50-90% in local small mammal populations.

Moeur and Guthrie (1984) examined the "Effects of Clearing Fire-Killed Trees on Wildlife" in the upper Frijoles Mesa area, comparing an unmanipulated Bandelier National Monument site to a salvage-logged site across the road on LANL land. In the summer of 1979 they found slightly more herbaceous cover on the Bandelier site, and no differences in insect or small mammal populations between sites. They document greater diversity and abundance of birds on the Bandelier site, presumably due to the increased structural diversity of the habitat where dead and downed trees were left in place.

Several other studies of the ecological effects of the La Mesa Fire were conducted but not written up for the symposium proceedings. Sivinski (1979) and Conley et al. (1979) used a network of 70 pellet transects in Bandelier to document "Responses of elk and mule deer to wildfire: Changes in utilization and migration patterns." They found low initial numbers of elk in fall 1977, with continuous increases through 1979. During that time they believed that 100 to 300 elk used Bandelier, and then only in winter, with use focused in the La Mesa Fire area.

Three companion studies on elk were presented at the 1981 symposium but published elsewhere. G. White (1981) used "Biotelemetry Studies on Elk" to show that local elk used burned areas heavily in the winter, especially the La Mesa Fire area. Rowland (1981) and Rowland et al. (1983) studied comparative winter diets of elk wintering in Bandelier's La Mesa Fire area and an unburned area on the Baca Ranch. The seeded grass sheep fescue dominated diets in the burned area, but nearly equal proportions of browse and grass were eaten by the Baca elk. The grass-dominated diet of the Bandelier elk had relatively high digestible

Table 2. Schedule, La Mesa Fire Symposium, March 29-31, 1994.

TUESDAY 3/29/94	
9:00	Registration
10:00	Welcome—Mary Bradford, Deputy Regional Director, NPS
10:10	Description of the La Mesa Fire, John Lissoway
11:00-12:00	Overview of La Mesa Fire Studies, Craig Allen
1:30-5:00	Field Trip to the La Mesa Fire Area, Terry Foxx, John Lissoway, Craig Allen
WEDNESDAY 3/20/94	
8:30-9:00	Tom Swetnam, Temporal and Spatial Variation in Southwestern Fire Regimes
9:00-9:30	Ramzi Touchan, Fire History and Climatic Patterns in Ponderosa and Mixed Conifer Forests of the Jemez Mountains
9:30-10:00	Craig Allen, Fire History and Landscape Change in the Frijoles Watershed, Bandelier National Monument
10:15-11:00	Teralene Foxx, The La Mesa Fire, Seventeen Years After: Post-fire Vegetation Changes
11:00-11:30	Alex McCord, Flood History Reconstruction in Frijoles Canyon Using Flood-Scarred Trees
12:45-1:30	Carlton S. White, The Effects of Fire on the Nitrogen Cycle Processes in Bandelier National Monument
1:30-2:15	William White, Geomorphic Response of Six Headwater Basins Sixteen Years After the La Mesa Fire
2:30-3:15	Sam Loftin, Potential Nitrogen Contribution of Soil Cryptogams to Post-Disturbance Forest Ecosystems
3:15-3:30	David Lightfoot, A Comparison of Ground-Dwelling Arthropod Assemblages Among Different Habitats Resulting from the 1977 La Mesa Fire
3:45-4:15	Nelson Jarmie, Diversity of Macromycetes in Bandelier National Monument - A Survey
4:15-4:45	Tom Cartledge, Heritage Resources and Fire Management: A Cooperative Co-Existence
THURSDAY 3/31/94	
8:30-9:00	Craig Allen, Elk Response to the La Mesa Fire and Current Status in the Jemez Mountains
9:00-9:30	Gale Wolters, Elk Effects on Meadows and Grasslands in Bandelier National Monument
9:30-10:15	Terry Johnson, Avifaunal Response After the La Mesa Fire
10:30-11:00	John Peterson (USFS Jemez District Ranger) and John Lissoway, Current US Forest Service and Bandelier National Monument Fire Programs in the Jemez Mountains
11:00-11:30	Charisse Sydoriak (Chief, Resources Management, Bandelier), Bandelier's Fire Monitoring Program
11:30-12:00	Milford Fletcher and Craig Allen, Research Summary and Management Lessons from the La Mesa Fire
12:00	End

energy values, which Weber (1981) and Weber et al. (1984) showed led to higher body weights and better nutritional status (as determined by blood metabolites).

As indicated previously, Pippin and Nichols (This Volume) presented a paper at the 1981 symposium describing "Observations of Arthropod Populations Following the Bandelier National Monument Fire of 1977," but it was inadvertently not included in the proceedings volume. They found that the diversity and abundance of arthropods was markedly reduced in an intensely burned area.

RECENT LA MESA FIRE STUDIES

As noted earlier, three years ago Milford Fletcher began to support another round of studies on the La Mesa Fire. Most of the work has been conducted the past two field seasons, and we have been fortunate to have several of the original investigators return for long-term followup work on their old topics (Table 1). One component of all the recent studies has been significant efforts to carefully record study site locations and archive all of the collected data at Bandelier, so that future studies can continue to follow the progress of post-fire ecosystem changes.

This symposium represents one effort to make current information on fire effects available to resource managers. The symposium schedule (Table 2) illustrates the diversity of studies which have been conducted. The researchers featured here have worked long and hard on their respective projects, particularly given the limited funding which was available. It has been a pleasure to work with this dedicated group of researchers. We hope you find the presented results interesting and useful.

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Remembering the La Mesa Fire

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Abstract.—In June, 1977, the La Mesa Fire burned across 15,444 acres of land in and around Bandelier National Monument. This was the largest and most intense fire to have occurred in the Jemez Mountains during the 20th Century. The conditions which led to, and occurred during, the La Mesa Fire are reviewed here.

BACKGROUND

I've been working at Bandelier National Monument since 1975, two years before the La Mesa Fire occurred. I participated directly in the La Mesa Fire and its aftermath. This is an introductory overview of the fire which led to the research presented in this symposium.

The La Mesa Fire of June, 1977 was in many ways a "wake up call" for the community of Los Alamos as well as the various land management agencies in the area. The La Mesa Fire also attracted national attention because of the multiple interesting issues raised by this large-scale, high-intensity crownfire which threatened an urban area, an internationally recognized center for scientific research, and a National Park System unit with significant natural and cultural resource values.

There were several significant circumstances connected with the La Mesa Fire to be aware of: (1) The ICS (Incident Command System) for dealing with complex fire emergencies was not yet functional; (2) this was the first major wildfire situation in which archeologists played a significant role in the suppression effort; (3) the term "urban-wildland intermix" had not yet been invented; and (4) the effects of this fire were subject to one of the most intensive series of studies of any National Park System fire up to that time.

The Los Alamos area is perched on a gently sloping, east-facing landform known as the Pajarito Plateau - a broad apron dissected by west-to-east trending canyons which drain into the Rio Grande. This plateau skirts the base of the higher slopes of the eastern Jemez Mountains. Much of the area is heavily forested, ranging from spruce-fir and mixed conifer forests in the mountains to ponde-

rosa pine forests and piñon-juniper woodlands on the mesas of the Pajarito Plateau. Canyon bottoms of the Plateau support diverse riparian communities. A zone of nearly pure ponderosa pine forest is found between roughly 6500 feet and 8200 feet elevation in the Bandelier area. This is the primary vegetation zone affected by the La Mesa Fire.

As is known from fire history studies dating back to the late 1400's, fire played a crucial role in shaping and maintaining forest ecosystems in the Jemez Mountains (see Touchan et al. - This Volume). We also know that since the late 1800's, the pre-European settlement fire return interval of around 5-12 years has changed markedly. Human influences on the landscape, including the gradual establishment of policies such as suppression of all wildfires, altered the natural patterns of fire occurrence - markedly changing vegetative communities. These changes in fire history and ecology are covered in various papers in this symposium.

Bandelier was added to the National Park System in 1916 by Presidential Proclamation. Monument administration was provided by the Forest Service until 1932. Although rich in natural resources, the monument was officially set aside to preserve and protect relicts of the earlier culture of the ancestral Puebloan (Anasazi) peoples who occupied the canyons and mesas of the Pajarito Plateau from the 1100's through the 1500's. These people left over 3000 archeological sites across Bandelier's 32,727 acres.

National Park Service policy of non-consumptive resource utilization combined with aggressive fire

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suppression had its own unique impacts in many park units: Bandelier was no exception. By the mid-1970's, it was becoming rather disturbingly clear to Bandelier's management that much of this dense and stagnating forested area within the park was viewed at high risk for what many fire people call a real "ripper".

PRELUDE TO THE FIRE

Prior to the La Mesa Fire, the effects of fire suppression practices on Bandelier's resources were just beginning to be documented by researchers such as Dr. Loren Potter of the University of New Mexico and Teralene Foxx, a local plant taxonomist. Within the pre-La Mesa landscape, forest density often exceeded 2,000 stems per acre of even-aged and stagnating mature trees. This in-turn produced a canopy cover estimated in the 80-100% range - suitable for a stand-destroying crownfire under the right conditions. Other obvious effects of fire suppression included lack of herbaceous understory and an expanding infestation of dwarf mistletoe in the largely ponderosa pine overstory.

Annual precipitation at the Bandelier Fire Tower (6500 ft. elevation) averages about 16.5 inches, largely derived from summer rainfall and winter snowfall. A poor snowpack from November 1976 through April 1977, yielding under 5 inches of total precipitation, provided for increasing drought-like conditions. The precipitation in May, combined with the first two weeks of June, added to a scant 0.64 inches. Fuel moistures for the over 3-inch diameter dead and down materials, an indicator of long-term drought, declined rather sharply from 15% on May 1 of 1977 to 6% (extremely volatile) on June 16. The afternoon, average, minimum relative humidity measured at the Bandelier Lookout dropped one week before the fire from 17% to 5%. The average high temperature for June that year was 88 degrees F, about 6 degrees above normal for the month.

The burning index, or "BI", represents one of many predictive fire danger parameters, and gives the fire program manager a good idea of how to preplan initial attack resources. The BI is computed daily from weather observations to characterize the potential behavior of the "initiating fire". This number, after specifying inputs such as fuel moistures, humidity, wind and other factors, can predict flame-lengths at the fire's leading edge. In other words, a normal BI for this time of the season might be in the neighborhood of 35, which tells fire

people that flame length in the fuel type of concern will be about 3.5 feet. A BI of 40 is 4 feet, and so on. Fire managers generally consider flame lengths of over 4 feet to be the upper limit of human direct attack on the fire's edge with handtools.

The conditions for June of 1977 looked grim. The average BI for the month of May was 58, already in the zone of high escape potential for initial attack forces in the daytime. On the 15th of June, the BI from afternoon weather observations was calculated at 92.

THE FIRE

At approximately 3:55 P.M. on June 16, 1977 under a cloudless sky, a USFS contract helicopter with helitack crew (based near Jemez Springs) responded to a smoke report on Mesa del Rito on the Jemez District of the Santa Fe National Forest, just west of the park boundary. It became clear to many that afternoon that nature's "balloon payment" in this severely altered, drought-impacted forest was about to come due.

Bandelier's engine crew responded immediately. Other engines and crews were also rolling. By 5:30 P.M., according to the aerial recon observer, the fire was now estimated at over 50 acres. By 6:00 P.M., fire size was estimated at 100 acres with average rates of spread later calculated at over 24 feet/minute. By nightfall on the 16th, the fire had dropped into the narrow and heavily wooded upper Alamo Canyon. To avoid the extreme potential for firefighter entrapment, the decision was made not to send people down into that canyon during the night.

On the 17th, humidities were hovering at 5%, temperatures during the day in the low 90's and winds were southwesterly at 15-18, gusting to 35 at treetop level. These conditions led to a major fire run up and out of Alamo Canyon, with long-range spotting, intermittent to sustained crowning (where fire leaves the surface and spreads most rapidly through the treetops), and a well organized convection column which lofted heat and fire brands to well over 20,000 feet. Spread was primarily to the northwest, approaching the rim of Frijoles Canyon. By late afternoon, a spotfire estimated at over 20 acres on the north rim of Frijoles was confirmed. The main fire's estimated size at this time was 2,000+ acres. A Class I fire management team was ordered along with a full complement of support resources, crews, engines, helicopters, and overhead. Park management was also

making campaign plans. The Bandelier backcountry was evacuated and the park was ordered closed as of June 18.

Late on the 18th a Class I team from California assumed management of the fire from the local Fire Boss, Orlando Romero of the Santa Fe National Forest. A dozer fireline was completed across Escobas Mesa from near the Ponderosa Campground, and engines were positioned defensively along this planned control line. However, nature had other ideas for the overhead team. By the start of what is termed by fire people as the daily "burning period" (approximately 10 A.M.), the winds had increased to 20-30 mph from the southwest, the relative humidity dropped to 3%, and estimated rates of spread were approaching 38 chains/hour (1 chain=66 feet). These conditions gave rise to one of the most spectacular high-intensity, sustained, crown-fire runs in recent history for the region. With flame lengths often exceeding 200 feet through these dense, dog-hair thickets, engine crews working along the two dozer blade-wide fireline quickly cut their hoses and rolled out to escape this unstoppable fire. They left in their wake a mile-plus wide fire front heading towards State Route 4 and Los Alamos Scientific (now National) Laboratory lands beyond. This fire was now consuming everything combustible in its path, often down to bare mineral soil.

By 12:30 P.M. that afternoon, the fire had reached Highway 4 east of Bandelier's Ponderosa Campground after nearly entrapping several engine and handcrews. Spotting distances during the day were estimated at 1/2 to 2 miles, with total fire size at this time estimated to exceed 5,000 acres. Structural fire apparatus crews from Los Alamos hastily retreated north into Laboratory technical area sites to deal with numerous spotfires. Management of the fire had reached another dimension now, with a third agency becoming involved in the incident. As the fire moved from heavily forested fuels into more open and discontinuous fuels, combined with dissipating late afternoon winds, the fire's intensity decreased in the Laboratory area.

On June 19th the fire weather forecast called for another day of extreme spread rates through ponderosa pine forests, with spotting, crownfire behavior, and 25,000 ft. convection column development predicted. By mid-morning however, handline was completed along the western boundary of the fire, with engine crews burning out westerly along Highway 4 from Backgate to the Los Alamos-Sandoval County line. Good progress was also

being reported along the southern and eastern portions of the fire's perimeter.

Archaeologists were a familiar site on the fire now - leading equipment, marking sites or features to be avoided, and talking to fire crews tempted to collect souvenirs.

On the 20th of June, the first significant weather break was indicated in the forecast. Although winds were continued high with low humidities during the day, the night shift called for possible thunderstorms with much higher humidities. This proved to be the first major break for crews in making progress toward containment. On the 21st, there was a heavy cumulus cloud buildup with late afternoon humidities building to around 70%. The estimated burned area was up to 11,000 acres, with a fire perimeter of nearly 18 miles. The now weary management team, along with the 1,000-plus "ground pounders", could finally catch a glimmer of hope.

On June 22 at 4:00 P.M., six long days and nights after the initial smoke report and action, the fire was declared contained. This meant that a fireline had been established completely around the fire. Full control of this fire would not come for another 3 days.

In all, 1370 personnel, 9 dozers, 23 engines, 5 air tankers, and 5 helicopters were committed to this incident. There was one fatality. Long-time Bandelier employee Johnny Aldaz died of a heart attack on June 18 while assigned to an engine crew. His memorial is located near the Bandelier Entrance Station.

THE AFTERMATH

The final acreage for the La Mesa Fire was set at 15,444, with over 10,230 on National Park Service, 2,684 on Santa Fe National Forest, and the remaining 2,530 on Los Alamos National Laboratory lands. This was the largest and most intense fire to have burned in the Jemez Mountains since the late 1800's. Total cost to the taxpayers of the La Mesa Fire was approximately 3 million dollars, or roughly \$190 per acre. The average cost of fire suppression has now climbed to well over \$600 per acre.

Impacts resulting from the fire's intensity and duration on vegetation, wildlife habitat, watersheds and soils, riparian systems, aesthetics, and non-renewable cultural resources ranged from

minimum to very severe. For the intensely burned areas, a rehabilitation plan was prepared. Among the first of this kind in the National Park System, the priorities were:

(1) to immediately stabilize the bare soils, handlines and dozer lines (remembering that onset of the summer monsoons was only days away);

(2) to assess the extent of damage to cultural resources, from both direct fire effects and human suppression activities; and

(3) clear visitor use trails, bridges, damaged facilities and cleanup debris.

To accomplish these priority tasks the Park Service, in cooperation with the Santa Fe National Forest, reseeded all but some 2,000 acres of burned

area on lands managed by Los Alamos National Laboratory. Archaeologists from the NPS Regional Office in Santa Fe conducted a fire effects study on cultural sites and materials, and developed perhaps the first study-based recommendations for managing wildland fire on a cultural landscape (see Cartledge - This Volume).

National Park Service Regional Chief Scientist Roland Wauer at that time had a notion of the enormous scientific study potential contained on the mesas and in the canyons of the La Mesa Fire area. He and his staff were instrumental in organizing and securing funding for a variety of ensuing research studies. This symposium presents followup results, as well as new studies, on the enduring effects of the La Mesa Fire.

Historical Fire Regime Patterns in the Southwestern United States Since AD 1700

Thomas W. Swetnam and Christopher H. Baisan¹

Abstract.—Fire-scar chronologies from a network of 63 sites in the Southwestern United States are listed and described. These data characterize the natural range and variability of fire regimes from low elevation pine forests to higher elevation mixed-conifer forests since AD 1700. A general pattern of increasing length of intervals between low intensity surface fires was observed along gradients of low to high elevations, and from the relatively drier pine sites to the wetter mixed-conifer sites. However, large variability in the measures of central tendency and higher moments of the fire interval distributions suggest that elevation and forest type were often weak determinants of fire frequency. Some of the variations in fire interval distributions between similar elevation or forest types were probably due to unique site characteristics, such as landscape connectivity (i.e., ability of fires to spread into the sites), and land-use history. Differences in the sizes of sampled areas and fire-scar collections among the sites also limited our ability to compare and interpret fire interval summary statistics.

Comparison of both the fire-scar network data (1700 to 1900) and documentary records of area burned on all Southwestern Region National Forests (1920 to 1978) with a Palmer Drought Severity Index time series clearly shows the association between severe droughts and large fire years, and wet periods and small fire years. Moreover, important lagging relations between climate and fire occurrence are also revealed. In particular, large fire years in ponderosa pine dominated forests were typically preceded by wet conditions in the prior one to three years. In contrast, large fire years in mixed-conifer forests were associated with extreme drought years, but no consistent lagging relations were observed. We hypothesize that both fuel production (especially grasses and pine needles) and fuel moisture were important climate-linked factors in ponderosa pine fire regimes, while fuel moisture was the primary factor controlling mixed-conifer fire regimes.

These results provide two important types of information for management: (1) Baselines of fire regime ranges and variations are documented across the most economically important and widespread forest types in the Southwest. These data will be useful for guiding, developing, and justifying ecosystem management plans, particularly for the restoration of fire regimes and forest structures to improve forest health and sustainability. (2) The fire-climate relations suggest that a long-range fire hazard forecasting model could be developed that would be a valuable tool for planning and implementing both prescribed fire and fire suppression programs in the Southwest.

INTRODUCTION

On June 2, 1900, Gifford Pinchot was riding horseback through park-like stands of ponderosa pine on the Mogollon Rim near Chevlon, Arizona.

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As he rode up onto a ridge he noticed a fire-scarred tree that appeared to have recently died. He dismounted, and taking a hatchet he chopped into one side of the "cat face." On the cut surface he could see the annual tree rings and the successive scars that had formed by the re-burning of the resinous scar boundaries each time a surface fire swept past the tree. He counted the tree rings between the scars, and then he estimated the dates of each fire. In all he counted 14 separate fires, the most recent in 1898 and the earliest in 1785 (photograph and notes on file in Forest Service, Southwestern Region Office, Albuquerque, NM). Pinchot, the future first Chief of the Forest Service, saw for himself the unequivocal evidence that surface fires were an ancient and recurrent forest disturbance, but his interpretation of the role they played was primarily negative. Years later in his book *Breaking New Ground* (1947) he made clear his view of fire in Arizona pine forests: "We looked down and across the plain. And as we looked there rose a line of smokes. An Apache was getting ready to hunt deer. And he was setting the woods on fire because a hunter has a better chance under cover of smoke. It was primeval but not according to the rules."

The scarcity of tree seedlings and the open canopy condition of pine forests convinced Pinchot and most early foresters that the frequent surface fires had kept forests "understocked." They also recognized that many years of abusive grazing practices were partly responsible for the poor tree regeneration. Elimination of fires and control of the grazing situation became the prime directives for the tough, young rangers charged with setting up the National Forest System on the ground.

Now, more than ninety years later we are experiencing a sea change in attitudes and policy towards fire. This change, most recently embodied in the concepts of "ecosystem management," has been driven by accumulated historical and ecological evidence demonstrating that fire is a keystone ecological process in most forest types, and that its exclusion, combined with other factors, has led to significant "forest health" problems. The 1977 La Mesa burn was a wake-up call to perhaps the most pressing forest health problem in Southwestern forests — historically anomalous, catastrophic wildfire in ponderosa pine — created by many decades of fire exclusion.

Prescribed fire has been a part of the fire manager's tool kit since before the La Mesa burn, but even with the greater acceptance and changes in policy over the past two decades the total

amount of area treated with prescribed burning (either "natural" or "planned") is minuscule compared to the amount of forest area that would benefit from such treatment. If we are to restore degraded forest ecosystems to conditions of better health and sustainability, and if fire is to be a primary restoration tool, then prescribed burning must be carried out at much larger spatial scales. However, problems of funding, smoke, and the hazards of escaped fires will surely limit the extent to which landscape-scale fire can be reintroduced in the Southwest. The task of researchers and managers is to identify the minimal level of fire re-introduction required for maximal ecological health and sustainability, but also practical and safe given our economic and social limitations.

The paradox of fire management in conifer forests is that, if in the short term we are effective at reducing fire occurrence below a certain level, then sooner or later catastrophically destructive wildfires will occur. Even the most efficient and technologically advanced fire fighting efforts can only forestall this inevitable result. It is clear from many years of study and published works that the thinning action of pre-settlement surface fires maintained open stand conditions and thereby prevented the historically anomalous occurrence of catastrophic crown fires that we are experiencing in today's Southwestern forests (Weaver 1951; Cooper 1960; Swetnam 1990; Covington and Moore 1994; Sackett et al. 1994). The ecosystem management approach explicitly recognizes that these conditions are untenable for the goal of long-term sustainability, and therefore we should strive to reintroduce keystone ecological processes such as fire, or substitute for them with silvicultural treatments such as mechanical thinning (Allen 1994; Kaufmann et al. 1994). The degree to which thinning or other silvicultural treatments can substitute for the fire process is open to debate.

If we are going to re-introduce fire processes we need to learn as much as possible about long-term fire history and fire effects within the forest types to be managed. Ideally, we should have specific knowledge for the particular management units where we are planning the re-introduction. A baseline description of historical conditions provides a view of the "natural range of variability" of the important processes controlling the dynamics and structure of ecosystems (Swanson et al. 1994). This baseline is useful as a reference, but not necessarily as an exact blueprint, for disturbance re-introduction (Morgan et al. In Press). In some cases the natural range and variability define the bounds

of the disturbance processes that are most likely to produce a long-term sustainable forest. How do we know that such conditions are sustainable? From a very long temporal perspective of centuries to millennia no forest ecosystem may be considered equilibrium (i.e., sustainable) because climatic, geologic, or anthropogenic fluctuations inevitably lead to ecosystem changes (Botkin 1990; Sprugel 1991; Swetnam 1993). On the other hand, we should remember that the open, park-like stands of ponderosa pine that were both so impressive to our pioneer predecessors, and which have provided the bulk of the timber cut during the settlement era and since, were primarily composed of trees that germinated and survived with such fire regimes for many centuries. Thus, the historical (i.e. "natural") range of variability of pre-settlement forests may be the best, and perhaps the only template we have for long-term sustainability.

The purpose of this paper is to review some of the facts that we have learned from intensive fire history studies in Southwestern ponderosa pine and mixed-conifer forests. After Pinchot's initial fire-scar counting in 1900, Harold Weaver, a forester with the Bureau of Indian Affairs, was apparently the next person to investigate Southwestern fire history patterns in tree rings (Weaver 1951). In the 1970s, Research Scientist John H. Dieterich of the U. S. Forest Service, Rocky Mountain Forest and Range Experiment Station, and Professor Marvin A. Stokes of the Laboratory of Tree-Ring Research, University of Arizona began collecting and dating fire-scarred specimens from throughout the region. In recent years, we (the authors, our students, and collaborators) have greatly expanded these collections. We are currently assembling an even larger fire history network that will encompass the full range of Southwestern woodland and forest types (e.g., pinyon-juniper and oak-pine woodlands up to the spruce-fir zone). We plan to conduct more systematic statistical analyses and modeling using these data. Our goal is to document and understand the natural range of variability of fire regimes across multiple temporal and spatial scales, and to use this knowledge to guide and support ecosystem management programs. We are especially interested in the fundamental causes and mechanisms of fire regime variability, particularly the role of climate and human land-use practices. Here we present a listing of 63 fire history reconstructions in the Southwestern U. S. (mainly Arizona and New Mexico) and some general descriptions of fire regime patterns and associations that we observe in these data.

METHODS

Sampling Considerations

Fire-scarred trees are relatively abundant in forests of the Southwest, but the most informative and useful specimens for fire history reconstructions are somewhat rare. They usually comprise less than about five percent of all standing trees, and a much smaller percentage in stands that have been harvested. Among the few trees with fire-scarred boles an even smaller proportion contain well-preserved, multiple fire scars. We have seen many instances of two fire-scarred trees of approximately the same age growing side-by-side; one of the trees contains a visible record of many fire scars, while the other tree has only one or a few fire scars. Based on these and other observations, it is clear that fire-scarred trees are not all equally consistent and reliable recorders of fires that have burned around their bases. Therefore, it is inefficient and inappropriate to sample fire-scarred trees as if they all belong to the same statistical population.

Many factors are involved in the repeated, consistent scarring of individual trees and the preservation of the fire scars formed on them (e.g., position of the tree on the landscape, bark thickness, lean of the tree, decay of the wood in the fire-scar wound, burning-off of older fire scars by subsequent fires, vigor of the tree and its ability to heal over wounds, production of resin at the wound boundaries, etc.). Historical factors are also important in determining abundance of useful fire-scarred material, such as past timber or fuelwood harvesting. In addition to living fire-scarred trees, snags and logs ("remnants") often contain very long and detailed records of past fires. Remnant specimens can be dendrochronologically dated (i.e., by crossdating, [Stokes and Smiley 1968; Swetnam et al. 1985]) thereby lengthening and replicating the fire-scar record for individual sites (Baisan and Swetnam 1990). Unfortunately, fires in the late twentieth century, including prescribed burns, usually consume the accumulated fire-scar evidence, especially the record preserved in remnants. Salvage of ancient fire-scar records before initiation of prescribed burning programs should therefore be a priority (Van Pelt and Swetnam 1990).

In developing a replicated and complete fire history reconstruction it is necessary to diligently search for and sample many trees with multiple, well-preserved fire scars distributed spatially throughout the sampling unit. Usually 10 to 30

trees or more are sampled within each selected forest stand (hereafter referred to as "sites"). Almost all of our sites range in size from approximately 10 to 100 ha, and a few are up to about 1000 ha. Relatively homogenous sites with little variation in topography or forest type are best. These sites are usually selected as "case studies" of fire history within particular forest types or certain landscape situations. At watershed or mountain range spatial scales, sites may be selected to achieve sufficient spatial dispersion to infer larger fire extent patterns (see discussion below).

The goal of our sampling has been to obtain a fire event "inventory" within sampled sites that is as long and complete as possible; i.e., to identify all or nearly all dates of fires that occurred within the sampled unit for a maximum length of time before the present. Contrary to the views of Johnson and Gutsell (1994) we do not believe that it is necessary, practical, or efficient to randomly sample sites or fire-scarred trees *in all circumstances* in order to obtain complete and un-biased fire history reconstructions. In fact, a random sampling scheme of all fire-scarred trees within sites that sustained high frequency surface fire regimes would not result in a complete or unbiased record *unless the record is preserved in those sites*, and the sampling involved very large numbers of trees; probably hundreds of trees would be required for sites of 100 to 1000 ha.

In many ways, fire-scarred trees are similar to fossils that paleontologists search for to inventory and reconstruct the ancient flora or fauna of an area. In most cases the rarity and the unevenness of the paleorecord, both in quality and quantity, precludes a strict random sampling. There simply are not enough old, well-preserved fossils distributed across the landscape to reasonably assume that a randomly selected set of sites, or of fossils within sites, would provide a clear or complete long-term picture of the past. Moreover, landscapes are often far too heterogeneous to have any hope of sampling, within the lifetime of a researcher, a sufficient number of sites or fossils (trees in our case) to produce a robust statistical description of histories in all landscape types. To reiterate, our objective is not to statistically sample the "population" of landscape types or of fire events that have occurred, but rather to obtain as complete an inventory as possible of all fire events (dates) that have occurred within selected units (i.e., case studies) as far back in time as possible. This is most efficiently accomplished by finding and sampling old living trees and remnants that have recorded and preserved

the maximum amount of fire history information at many different points in space.

Fire-scar records are fundamentally a spatial "point record" of fire occurrence. In ponderosa pine forests it is not possible to reconstruct the exact perimeter of low intensity burns that occurred more than a few years before the present. There is no clearly preserved record of the precise extent of the many dozens of individual burns that swept through old-growth ponderosa pine forests in past centuries. This is in sharp contrast to lower fire frequency, stand-replacement fire regimes (such as in chaparral or spruce-fir forests) where the extant stand structure (e.g., ages or heights of trees, or other visible clues) can be used to estimate the perimeters of some past burns, although these methods have serious limitations as well (Heinselman 1973, Tande 1979, Minnich 1983, Johnson and Gutsell 1994). Surface fires in ponderosa pine were of such low intensity that their direct influence on the overstory canopy structure was negligible, or very spatially patchy. Even though surface fires had minimal direct effects on most mature overstory trees, this does not mean they were ecologically unimportant. The individual and cumulative impacts of the frequent, low intensity surface fires had a profound influence on tree seedling dynamics, low and mid-level canopy structures, understory plant species diversity, nutrient cycling and other soil properties, plant growth, and many other ecosystem properties (e.g., diversity of vertebrate and invertebrate fauna).

Localized high intensity burns probably occurred in some places within both ponderosa pine and mixed-conifer forests, such as around recently dead snags with accumulated litter, bark, and branches at their base. The typically longer intervals between fires in mixed-conifer forests, and more extreme drought conditions when fires did occur (see results section), led to a mosaic pattern of variable size patches of high-intensity stand replacement burns within a larger matrix of surface burn (Baisan and Swetnam, In Press).

Although we cannot reconstruct the precise perimeters or prepare detailed maps of past surface fires in Southwestern ponderosa pine and mixed-conifer forests, we can study the *relative* extensiveness of fires at various spatial scales (Figure 1). Patterns of synchrony and asynchrony of fire dates among trees and among sites can be used to infer the relative extent of fire events across these different spatial scales. For example, temporally synchronous fire dates recorded throughout sites by

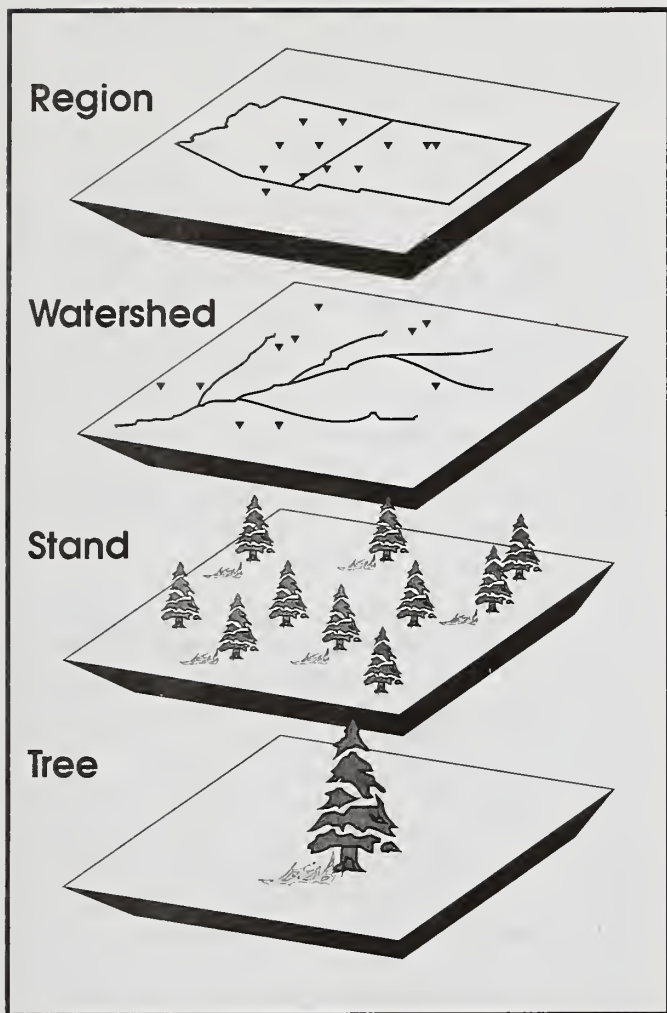


Figure 1.—Spatial scales of fire history analysis. Fire-scar records on individual trees must be carefully selected and sampled in order to maximize the completeness of the fire date inventory within sites. The patterns of synchrony and asynchrony of fire records among spatially dispersed trees within sites, among sites within watersheds (or mountain ranges), and among sites within the region can be evaluated to identify patterns of relative fire size, spread, extensiveness, and associations with climatic variation and land-use history.

many sampled fire-scarred trees can be reasonably inferred to have been burns of larger spatial extent *within the sampled site* than fire dates recorded by only one or a few trees. Similarly, synchronous fire dates recorded in many different sites at watershed or larger spatial scales (Figure 1) probably represent larger areas burned during those years than fire dates recorded in smaller numbers of sites. It is possible that synchronous fire dates recorded on different trees (or in different sites) were not caused by the same contiguous burn. Multiple fire ignitions by lightning or people could have started many different fires during the same year. Nevertheless, the same fire dates recorded at many differ-

ent points in space would still probably represent larger amounts of area burned during those particular years than fire dates recorded by smaller numbers of trees or sites.

It is also possible that fire intensity is a factor determining synchronicity of the recorded fire dates (i.e., hotter fires may be more likely to scar trees). However, we have observed that even low intensity prescribed burns usually re-scar trees that already have been scarred at least once. In contrast to un-scarred trees, the easily ignited exposed wood and seeping resin on previously scarred trees make them especially "sensitive" to being re-scarred by subsequent fires of any intensity. The vast majority of fire-scar dates in our data sets were recorded on trees that had already incurred one or more scars and had an open wound (i.e., they were already sensitive fire recorders). Hence, with a well-replicated sample set of fire-scarred trees and sites even low intensity, but widespread fires should still be evident as synchronous dates. Moreover, it is probable that during years when fires were likely to spread over large areas they were also likely to be more intense. For example, during drought years fuels are dry and burn intensely and rapidly over large areas. Also, following relatively long periods without fire the fuels accumulate and become more continuous across the landscape, and so when fire occurs it tends to burn intensely and spread over large areas. Thus, the direct association between fire intensity and extensiveness we observe in the present certainly existed in the past, but this relationship does not contradict our interpretation that, within a given area, synchronous fire dates generally represent larger areas burned than asynchronous fire dates.

This idea of assessing patterns of synchrony and asynchrony across different spatial and temporal scales has a direct scientific lineage from the earth sciences, and dendrochronology in particular. Geologists have long used the principle of uniformity ("the present is the key to the past") in reconstructing earth history from matched spatial and temporal patterns of layered records (e.g., sediments). Dendrochronologists rely upon "crossdating" (i.e., synchrony) of annual tree-ring widths among trees and sites to identify the exact chronological placement of tree-rings, as well as for distinguishing the influences of climate on tree growth from the influences of more locally specific factors. The strength of the dendrochronological approach lies in the exactness of the time sequences that are assembled at multiple points in space. This exactness enables us to spatially aggregate the time series and thereby identify patterns of synchrony and

asynchrony with high resolution at multiple spatial and temporal scales. Such information on *keystone processes* (*sensu* Holling 1992) spanning seasons to centuries and individual trees to regions is rare in ecology. This approach has proven fruitful in a variety of applications (Fritts and Swetnam 1989), including fire history and fire climatology (Swetnam and Dieterich 1985; Swetnam et al. 1989; 1992; Swetnam and Betancourt 1990; 1992; Swetnam 1993; Baisan and Swetnam 1990; Brown and Swetnam 1994; Grissino-Mayer and Swetnam, In Press; Grissino-Mayer et al. In Press; Touchan et al. In Press; Touchan et al. This Volume), insect outbreak studies (Swetnam and Lynch 1989; 1993; Swetnam et al. In Press) and in tree demography studies (Swetnam and Brown 1993; Betancourt et al. 1993).

Data Compilation and Statistical Description

Master fire-scar chronologies (Dieterich 1980; Dieterich and Swetnam 1984) were developed from more than 1,200 fire-scarred trees sampled in 63 sites located in Arizona, New Mexico, Texas, and Sonora Mexico (Figure 2, Table 1). This is currently the world's largest and longest regional-scale fire history network composed entirely of fire event chronologies accurately dated to annual or seasonal resolution. These tree-ring data were collected and crossdated by many individuals. Some of the detailed fire histories for individual sites are described in published papers (see Swetnam 1990 for a partial list), while others are described in unpublished reports on file at the Laboratory of Tree-Ring Research (LTRR). Other descriptions are contained in papers, theses, and dissertations that are currently in preparation by the authors, our students, and colleagues.

All of the fire dates for each sampled tree in each site were entered in database files. These files were processed through a fire history analysis software package called FHX2, written by Mr. Henri Grissino-Mayer of LTRR. FHX2 computes a variety of descriptive statistics for fire interval and fire frequency data. All of the chronologies compiled for this paper were analyzed for the time period AD 1700 to 1900. Much longer fire-scar data were included in many of the sites, but the post-1700 time period included most of the sampled trees in most sites, and therefore was the best replicated period. Very few fire dates were recorded after about 1900 in most sites due to the advent of intensive livestock grazing, which removed fine fuels (i.e., grasses and herbs) necessary for fire spread, and/or because of organized fire suppression by

land management agencies. Thus, the fire-scar analyses concentrate on a two century "pre-settlement period" preceding AD 1900.

The fire interval statistics computed and reported here include (1) measures of central tendency: mean fire interval, median fire interval, Weibull median probability interval (WMPI); and (2) measures of range and variability (or higher moments of the distribution): minimum and maximum intervals, standard deviation, coefficient of variation, skewness, and kurtosis. The WMPI is the estimated fire interval (in years) at which there is a 50 percent probability of longer (or shorter) fire intervals occurring — based on the fitting of a Weibull-type curve (model) to the fire interval distributions (see Johnson and vanWagner [1985] for a description of these models).

The fire interval statistics were computed on three different levels of fire-scar dates. These were: (1) fire dates recorded within each site by any tree; (2) fire dates recorded by 10 percent or more of the fire-scarred trees within each site; and (3) fire-scar dates recorded by 25 percent or more of the fire-scarred trees within each site. An additional criterion for the 10 and 25 percent sortings was that at least two trees within each of the sites recorded the fire dates used to compute the descriptive statistics. This sorting (or filtering) of fire dates recorded by increasing percentages of the trees within each site is a means of assessing patterns of fire frequencies and extent associated with fire events that probably burned progressively greater areas within sites (see discussion in previous section). For example, in some sites many fires were recorded by only one or a few sampled trees, but a few fires were consistently recorded by many or nearly all sampled trees. In these cases the different sortings would show greatly different fire frequencies. In contrast, in some sites most fires were recorded by most sampled trees, and hence fire frequencies varied only slightly among the different sortings. In each type of case a different interpretation may be made regarding the frequencies and extensiveness of fires.

After computing fire interval statistics for all master fire chronologies, the data were sorted by elevation and forest type and plotted to assess patterns that may be related to these two factors. Forest types were broadly categorized as: (1) pine/pinyon-juniper/oak [PINE/PJ/OAK] (2) ponderosa pine [PIPO] (3) ponderosa pine/mixed-conifer [PIPO/MC] (4) mixed-conifer [MC]. The PINE/PJ/OAK category included sites with ponderosa pine, or other pine species (such as Chihuahua pine or

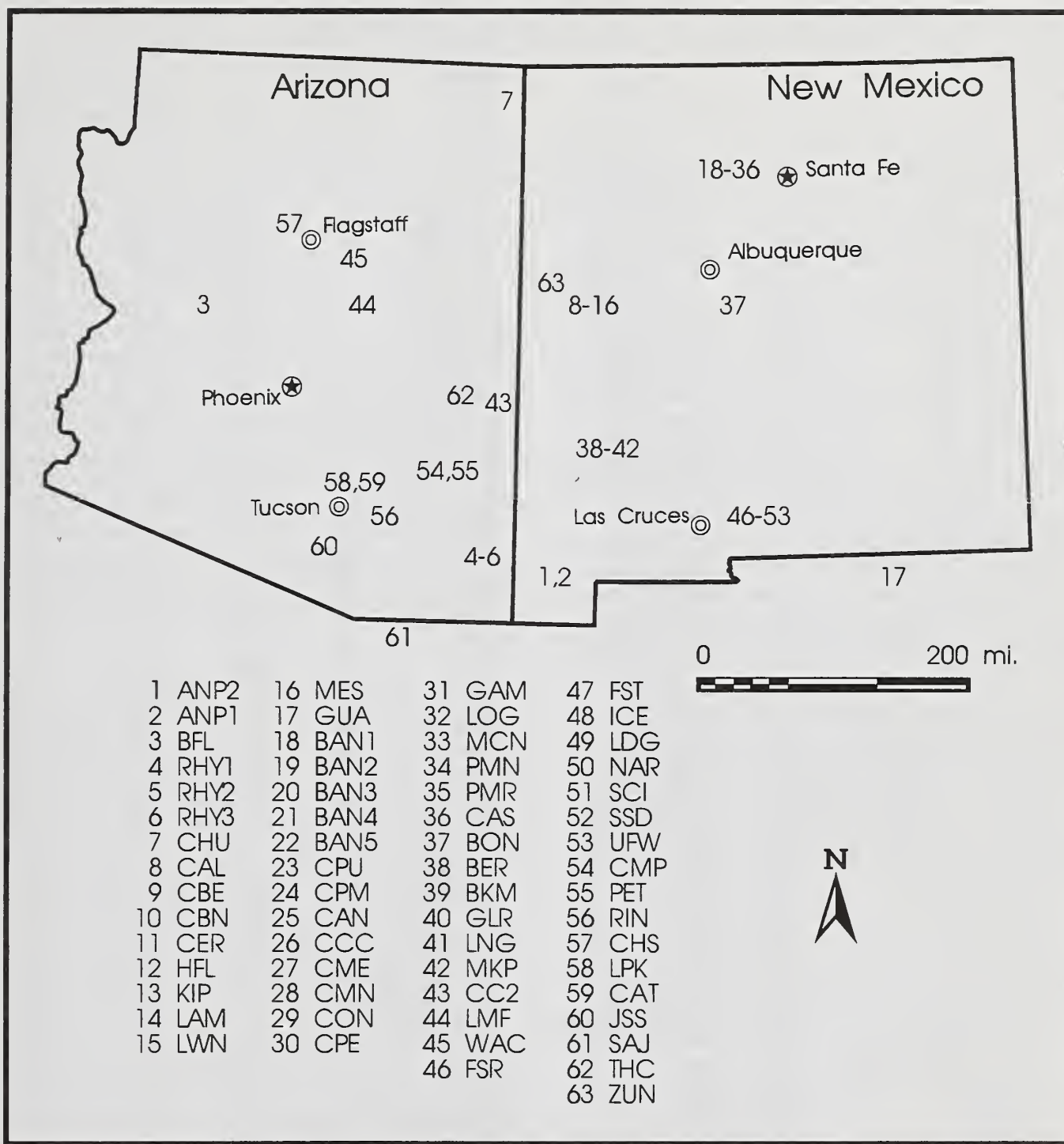


Figure 2.—Map of Arizona and New Mexico showing locations of all fire history sites reported in this paper. The numbers on the map refer to the site codes which are listed below and in Tables 1 to 4. The U.S. Forest Service Southwestern Region [Region 3] is located primarily in these two states.

Apache pine in Southern Arizona) as the major source of fire-scarred samples, but also mixed within the stand were pinyon, juniper, or various oak species. The PIPO category included sites that were pure or nearly pure stands of ponderosa pine.

The PIPO/MC category were sites with ponderosa pine as the primary dominant tree species and some combination of Douglas-fir, or true firs (*Abies*) were also present, but in smaller proportions (density or crown cover) than the ponderosa

Table 1.—Listing of 63 fire-scar sites in Southwestern fire history network. See text for explanation of forest type. Ownership is National Forest (NF), National Park (NP), National Monument (NM), The Nature Conservancy (TNC), or other.

Site Code	Site Name	State	Ownership	Mountain Range of Region	No. of Fire-Scar Samples	Forest Type	Lowest Elevation (Feet)	Highest Elevation (Feet)
ANP2	ANIMAS PEAK—SOUTH	NM	GRAY RANCH (PRIVATE)	AMIMAS	56	PIPO/MC	8000	8100
ANP1	ANIMAS PEAK—NORTH	NM	GRAY RANCH (PRIVATE)	ANIMAS	18	PIPO	8000	8400
BFL	BATTLE FLATS	AZ	PRESCOTT NF	BRADSHAW	7	PIPO/CHAP	5000	5200
RHY3	RHYOLITE CANYON—LOWER	AZ	CHIRICAHUA NM	CHIRICAHUA	12	PINE/OAK	5600	5920
RHY2	RHYOLITE CANYON—MIDDLE	AZ	CHIRICAHUA NM	CHIRICAHUA	30	PIPO/MC	5920	6300
RHY1	RHYOLITE CANYON—UPPER	AZ	CHIRICAHUA NM	CHIRICAHUA	16	PIPO/MC	6800	7000
CHU	CHUSKA	AZ	NAVAJO RESERVATION	CHUSKA	16	PIPO/MC	8800	8900
CBE	CERRO BANDERA EAST	NM	EL MALPAIS NM	EL MALPAIS	32	PIPO	7900	8360
CBN	CERRO BANDERA NORTH	NM	EL MALPAIS NM	EL MALPAIS	35	PIPO	7860	8100
CER	CERRO RENDIJA	NM	EL MALPAIS NM	EL MALPAIS	11	PIPO	7900	8140
CAL	EL CALDERON	NM	EL MALPAIS NM	EL MALPAIS	5	PIPO	7200	7260
KIP	HIDDEN KIPUKA	NM	EL MALPAIS NM	EL MALPAIS	13	PIPO	7375	7440
HFL	HOYA DE CIBOLA LAVA FLOW	NM	EL MALPAIS NM	EL MALPAIS	23	PIPO	7500	7500
LAM	LA MARCHANITA	NM	EL MALPAIS NM	EL MALPAIS	37	PIPO	7700	8000
LWN	LOST WOMAN	NM	EL MALPAIS NM	EL MALPAIS	20	PIPO	7660	7960
MES	MESITA BLANCA	NM	EL MALPAIS NM	EL MALPAIS	26	PIPO/PJ	7370	7420
GUA	GUADALUPE MTNS.—THE BOWL	TX	GUADALUPE MTNS NP	GUADALUPE	26	PIPO/MC	7546	8202
CME	CAMP MAY EAST	NM	SANTA FE NF	JEMEZ	6	PIPO	8900	9080
CMN	CAMP MAY NORTH	NM	SANTA FE NF	JEMEZ	20	MC	9720	10020
CAN	CANADA BONITA NORTH	NM	SANTA FE NF	JEMEZ	28	MC	9720	9840
CAS	CANADA BONITA SOUTH	NM	SANTA FE NF	JEMEZ	31	PIPO	9120	9220
CPM	CAPULIN CANYON MIDDLE	NM	BANDELIER NM	JEMEZ	15	PIPO	6650	6940
CPU	CAPULIN CANYON UPPER	NM	BANDELIER NM	JEMEZ	8	PIPO/MC	8370	8430
CPE	CERRO PEDERNAL	NM	SANTA FE NF	JEMEZ	26	PIPO	8800	9190
CCC	CLEAR CREEK CAMPGROUND	NM	SANTA FE NF	JEMEZ	20	PIPO	8202	8300
CON	CONTINENTAL DIVIDE	NM	SANTA FE NF	JEMEZ	24	PIPO	9350	9400
GAM	GALLINA MESA	NM	SANTA FE NF	JEMEZ	25	PIPO/MC	8520	9180
LOG	LOS GRIEGOS	NM	SANTA FE NF	JEMEZ	15	MC	9250	9500
MCN	MONUMENT CANYON NATURAL AREA	NM	SANTA FE NF	JEMEZ	30	PIPO	8200	8420
PMN	PAJARITO MOUNTAIN NORTH	NM	SANTA FE NF	JEMEZ	28	MC	9340	10080
PMR	PAJARITO MOUNTAIN RIDGE	NM	SANTA FE NF	JEMEZ	23	PIPO	9380	9740
BAN1	RITO DE LOS FRIJoles—GROUP 1	NM	BANDELIER NM	JEMEZ	9	PIPO/PJ	6660	6750
BAN2	RITO DE LOS FRIJoles—GROUP 2	NM	BANDELIER NM	JEMEZ	13	PIPO/MC	7100	7700
BAN3	RITO DE LOS FRIJoles—GROUP 3	NM	BANDELIER NM	JEMEZ	18	PIPO	8235	8640
BAN4	RITO DE LOS FRIJoles—GROUP 4	NM	BANDELIER NM	JEMEZ	23	PIPO/MC	9154	9620
BAN5	RITO DE LOS FRIJoles—GROUP 5	NM	BANDELIER NM	JEMEZ	12	PIPO	7267	7430
BON	MANZANO MTNS—NORTH	NM	CIBOLA NF	MANZANO	19	PIPO	7300	7400
BER	"BEARWALLOW, GILA"	NM	GILA NF	MOGOLLON	13	MC	9000	9600
BKM	BLACK MOUNTAIN	NM	GILA NF	MOGOLLON	27	PIPO/ MC	8400	9300
GLR	GILITA RIDGE	NM	GILA NF	MOGOLLON	10	PIPO	8300	8300
LNG	LANGSTROTH MESA	NM	GILA NF	MOGOLLON	18	PIPO/MC	7800	8400
MKP	McKENNA PARK	NM	GILA NF	MOGOLLON	12	PIPO	7640	7800
CCA	CASTLE CREEK	AZ	APACHE NF	MOGOLLON RIM	17	PIPO	8000	8200
LMF	LIMESTONE FLATS	AZ	COCONINO NF	MOGOLLON RIM	13	PIPO	6900	6900
WAC	WALNUT CANYON	AZ	WALNUT CANYON NM	MOGOLLON RIM	18	PIPO/PJ	6660	6800
SCI	FILLMORE SIDE CANYON 1	NM	TNC	ORGAN	7	PIPO	7200	7500
FST	FILLMORE SIDE CANYON 2	NM	TNC	ORGAN	8	PIPO/MC	7200	7700
FSR	FILLMORE SIDE CANYON 3	NM	TNC	ORGAN	10	PIPO	7200	7800
ICE	ICE CANYON	NM	TNC	ORGAN	7	PIPO	7500	7800
LDG	LEDGE SITE	NM	TNC	ORGAN	7	PIPO	7800	7900
NAR	NARROWS	NM	TNC	ORGAN	8	PIPO/PJ/OAK	7000	7300
SSD	SNAG SADDLE	NM	TNC	ORGAN	4	PIPO	7800	8000
UFW	UPPER FILLMORE WEST	NM	TNC	ORGAN	24	PIPO/MC	7800	8200
CMP	CAMP POINT	AZ	CORONADO NF	PINALENO	50	MC	7546	9600
PET	PETER'S FLAT	AZ	CORONADO NF	PINALENO	40	MC	9200	9450
RIN	MICA MOUNTAIN	AZ	SAGUARO NP	RINCON	44	PIPO/MC	6791	8530
CHS	CHIMNEY SPRINGS	AZ	COCONINO NF	SAN FRANCISCO	8	PIPO	7325	7425
LPK	LEMMON PEAK	AZ	CORONADO NF	SANTA CATALINA	15	MC	8750	8960
CAT	ROSE CANYON + PALISADES	AZ	CORONADO NF	SANTA CATALINA	11	PIPO/MC	7000	7600
JSS	JOSEPHINE SADDLE	AZ	CORONADO NF	SANTA RITA	17	PINE/OAK	6800	7200
SAJ	SIERRA AJOS	—	"SONORA, MEXICO"	SIERRA AJOS	18	PINE/OAK	6890	7218
THC	THOMAS CREEK	AZ	APACHE NF	WHITE	26	MC	8300	9200
ZUN	ZUNI MOUNTAINS	NM	CIBOLA NF	ZUNI	7	PIPO	8000	8400

pine. The MC category were mixed-conifer stands where ponderosa pine or other pines (e.g., Southwestern white pine) were secondary dominants, and generally in much smaller proportions than Douglas-fir, true firs, or spruce.

These forest type categorizations were imperfect for a number of reasons. One problem was that tree species composition and density has changed greatly in many of these stands because of twentieth century fire suppression or harvesting. For example, Douglas-fir and true firs have clearly increased in density in many areas — in some cases converting what were previously pure ponderosa pine stands to mixed-conifer. Generally, we tried to categorize the sites according to the apparent structure of the stands prior to the settlement and fire suppression era (i.e., before ca. 1900). Thus, composition of mature overstory trees that were likely to be older than about 100 years of age were given more weight in the classification. Another problem was that a few sites simply did not fit neatly into these categories because of unique tree species compositions and/or because they were in special locations, such as in riparian canyon bottoms.

Drought—Fire Relations

Temporal patterns of fire occurrence among all sites in the Southwest were compared with regional drought patterns. This analysis was conducted by compiling a set of recent dendroclimatic reconstructions based a large network of climatically sensitive tree-ring chronologies from Arizona and New Mexico (Cook et al., In Press). These reconstructions were arrayed in a spatial grid over the Southwestern Region. Each of the 13 grid points, consisting of reconstructed time series of Palmer Drought Severity Indices (PDSI) for the summer season (June, July, and August), were based on a multiple regression model using PDSI derived from meteorological station data for the period 1928 to 1979 as independent data, and sets of tree-ring width chronologies as dependent data. These models explained between 41 and 72% of the variance (adjusted r^2) in the tree-ring data (calibration period). A regionalized PDSI time series was computed by averaging the 13 grid point time series into a single time series representing annual drought magnitude fluctuations over the whole Southwest from AD 1700 to 1978 (recent decades were not reconstructed because not all tree-ring chronologies extended to the present). PDSI time series were normalized, so that values were expressed in standard deviation units.

A regional compilation of numbers of sites recording individual fire years was computed for the period 1700 to 1900. An additional regional times series of area burned per year for all National Forests in Arizona and New Mexico (Forest Service Region 3) was compiled for the period 1920 to 1978 from U.S. Forest Service documents (Swetnam 1990; Swetnam and Betancourt 1990). The regional time series of (a) numbers of sites recording fire scars and (b) area burned per year were sorted from largest to smallest fire years and sets of the largest and smallest fire years in the fire time series were compared with the regional PDSI time series. The comparisons included plotting the occurrences of the largest and smallest fire years on a line graph of the PDSI time series, and by conducting a "super-posed epoch analysis" (SEA) (Baisan and Swetnam 1990; Swetnam 1993). The SEA involved computing the mean PDSI values during all of the 20 largest and smallest regional fire years in (a) and 10 of the largest and smallest fire years in (b). The mean PDSI values were also computed for each of the five years preceding and two years following the sets of fire years. A Monte Carlo "bootstrapping" simulation was used to estimate confidence intervals on the observed mean values (Mooney and Duvall 1993; Swetnam 1993).

The analysis was run on the largest and smallest fire years based on all sites, and also on a separate sorting of largest and smallest fire years among MC and PIPO/MC sites in one group and PIPO sites in another group. The purpose of this sorting was to determine if different lagging patterns in drought-fire relations might be observed between the wetter and generally more productive MC, PIPO/MC group and the drier and relatively less productive PIPO group. Hypothetically, without regard to forest type, we expected to see that largest fire years were dry and smallest fire years (i.e., years with fewest numbers of sites recording fire events) were relatively wet. We also expected to see some pattern of dry or wet conditions preceding largest or smallest fire years that pre-conditioned Southwestern forests for more or less extensive fires by affecting fuel production. Finally, we did not expect post-fire years to be significantly wet or dry.

RESULTS

Fire Interval Statistics

Fire interval statistics are presented for all fire dates regardless of the number or proportion of

sampled trees recording them within sites (Table 2), for fire dates recorded by more than one tree and 10 percent or more of the sampled trees within sites (Table 3), and for fire dates recorded by more than one tree and 25 percent or more of sampled trees within sites (Table 4). Generally, these tables represent measures of central tendency, range and variation of all recorded fires regardless of size (Table 2), and those fires that probably burned over relatively larger proportions (or all) of the sampled sites (Tables 3 and 4). Tables 3 and 4 could be considered more conservative (i.e., longer) estimates of mean fire intervals in that these statistics discount fires that were probably smaller. On the other hand, as previously mentioned, the many apparently smaller fires that are included in Table 2 could have been ecologically very important as well, both cumulatively, and individually. Furthermore, even when including all recorded fires, it is still likely that some of the fire interval estimates were conservative because, despite our efforts to obtain a complete inventory of fire events within sites, we probably still missed sampling some fire dates. This was probably a more important problem in the highest fire frequency sites (i.e., fire intervals less than about 5 years), where fire extent also tended to be very patchy (see a discussion of this pattern in millennia length records in giant sequoia, Swetnam 1993).

The different measures of central tendency (mean, median, WMPI) were usually within one to about three years of each other, and the median was usually closer in value to the WMPI than the mean (Tables 2, 3, and 4). Large differences were observed in only a few cases. Advantages of the WMPI estimate are that it is based on a model that conforms to the typical non-normal shape of most fire interval distributions, and the statistic can be interpreted in terms of probability, which could be useful in simulation modeling or other prediction schemes. The skewness statistic demonstrates that most of the fire interval distributions were moderately positively skewed, i.e., fire dates were often clustered to the "left" with a long tail to the "right" representing many relatively short intervals and fewer unusually long intervals between fires. Thus, because of the skewness of most fire interval distributions the simple mean and median measures of central tendency were usually less statistically robust than the WMPI.

The kurtosis statistic was more variable than the skewness statistic among the sites and among the different sortings by percentage of trees scarred (Tables 2, 3, and 4). Kurtosis measures "peaked-

ness" of the distribution, with positive values indicating relatively highly peaked distributions (i.e., many values clustering near the central tendency) while negative values indicate a relatively flat distribution. Generally, more of the sites showed positive kurtosis in the computations involving all fire dates than the 10 and 25 percent sortings.

Given the large ranges and variability of the fire intervals within and among sites, we believe it would be a mistake to over-emphasize the importance of, or to over-interpret the ecological meaning of statistical summaries. While the fire process can be described with various levels of accuracy and bias by many different statistical summaries, such measurements are only one means of assessing fire regime properties. Other, and perhaps more important temporal characteristics of fire regimes are the historically unique or "time explicit" patterns. By this we mean the chronological and specific occurrence of individual fires, or the unusual short and long intervals between fires; i.e., the historical and contingent aspects of fire regimes. Particular events, and the ordering of these events in relation to other environmental factors and processes (e.g., climate, plant recruitment and mortality, and human-related events), may be more important than any summary statistic for understanding the past dynamics and current structure of ecosystems.

Despite the large intra-site variation in fire intervals, we can still visually detect some patterns in the measures of central tendency when plotted across gradients of elevation (Figure 3) or forest type (Figure 4). There is a general tendency for increasing length of fire intervals from lowest to highest elevations and from PINE/PJ/OAK to MC forest types. However, these patterns appear to be relatively weak in that the ranges of the measures of central tendency among sites at different elevations and forest type broadly overlap. Again, the uniqueness of individual sites and their special histories probably explains some of the overlap in these measures (see Discussion section).

An interesting deviation from the general pattern of increasing length of fire intervals from the drier to wetter forest types is the tendency for somewhat shorter intervals in the PIPO/MC type than in the PIPO type (Figure 4). We speculate that this may be related to higher productivity levels in the relatively mesic PIPO/MC sites. Fuel levels may recover quickly in these types following fire, while the presence of long-needle ponderosa pines assures high flammability of the fuel substrate.

Table 2.—Listing of fire interval statistics for 63 Southwestern fire-scar chronologies. Fire dates were based on fires recorded by any sampled tree within each site, AD 1700 to 1900.

Fire Intervals (years)—All Fire Scar Dates										
Site Code	No. of Intervals	Mean	Median	WMPI	Minimum	Maximum	Standard Deviation	Coeff. of Variation	Skewness	Kurtosis
ANP2	26	7.42	6	6.61	1	21	5.021	0.676	1.047	0.408
ANP1	37	5.35	4	4.31	1	16	4.392	0.821	0.919	-0.325
BFL	96	2.07	1	1.74	1	17	2.381	1.149	4.013	18.294
RHY3	29	6.17	6	5.41	1	15	3.799	0.616	0.262	-0.800
RHY2	23	8.30	7	6.78	1	33	7.283	0.877	1.727	3.383
RHY1	24	7.96	6	6.66	1	31	6.676	0.839	1.843	3.773
CHU	44	3.93	3	3.14	1	23	4.256	1.082	2.821	8.696
CBE	35	5.63	5	5.22	1	12	3.030	0.538	0.216	-0.956
CBN	36	5.33	5	4.95	1	13	3.089	0.579	0.716	-0.348
CER	19	9.32	9	7.81	1	25	6.840	0.734	0.603	-0.692
CAL	14	13.14	10	11.21	1	30	8.917	0.678	0.464	-0.947
KIP	12	16.50	12	13.27	3	55	15.294	0.927	1.390	0.955
HFL	15	12.00	10	10.83	2	31	8.018	0.668	0.940	0.002
LAM	27	7.30	7	6.79	2	21	4.479	0.614	1.279	1.478
LWN	22	8.96	7	7.70	2	30	7.569	0.845	1.689	1.965
MES	21	9.10	8	8.61	2	22	5.039	0.554	0.842	-0.017
GUA	36	5.11	4	4.36	1	15	3.882	0.760	1.038	0.026
CME	10	17.10	14	13.83	1	46	13.470	0.788	0.860	-0.193
CMN	6	25.17	14	14.35	1	89	32.872	1.306	1.310	-0.054
CAN	8	19.50	16	16.84	4	52	15.712	0.806	1.086	-0.104
CAS	19	10.05	7	8.95	2	29	7.322	0.728	1.313	0.977
CPM	20	9.45	10	8.57	1	21	5.708	0.604	0.565	-0.516
CPU	20	9.45	9	7.92	1	21	6.650	0.704	0.539	-0.878
CPE	11	14.36	11	13.07	4	28	9.102	0.634	0.392	-1.484
CCC	31	5.84	3	4.43	1	24	5.693	0.975	1.463	1.535
CON	25	7.80	4	5.38	1	28	8.588	1.101	1.391	0.534
GAM	43	4.54	4	4.10	1	12	2.922	0.644	0.983	0.300
LOG	12	15.75	13	13.74	1	33	10.217	0.649	0.375	-1.189
MCN	35	5.57	5	5.37	1	12	2.627	0.471	0.509	-0.248
PMN	13	12.00	10	10.45	3	32	8.803	0.734	0.819	-0.313
PMR	28	6.21	5	5.68	1	21	4.149	0.668	1.672	3.559
BAN1	23	8.26	7	7.04	1	25	6.398	0.774	1.190	0.516
BAN2	28	6.79	5	5.72	1	24	5.600	0.825	1.593	2.072
BAN3	34	5.59	5.5	5.01	1	13	3.431	0.612	0.393	-0.961
BAN4	40	4.75	4	4.11	1	17	3.455	0.727	1.297	2.000
BAN5	21	8.00	8	7.26	1	24	4.980	0.622	1.324	2.898
BON	19	9.16	7	7.69	2	38	8.308	0.907	2.206	5.244
BER	29	6.00	5	5.01	1	21	5.007	0.835	1.589	2.341
BKM	66	2.98	3	2.64	1	15	2.557	0.857	3.020	10.526
GLR	43	4.51	4	4.12	1	18	3.232	0.716	2.147	5.482
LNG	7	12.29	13	10.38	1	31	9.358	0.762	0.995	0.043
MKP	55	3.47	3	3.09	1	10	2.218	0.639	0.596	-0.266
CCA	56	3.45	3	3.18	1	11	2.165	0.628	1.298	1.504
LMF	71	2.51	2	2.27	1	12	1.889	0.753	2.596	8.903
WAC	50	3.72	3.5	3.50	1	10	2.080	0.559	0.986	0.703
SCI	34	4.85	3	3.98	1	21	4.900	1.010	2.229	3.973
FST	31	5.90	5	5.23	2	19	4.460	0.755	1.412	1.091
FSR	31	5.52	3	4.65	1	23	4.891	0.887	1.953	3.789
ICE	24	7.38	5	5.89	1	33	7.829	1.062	2.344	4.604
LDG	16	11.25	12	10.64	2	23	5.756	0.512	0.213	-0.722
NAR	30	6.27	3	4.47	1	34	7.465	1.191	2.180	4.571
SSD	24	4.54	4	4.18	1	9	2.484	0.547	0.086	-1.139
UFW	59	2.93	2	2.61	1	15	2.399	0.818	2.801	9.990
CMP	27	6.82	5	5.75	1	23	5.299	0.778	1.335	1.540
PET	31	6.10	4	5.24	1	22	4.686	0.769	1.455	2.175
RIN	65	2.95	3	2.67	1	9	1.940	0.657	1.067	0.673
CHS	71	2.62	2	2.14	1	13	2.669	1.019	2.398	5.523
LPK	28	6.60	6	6.03	1	17	4.080	0.582	0.554	-0.570
CAT	36	5.50	5	5.26	1	15	2.923	0.531	1.315	2.095
JSS	29	6.59	5	6.26	2	18	3.756	0.570	1.254	0.953
SAJ	55	4.04	3	3.79	1	22	3.050	0.464	0.565	0.075
THC	68	2.94	2	2.52	1	9	2.304	0.783	1.235	0.633
ZUN	29	5.86	5	4.84	1	17	4.478	0.764	0.821	-0.232

Table 3.—Listing of fire interval statistics for 63 Southwestern fire-scar chronologies. Fire dates were based on fires recorded by 10% or more of sampled trees within each site, AD 1700 to 1900.

Fire Intervals (years)—Fire Scar Dates Recorded by 10% or More of Sampled Trees										
Site Code	No. of Intervals	Mean	Median	WMPI	Minimum	Maximum	Standard Deviation	Coeff. of Variation	Skewness	Kurtosis
ANP2	12	14.33	14	12.66	2	32	9.267	0.647	0.343	-1.058
ANP1	14	14.14	9	11.92	3	36	11.114	0.786	0.764	-0.867
BFL	37	4.13	3	3.37	1	22	4.650	1.124	3.097	9.171
RHY3	20	8.75	9	8.03	1	17	4.610	0.527	-0.004	-0.841
RHY2	12	15.25	13	14.20	4	50	11.419	0.749	2.446	4.897
RHY1	14	12.64	12.5	12.21	4	31	6.675	0.528	1.364	1.793
CHU	23	7.22	4	5.30	1	41	8.733	1.210	2.695	7.464
CBE	25	7.08	7	6.87	2	13	3.095	0.437	-0.016	-1.006
CBN	31	6.19	5	5.89	2	13	3.240	0.523	0.603	-0.695
CER	14	12.64	10.5	10.13	3	43	11.256	0.890	1.333	1.339
CAL	7	21.86	17	20.81	8	37	12.116	0.554	0.184	-1.882
KIP	4	36.25	26	33.57	17	76	27.439	0.757	0.815	-1.399
HFL	12	13.58	13	12.14	2	31	8.681	0.639	0.466	-0.786
LAM	19	10.37	9	10.00	4	21	5.134	0.495	0.627	-0.654
LWN	14	14.07	13	13.02	3	30	8.471	0.602	0.669	-0.611
MES	14	13.64	13.5	13.14	4	24	6.404	0.469	-0.041	-1.237
GUA	20	8.75	6.00	7.218	1	26	7.085	0.810	0.987	-0.062
CME	7	24.29	20	23.85	13	46	11.842	0.488	0.808	-0.819
CMN	2	16.00	—	16.00	14	18	2.828	0.177	0.000	-2.500
CAN	4	23.00	23	23.32	14	32	7.528	0.327	0.000	-1.635
CAS	8	23.00	23	23.13	13	33	7.672	0.334	0.000	-1.606
CPM	12	14.00	12.5	13.06	3	29	7.909	0.565	0.404	-0.960
CPU	11	14.27	10	13.90	6	24	6.665	0.467	0.166	-1.790
CPE	7	22.57	21	20.35	4	50	15.054	0.667	0.637	-0.670
CCC	19	8.26	6	6.97	1	24	6.154	0.745	0.891	0.072
CON	16	11.94	6.5	7.74	2	48	15.013	1.258	1.618	1.105
GAM	25	7.80	8	7.36	1	15	3.979	0.510	0.243	-0.980
LOG	7	26.14	25	25.82	10	45	11.379	0.435	0.264	-1.000
MCN	29	6.48	6	6.40	2	12	2.572	0.397	0.291	-0.767
PMN	5	15.60	14	14.93	4	25	8.019	0.514	-0.282	-1.381
PMR	20	8.30	7.5	7.72	1	21	4.846	0.584	0.905	0.417
BAN1	13	14.08	12	12.52	2	25	8.539	0.607	-0.037	-1.665
BAN2	18	10.22	9.5	9.46	1	24	5.897	0.577	0.728	-0.062
BAN3	26	7.31	7.5	6.60	1	23	4.541	0.621	1.330	3.337
BAN4	26	7.31	6	6.28	1	23	5.312	0.727	1.285	1.523
BAN5	12	8.00	8	8.01	4	12	2.730	0.341	-0.080	-1.472
BON	10	17.40	15	15.98	2	38	10.265	0.590	0.565	-0.438
BER	10	16.30	11.5	14.46	2	32	10.904	0.669	0.446	-1.465
BKM	34	5.79	3.5	4.98	1	20	4.471	0.772	1.316	1.336
GLR	19	8.26	5	7.21	3	28	6.822	0.826	1.564	1.519
LNG	37	5.05	4.00	4.483	1	22	3.822	0.756	2.409	8.207
MKP	23	6.30	5	5.52	1	16	4.237	0.672	0.764	-0.167
CCA	26	7.08	7	6.77	1	14	3.346	0.473	0.061	-0.989
LMF	37	4.05	3	3.63	1	13	2.798	0.690	1.276	1.360
WAC	40	4.53	4	4.23	1	12	2.532	0.559	0.900	0.755
SCI	17	9.71	8	8.78	2	23	6.243	0.643	0.630	-0.825
FST	17	10.06	7	8.68	2	23	7.293	0.725	0.585	-1.200
FSR	11	13.73	13	13.55	4	23	5.569	0.406	0.048	-0.942
ICE	7	24.43	27	23.84	7	35	10.768	0.441	-0.469	-1.427
LDG	7	19.43	21	19.68	12	27	5.350	0.275	-0.205	-1.328
NAR	12	10.25	8	9.46	3	21	6.538	0.638	0.733	-1.104
SSD	5	18.80	20	18.66	9	27	8.106	0.431	-0.155	-1.924
UFW	43	4.02	3	3.38	1	23	4.132	1.027	3.022	9.660
CMP	27	8.52	8	7.73	2	23	5.600	0.672	0.818	-0.172
PET	20	9.45	8.5	8.91	3	22	5.296	0.560	0.753	-0.236
RIN	31	6.13	6	6.02	2	13	2.668	0.435	0.873	0.165
CHS	16	7.12	5.5	6.41	1	18	4.674	0.656	0.790	-0.282
LPK	23	8.61	9	7.94	2	17	4.793	0.557	0.061	-1.463
CAT	27	7.33	6	7.01	2	16	3.803	0.519	0.695	-0.451
JSS	21	8.24	7	7.94	3	21	4.242	0.515	1.167	1.593
SAJ	35	5.54	4	5.14	2	22	3.910	0.487	0.553	-0.704
THC	19	9.68	8	8.31	1	24	6.969	0.720	0.703	-0.769
ZUN	5	28.00	21	20.21	1	61	22.847	0.816	0.340	-1.400

Table 4.—Listing of fire interval statistics for 63 Southwestern fire—scar chronologies. Fire dates were based on fires recorded by 25% or more of sampled trees within each site, AD 1700 to 1900.

Fire Intervals (years)—Fire Scar Dates Recorded by 25% or More of Sampled Trees

Site Code	No. of Intervals	Mean	Median	WMPI	Minimum	Maximum	Standard Deviation	Coeff. of Variation	Skewness	Kurtosis
ANP2	7	24.57	22	22.82	4	46	13.710	0.558	0.075	-1.080
ANP1	12	16.50	12.5	14.65	4	41	11.767	0.713	0.808	-0.642
BFL	37	4.13	3	3.37	3	28	4.650	1.124	3.097	9.171
RHY3	19	9.21	10	8.77	4	25	4.354	0.473	-0.009	-0.756
RHY2	10	17.90	14.5	17.08	9	50	11.855	0.662	2.125	3.031
RHY1	13	13.08	13	12.67	4	31	6.739	0.515	1.291	1.600
CHU	10	9.30	10	8.31	4	16	6.019	0.647	0.286	-1.269
CBE	22	8.04	8.5	7.76	1	22	3.860	0.480	0.457	-0.529
CBN	28	6.79	6	6.57	4	40	3.178	0.468	0.417	-0.942
CER	14	12.64	10.5	10.13	2	48	11.256	0.890	1.333	1.339
CAL	7	21.86	17	20.81	10	41	12.116	0.554	0.184	-1.882
KIP	4	36.25	26	33.57	14	25	27.439	0.757	0.815	-1.399
HFL	10	16.30	17	15.91	8	37	7.558	0.464	0.422	-0.614
LAM	17	11.59	11	11.04	13	33	5.864	0.506	0.146	-1.444
LWN	10	15.80	15	15.70	2	16	6.443	0.408	0.800	0.182
MES	11	17.36	15	17.01	2	17	8.262	0.476	0.937	-0.189
GUA	5	27.40	22	25.04	2	13	22.018	0.804	1.209	-0.552
CME	7	24.29	20	23.85	10	53	11.842	0.488	0.808	-0.819
CMN	2	16.00	16	—	7	29	2.828	0.177	0.000	-2.500
CAN	3	20.00	21	20.42	3	34	5.568	0.278	-0.261	-2.000
CAS	8	23.00	23	23.13	7	35	7.672	0.334	0.000	-1.606
CPM	11	15.27	13	14.98	14	18	7.058	0.462	0.642	-1.019
CPU	11	14.27	10	13.90	13	46	6.665	0.467	0.166	-1.790
CPE	5	31.60	23	29.82	4	23	18.902	0.598	0.164	-1.911
CCC	11	13.18	13	12.64	2	64	6.954	0.528	0.593	-0.891
CON	9	17.22	9	10.60	6	24	22.543	1.309	1.305	-0.170
GAM	15	11.27	12	11.29	2	23	3.788	0.336	0.148	-0.700
LOG	7	26.14	25	25.82	5	19	11.379	0.435	0.264	-1.000
MCN	20	9.40	8	8.97	3	28	5.103	0.543	0.846	-0.598
PMN	4	19.50	19.5	19.86	12	66	4.655	0.239	0.000	-1.693
PMR	13	12.77	12	12.32	5	31	6.470	0.507	0.682	-0.375
BAN1	9	17.11	20	16.16	3	42	8.623	0.504	-0.263	-1.459
BAN2	16	11.50	10	11.05	5	25	6.240	0.543	1.235	0.916
BAN3	18	10.22	9	8.91	3	43	6.603	0.646	0.561	-0.561
BAN4	15	12.67	11	12.03	1	18	6.715	0.530	0.391	-1.128
BAN5	10	9.60	8.5	9.51	2	20	3.921	0.408	0.278	-1.113
BON	7	19.00	15	16.32	3	30	14.468	0.761	1.027	0.035
BER	7	23.29	19	22.75	17	76	11.280	0.484	0.333	-1.459
BKM	15	13.13	10	12.09	4	21	9.133	0.695	1.691	2.579
GLR	18	8.72	5.5	7.71	12	27	6.841	0.784	1.474	1.285
LNG	21	8.38	7	7.59	1	15	6.029	0.719	1.540	1.646
MKP	21	6.91	6	6.40	2	26	4.024	0.583	0.779	-0.089
CCA	17	10.82	8	9.51	10	45	9.416	0.870	2.257	4.731
LMF	28	5.36	5	5.03	2	24	3.200	0.597	1.418	1.797
WAC	23	7.65	6	6.85	7	30	5.581	0.729	1.547	1.700
SCI	17	9.71	8	8.78	14	25	6.243	0.643	0.630	-0.825
FST	17	10.06	7	8.68	7	35	7.293	0.725	0.585	-1.200
FSR	11	13.73	13	13.55	3	20	5.569	0.406	0.048	-0.942
ICE	7	24.43	27	23.84	1	16	10.768	0.441	-0.469	-1.427
LDG	7	19.43	21	19.68	3	21	5.350	0.275	-0.205	-1.328
NAR	12	10.25	8	9.46	3	22	6.538	0.638	0.733	-1.104
SSD	5	18.80	20	18.66	5	27	8.106	0.431	-0.155	-1.924
UFW	22	7.77	5	7.01	4	31	5.673	0.730	1.368	0.722
CMP	12	12.67	12	11.45	9	50	8.773	0.693	1.164	0.643
PET	15	12.60	12	12.35	3	22	5.248	0.417	0.033	-0.639
RIN	25	7.32	7	7.12	2	13	3.288	0.449	0.307	-1.175
CHS	16	7.12	5.5	6.41	2	22	4.674	0.656	0.790	-0.282
LPK	19	10.42	12	9.65	2	23	5.719	0.549	0.314	-0.303
CAT	27	7.33	6	7.01	2	16	3.803	0.519	0.695	-0.451
JSS	18	9.61	10	9.08	3	30	6.001	0.624	2.079	5.072
SAJ	25	5.88	5	5.47	2	22	4.050	0.582	1.774	3.668
THC	12	14.75	15	13.65	1	24	7.956	0.539	0.099	-0.853
ZUN	5	28.00	21	20.21	1	61	22.847	0.816	0.340	-1.400

Drought—Fire Relations

As we have observed in compilations of smaller sets of fire-scar chronologies from the Southwest (e.g., Swetnam 1990; Swetnam and Betancourt 1990; 1992) there was a remarkable synchrony of fire events across the region during the pre-settlement era (Figure 5). The maximum number of sites recording fires among the 63 sites was 41 in the year 1748. The next largest regional fire year was 1851 with 37 of the sites recording fires during that year (Figure 5). Overall, the regional fire occurrence times series from 1700 to 1900 shows a pattern of about 20 large regional fire years (more than 19 sites) occurring against a background of smaller fire years. An obvious decline in numbers of sites (Figure 5) around 1900 reflects the region-wide onset of intensive livestock grazing beginning in the late 1800s followed by the beginning of organized fire suppression efforts during the first decades of the twentieth century (Swetnam 1990; Touchan et al. This Volume).

The synchrony of large fire years and small fire years, as measured by the largest and smallest numbers of sites recording fires (Figure 5) is probably related to regional-scale year-to-year climatic oscillations. Climate is the only factor operating over such a large area that could produce such a consistent pattern. Obviously, human influences on fire occurrence, such as the fire decline since the late 1800s, were also important, but it is highly unlikely that Native Americans, for example, purposely synchronized the year-to-year timing of their burning practices in dozens of different mountain ranges over the Southwest. We will return to the issue of the importance of fires set by Native Americans versus lightning in the discussion section.

Both the overlay of large and small fire years on the PDSI time series (Figure 6) and the SEA (Figure 7) reveal that important current year and lagging relations existed between fire occurrence and climate. This pattern is fairly consistent in both the

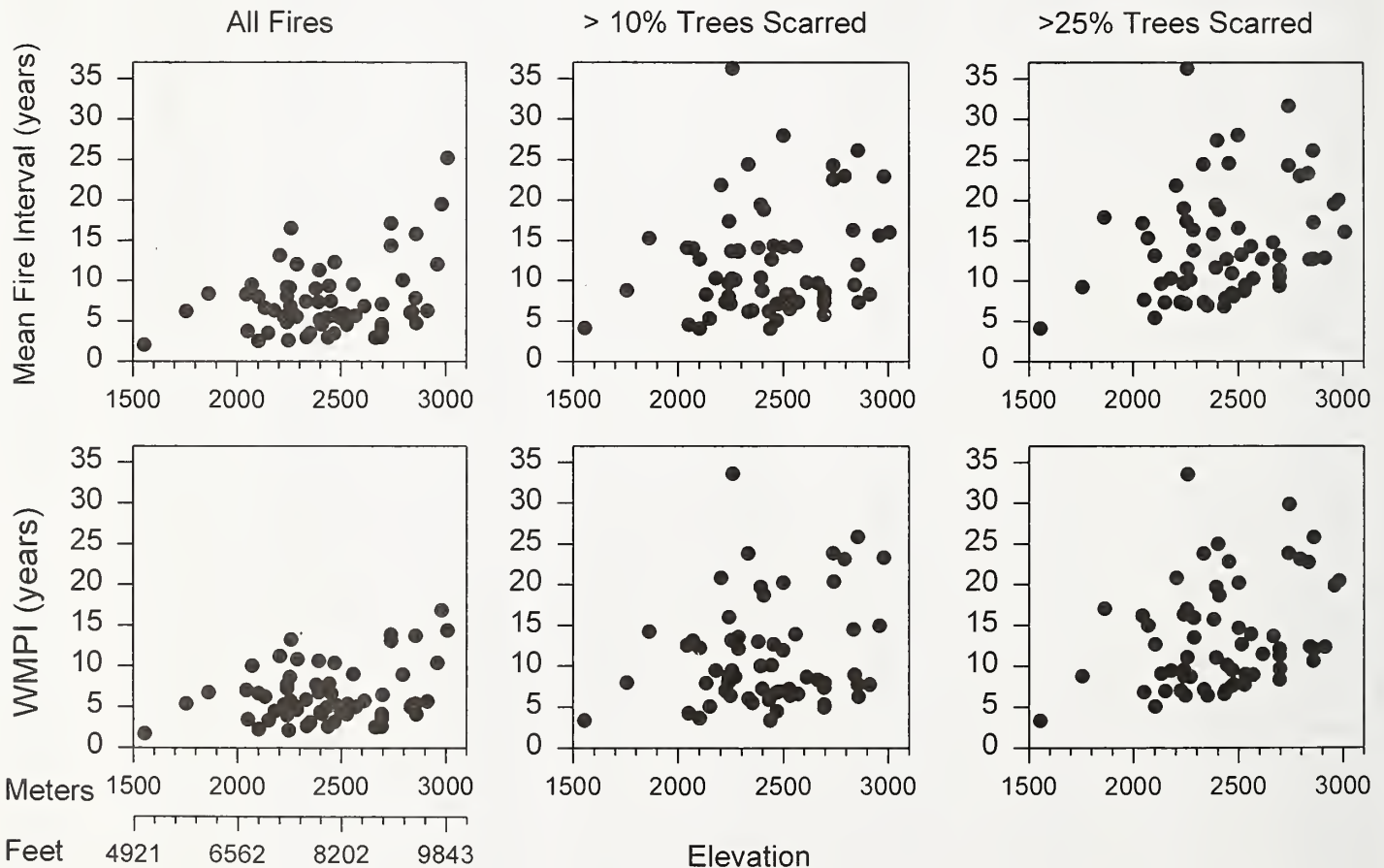


Figure 3.—Measures of central tendency of fire interval distributions - mean fire interval and Weibull median probability interval - versus elevation among the 63 fire history sites. The fire interval estimates were based on three sortings: (1) fires recorded by any number or percentage of trees within sites (All Fires), (2) fires recorded by at least two trees and ten percent or more of the sampled trees within sites, and (3) fires recorded by at least two trees and twenty five percent or more of the trees within the sites.

fire-scar record (pre-1900) and the area burned record from National Forests (post 1920) (Figure 6 and 7). There was a striking correspondence between severe drought years and the largest fire years, especially in the fire-scar record (Figure 6). There was a somewhat less consistent correspondence between the smallest fire years and wet years, particularly before about 1820 (Figure 6). Not all severe drought years were large regional fire years. A visual inspection of Figure 6 suggests that in many instances (particularly in the pre-1900 fire scar record) the largest fire years often followed within one to a few years an unusually wet year (or years) and/or one of the smallest fire years. For example, the largest fire year in the pre-1900 record—1748—was also one of the driest and it followed several very wet years (Figure 6).

The SEA statistically measures the average strength of these lagging relations among the set of largest and smallest fire years (Figure 7). The largest fire years (the 20 years with maximum numbers of sites recording fires) were typically very dry and the second and third years preceding these fire years were very wet (upper left plot Figure 7). The sorting of fire years by forest type demonstrates that this pattern was primarily driven by the fire-climate

relations in the ponderosa pine sites (middle right plot in Figure 7). In contrast, the largest fire years among the mixed-conifer sites were drier than the largest fire years among ponderosa pine sites, but preceding years had no consistent pattern (middle left plot in Figure 7). The smallest fire years among all sites were typically very wet and the years immediately preceding the smallest fire years were dry (upper right plot in Figure 7). A similar SEA of actual area burned per year on National Forests in the twentieth century shows that largest fire years were on average very dry, the smallest fire years were on average wet, and no significant wet or dry patterns preceded these years (Figures 6 and 7).

DISCUSSION

Fire Interval Variations

The large scatter of data points in the comparison of elevation and forest type versus WMPI or mean fire interval (Figures 3 and 4) suggests that a weak relationship may have existed between fire frequency (or interval distributions) and these fac-

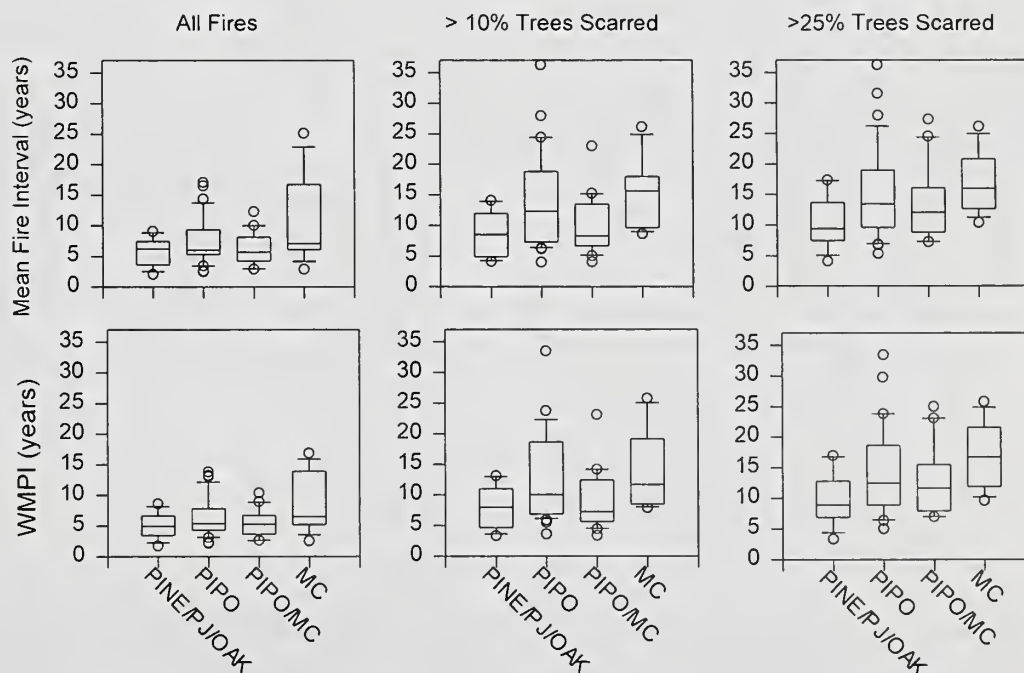


Figure 4.—Measures of central tendency and the variance of these measures sorted by forest type. See text for explanation of the types. The box plots show mean values as horizontal lines within the boxes, the upper and lower sides of the box are the 95% confidence levels, the horizontal lines at the ends of the vertical lines outside of the boxes are the 99% confidence levels, and the small circles above and below are the outliers beyond the 99% confidence levels.

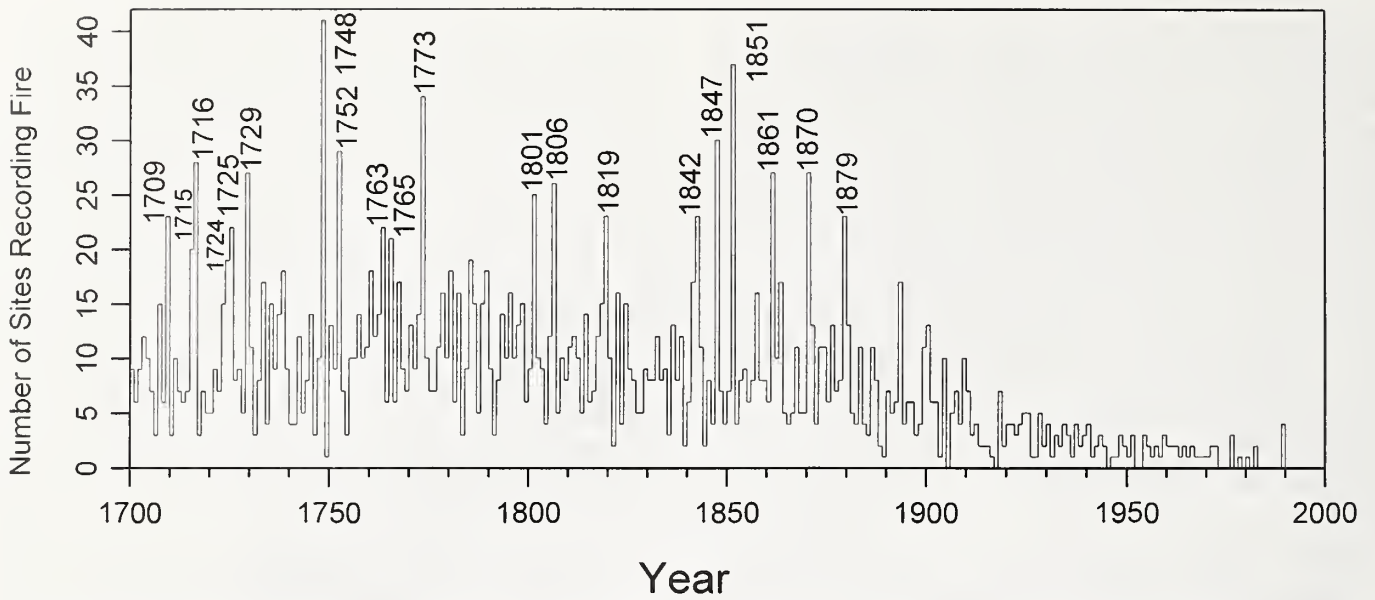


Figure 5. Regional fire occurrence time series from a network of 63 fire history sites in the Southwestern U.S. The largest 20 fire years are listed, based on the maximum numbers of sites recording these years.

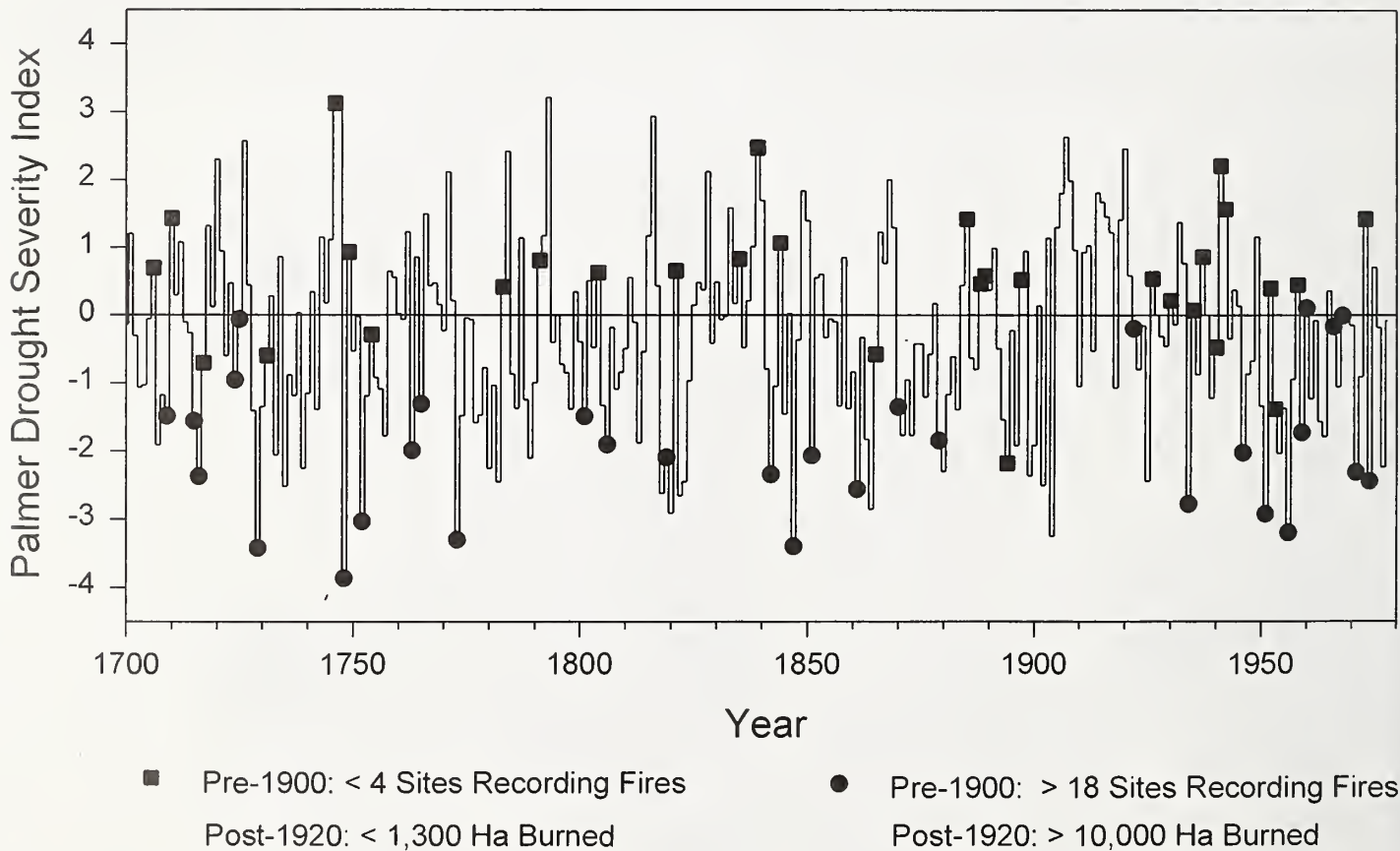


Figure 6. Palmer Drought Severity Index (PDSI) reconstruction (AD 1700 to 1978) for the Southwestern U.S. derived from tree-ring width chronologies (see text for explanation). The circles and squares show the largest and smallest fire years recorded by the regional fire-scar network (1700 to 1900, 20 years each) and the largest and smallest fire years recorded in the area burned per year record from all National Forest lands in the Southwest Region (1920 to 1978, 10 years each).

tors. This general pattern conformed to our initial expectations of longer intervals between fires in the higher, relatively mesic, mixed-conifer sites than in the lower, drier, ponderosa pine sites. However, because of the large scatter of the data points it must be recognized that associations observed here have little or no predictive power for specific sites. We have not yet proceeded with more sophisticated statistical tests and comparisons of these patterns because of various data limitations requiring more study. In particular, a probable cause of some of the variability observed in the fire interval statistics between sites of approximately the same elevation or forest type is the fact that the sampled sites encompassed (and represented) different size areas

and included different numbers of sampled trees. The problem is that as study area increases in size the estimated fire frequency for the entire sampled area is also likely to be higher (see Arno and Peterson 1981). Simply stated: larger areas were more likely to have been burned over at least partially by more fires. Number of trees sampled also affects fire frequency estimates if fires were relatively patchy within sites. Hence, some kind of statistical standardization of study area and sample size may be needed for a more rigorous comparison of fire interval distributions.

Differences in sampled areas among our sites was actually not very large — usually within an order of magnitude, ranging from about 10 ha to 100 ha (areas defined by a polygon with convex vertices determined by outermost sampled trees within sites, i.e., a “convex hull”). In many of our sites most fires were probably as large or larger than the sampled areas, as indicated by highly synchronous fire dates among sampled trees. In other cases, especially in the higher fire frequency sites, most fire dates were recorded by only one or a few trees. As previously pointed out, in these latter cases, sizes of the areas and numbers of trees sampled can have a more important effect on the estimated fire frequency. However, this effect might be small in terms of absolute values of estimated fire frequency because these values are approaching the limit of possible fire frequency anyway. For example, fire intervals based on all fire dates (Table 2) are about two to three years in the highest fire frequency sites. Expanded area or additional trees sampled in these stands could only increase these frequencies up to the maximum fire frequency we can estimate (and which may be ecologically possible), i.e., one fire each year.

A related problem is the estimation of the size of the area that is represented by a set of spatially dispersed fire-scarred trees. In some cases, very distinct fire barriers, such as cliffs or talus slopes, can help define the probable minimum boundaries of an area that the larger fires burned over. Fire spread simulation models (e.g., Finney 1994) also have potential for defining probable “firesheds” that would be useful in determining areas represented by spatial networks of sampled trees and sites. We are currently experimenting with various spatial statistics models involving tessellations, kriging, and distance measures that estimate *relative* areas that sampled fire-scarred trees might represent. Ultimately, we do not believe that these sampling problems are intractable. In fact, they offer the possibility of learning a great deal more

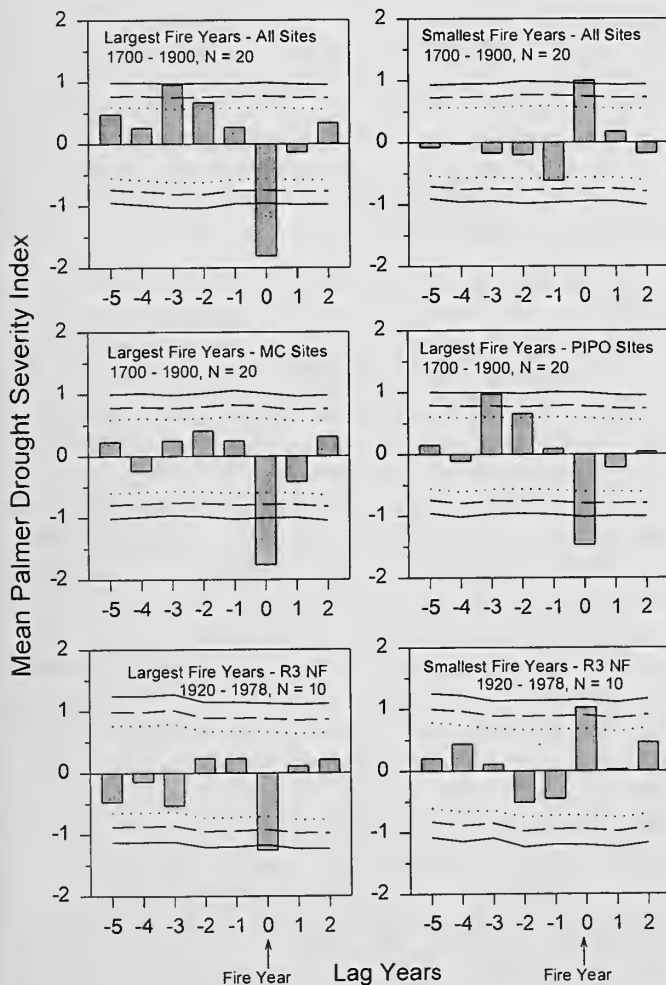


Figure 7. Results of superposed epoch analyses (SEA) using the PDSI reconstruction and sets of largest and smallest fire years recorded in the fire scar network (1700 to 1900) and in Forest Service documents of area burned per year on all National Forests in the Southwestern Region (1920 to 1978). The horizontal lines are confidence intervals (CL) estimated from a bootstrap simulation of 1000 trials of randomly selected sets of the same number of key dates. The dotted line is the 95% CL, the dashed line is the 99% CL and the solid line is the 99.9% CL.

about spatial patterns of past fires, as well as the limitations of paleo-fire reconstruction methods.

In addition to elevation and forest type, other landscape attributes were also important in controlling fire regime characteristics. For example, slope, aspect, and continuity (contiguity) with other landscape units can be very important, even to the extent of over-riding the importance of other factors (Swetnam et al. 1989; Grissino-Mayer and Swetnam, In Press; Grissino-Mayer et al., In Press; Touchan et al. This Volume). Similarly, land-use history can over-ride the importance of other landscape attributes. The onset or decline of intensive livestock grazing, and/or the initiation of organized fire suppression efforts usually resulted in the greatest single temporal change observed in most fire chronologies. These human influences were not all synchronous across the Southwest. For example, certain areas in northeastern Arizona and northern New Mexico were subject to intensive livestock grazing (especially by sheep and goats) at different times in the 18th and 19th centuries, resulting in complex temporal and spatial patterns of interrupted and resumed surface fire regimes. These patterns seem to correlate fairly well with establishments of land grants from the King of Spain to Hispanic colonists, initiation of intensive grazing, and hostilities between the colonists and Native Americans (Savage and Swetnam 1990; Touchan et al. In Press; Touchan et al., This Volume). The associations between patterns of historical livestock grazing, climatic variation, and fire occurrence all point to the importance of the production and moisture content of fine fuels (i.e., grasses, herbs, and tree needles) as key factors driving the pre-1900, surface fire regimes of the Southwest.

Fire Climatology

The patterns of association between drought and fire occurrence observed in the large network of fire histories (Figures 6 and 7) were also observed at smaller spatial scales (e.g., mountain ranges—see Baisan and Swetnam 1990, and Touchan et al. This Volume). Different responses of fire occurrence in pure ponderosa pine versus mixed-conifer, and consistency in these responses at different spatial scales (mountain ranges, and the region) strongly suggests that fuel types, amounts, and condition (e.g., moisture content) were key factors in this system. We hypothesize that the significant lagging relations in ponderosa pine reflects the *initial* importance of fine fuel production tied to

moisture levels in previous years (especially one to three years preceding large fire years). This mechanism apparently operated both through the production of higher fuel amounts during preceding wet years (upper left plot Figure 7) and in producing lower amounts of fuels in preceding dry years (upper right plot, Figure 7). This topic has not been studied in ponderosa pine forests, but similar patterns have been documented in lower elevations of southern Arizona (Rogers and Vint 1987). In the pre-settlement era grass production was probably very important to the spread of frequent fires through the open, park-like stands, but the interesting two to three-year lags that consistently show up in our analyses also suggest that tree needle production may also be important. Ponderosa pine typically holds needles on the branches for three to five years before they are abscised and fall to the forest floor. Hence, climatic oscillations on these time scales (e.g., the El Niño-Southern Oscillation) could be important mechanisms that synchronize fuel production, moisture content, and fire occurrence at large spatial scales (Swetnam and Betancourt 1990; 1992).

The lack of significant lagging relations in the mixed-conifer forests further supports the hypothesis that fuels and climate were primary controls of fire regimes. In these relatively high productivity, mesic forests with longer intervals between surface fires, it appears that *fuel amounts* were not limiting. Rather, it seems that *fuel moisture* was most important, as reflected in the very dry conditions that prevailed during the largest fire years (middle left plot Figure 6). Greater canopy cover in mixed-conifer than in ponderosa pine forests, because of greater shade tolerance of the dominant tree species, results in the snow pack persisting longer into the spring. Moreover, the shaded conditions limit the development grass cover, and the short needles of Douglas-fir and true firs tend to compact quickly on the forest floor. This results in a fuel substrate that is less conducive to fire spread than in the grassy understory and loose litter layer of long needles found in ponderosa pine forests. Needle retention is also longer in both Douglas-fir and true firs (five to seven years, or longer). The combination of these micro-environmental and fuel characteristics result in mixed-conifer fire regimes that were unresponsive to previous year's moisture levels and associated fuel productivity, and fires primarily occurred when conditions were very dry.

The twentieth century SEA confirmed the importance of drought conditions during largest fire years in National Forests, but not the importance of

preceding years (lower plots, Figure 7). These data, however, combine fire occurrence across a very broad range of forest, woodland, and grassland types in the Southwest and so important lagging relations might be obscured. It is also a fact that fire regimes and fuels across the Southwestern region have greatly changed in the twentieth century. The past one hundred or more years of grazing, fire suppression, logging, road building, recreation uses, etc. have directly altered fuel amounts and composition, ignition sources, and locations. Despite these changes, and the lack of patterns in the SEA documenting lagging patterns, recent fire patterns suggest that prior year's fuel production linked to wet years can be critically important determinants of year-to-year fire loads. The early 1990s are a case in point. An unusual El Niño event persisting for about two and a half years—starting in 1991 and lasting until 1993—resulted in excellent grass production across much of the Southwestern Region. Regional fire occurrence was relatively low during the El Niño years, then dry summer conditions in 1994 led to numerous very large wildfires, especially in southern Arizona and New Mexico.

The Role of Humans in Pre-Settlement Southwestern Fire Regimes

When discussing historical fire regimes it is necessary to point out that fire occurrence patterns were probably influenced to some degree by the intentional and un-intentional burning practices of Native Americans (see the Pinchot quote at the beginning of this paper). The fact that Native Americans did set fire to the Southwestern landscape is well established (Dobyns 1978; Pyne 1982; Bahre 1991). However, we question the implicit or explicit assertion that the use of fire by Native peoples was primarily controlling the dynamics of fire regimes in virtually all parts of North America or the Southwest. This is an over generalization.

In the first place, lightning strikes capable of igniting fires are far more prevalent than most people realize. The installation of lightning detection networks over the whole United States in recent decades clearly documents the fact that *hundreds or even thousands* of lightning strikes occur in single storms passing over mountain ranges. The Southwest has one of the highest incidences of lightning strikes, and the highest rate of lightning ignited fires in the U. S. (Schroeder and Buck 1970:168). The important question is: Were there enough lightning ignitions to account for the fire

frequencies that we document in the fire scar record? We believe that in *most cases* there are currently, and there were historically, enough lightning ignitions to produce the fire frequencies we estimate from fire-scar chronologies. This is based on a simple accounting of the rates of successful lightning fire ignitions within our mountain ranges today, as well as the fact that these fires, if not suppressed, would have had the opportunity to burn un-hindered for several months, thus spreading over enormous areas. In fact, the historical record (e.g., newspaper articles) contains many accounts of fires burning millions of acres in the Southwest during particular years (see Bahre 1985).

The data and results we have presented in this paper and elsewhere also support the hypothesis that fuel and climate were primary driving and regulating forces in pre-settlement fire regimes. It is likely that Native Americans set some of the fires that are documented in our fire-scar records, but these fires would not have burned over large areas if the fuels had not been present, and in the condition (e.g., moisture content) necessary for spread. Fundamentally, we argue that ignition sources (or amount of ignitions) were usually not limiting—*fuels and related climatic conditions were*. Hence, it is unnecessary in most cases to invoke human-set fires as an explanation or cause of fire regime patterns in the Southwest. We contend that, even if humans had never crossed the land bridge from Asia to North America, historical fire regimes in most Southwestern forests would still have been similar in most respects to the fire regimes that we have documented.

Now, having made a rather broad generalization of our own, a caveat is in order. We have in a several instances observed unusually high fire frequencies during some time periods in sites that were isolated topographically, so that spread of fires from outside of these areas had a low probability (unpublished data). Infrequent lightning ignitions in the twentieth century within these sites suggest that lightning probably could not account for the frequencies we documented. Furthermore, comparison with climatic data (e.g., SEA) indicated that fire-climate relations were weak or non-existent in these cases. Hence, supplemental fire ignitions by people is a reasonable explanation. The point here is that we do not deny the fact that people strongly influenced fire regimes in *some places and some periods*, but we emphasize that the role and importance of Native Americans in pre-settlement fire regimes of the Southwest were *very site and time specific*, and not ubiquitous.

CONCLUSIONS

Pre-1900 fire regimes of the Southwestern U.S. varied greatly in time and space. Some patterns of fire regime variation were evident across gradients of elevation and forest type, such as a decrease in frequency from low to high elevations and from drier ponderosa pine to wetter mixed-conifer forests. Additional study is needed, however, because fire history reconstructions come from areas of different size and are based on variable sample sizes, which could importantly affect inter-site statistical comparisons. Additional fire history reconstructions are also needed from lower and higher elevation forests and woodlands. For example, we have very little knowledge of fire regime patterns in pinyon-juniper and pine-oak woodlands and their ecotones with grasslands below and pine forests above. Similarly, we have limited fire chronology data from higher elevation mixed-conifer forests, and virtually none from spruce-fir forests. Fire history collections obtained systematically across the full span of the elevation gradient would be useful for evaluating inter-site (type) variations as well as historical fire spread patterns and relative fire extent across the landscape (Caprio and Swetnam, In Press).

Although elevation and forest cover type may ultimately explain more of the variance in fire frequency patterns than is evident in our current data sets, we expect that other landscape attributes (e.g., slope, aspect, landscape connectivity, etc.) will have greater or lesser importance in different instances. We believe this calls for a spatial modeling approach that makes use of historical fire occurrence data to "parameterize" the varying importance of multiple factors. Such a model could be used to map past and potential fire regime patterns across landscapes. Geographic information systems are logical tools to use in such a modeling effort. Even though such models will be very useful in assessing the role and importance of fire in ecosystem dynamics, we must remember that past fire regimes were linked to partially or totally unpredictable climatic patterns and human interventions. Thus, statistics that summarize general fire regime properties (i.e., mean fire interval, WMPI, etc.), or models that attempt to simulate fire regimes and forest structures based on statistics or mechanisms, cannot fully substitute for the historical record in terms of the explanatory power of *knowing what actually happened* within individual sites. This knowledge provides direct explanation and understanding of *how* and *why* past and current forest structures developed.

Finally, our data demonstrate that climatic variations, specifically drought fluctuations, were important in determining temporal and spatial patterns of fire occurrence across time scales of years to centuries and spatial scales from forest stands to the region. Climatic variation (yearly to longer time scales) is extremely complex and therefore difficult to predict. On the other hand, the El Niño-Southern Oscillation (ENSO), which has been called the single strongest control of global inter-annual climate variation, is currently being forecast several seasons in advance with fairly good skill by models and observations (Barnett et al. 1988; Ropelewski 1992). The linkage between ENSO, other climatic variations, and fire is at least partly through the production of fuels *preceding* fire seasons. Thus, the oscillatory and persistent behaviors of both the climate system and the bio-physical system of fire and fuels indicates that development of predictive fire hazard models operating at time scales of seasons to years should be attempted using new knowledge and modeling capabilities that are now available.

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Fire History and Climatic Patterns in Ponderosa Pine and Mixed-Conifer Forests of the Jemez Mountains, Northern New Mexico

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Abstract.—We reconstructed fire history in ponderosa pine and mixed-conifer forests across the Jemez Mountains in northern New Mexico. We collected fire-scarred samples from ten ponderosa pine areas, and three mesic mixed-conifer areas. Prior to 1900, ponderosa pine forests were characterized by high frequency, low intensity surface fire regimes. The mixed-conifer stands sustained somewhat less frequent surface fires, along with patchy crown fires. We also examined the associations between past fires and winter-spring precipitation. In both ponderosa pine and mixed-conifer forests, precipitation was significantly reduced in the winter-spring period immediately prior to fire occurrence. In addition, winter-spring precipitation during the second year preceding major fire years in the ponderosa pine forest was significantly increased. The results of this study provide baseline knowledge concerning the ecological role of fire in ponderosa pine and mixed-conifer forests. This information is vital to support ongoing ecosystem management efforts in the Jemez Mountains.

INTRODUCTION

Fire has played a dominant role in controlling the formation and maintenance of species and age structure patterns in forest communities (Weaver 1951; Dieterich 1983; Baisan and Swetnam 1990). In order to understand the modern landscape and to manage it effectively, fire managers require specific information about the spatial and temporal variability of past fire regimes (Allen 1994). Historical reconstructions, such as fire history analysis, provide specific information on the range and variability of the fire process, which can be a useful guide to reintroduction of fire for long-term sustainability of forests (Swanson *et al.* 1993; Kaufmann *et al.* 1994).

During the past century, the ecology of Southwestern forests, including the Jemez Mountains in northern New Mexico, has been altered by anthropogenic factors. Anthropogenic effects include intensive grazing by sheep and cattle and effective

fire suppression by the U.S. Forest Service (deBuys 1985; Carlson 1969; Allen 1989; Touchan *et al.* - in press). Natural factors also have an effect on fire regimes. On a regional scale, climate causes variations in fire regimes because it has a significant influence on fire frequency, extent, and intensity. On a local scale, topography, aspect, and elevation have site specific influences on fire regimes.

In this study we investigate the past fire regimes of ponderosa pine and mixed-conifer forest types in the Jemez Mountains. We employ dendrochronological methods to determine exact fire dates and approximate establishment dates of aspen stands. We assess and discuss the influence of land-

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use and topography on observed fire regime patterns. We also identify year-to-year climatic variations associated with fire occurrence in each forest type by comparing tree-ring reconstructions of fire history and climatic variations (Baisan and Swetnam 1990; Swetnam and Betancourt 1990; Swetnam 1993).

STUDY AREA

The Jemez Mountains are located in north-central New Mexico (Figure 1). Elevations range from

1,590 m at the Rio Grande to 3,526 m at the summit of Tschicoma Peak (the highest point in the Jemez Mountains), with a geologic boundary enclosing about 543,522 ha (Smith *et al* 1976). The elevation of the sampled area varies between 2,250 m and 3,000 m (Table 1). Soil parent material varies from rhyolites and andesites with some dacites and latites, to tuff and pumice on the plateaus and basalt near the Rio Grande (Nyhan *et al* 1978).

The length of the frost-free growing season in Los Alamos is 157 days, or around five months (Bowen 1989). July is the warmest month at Los

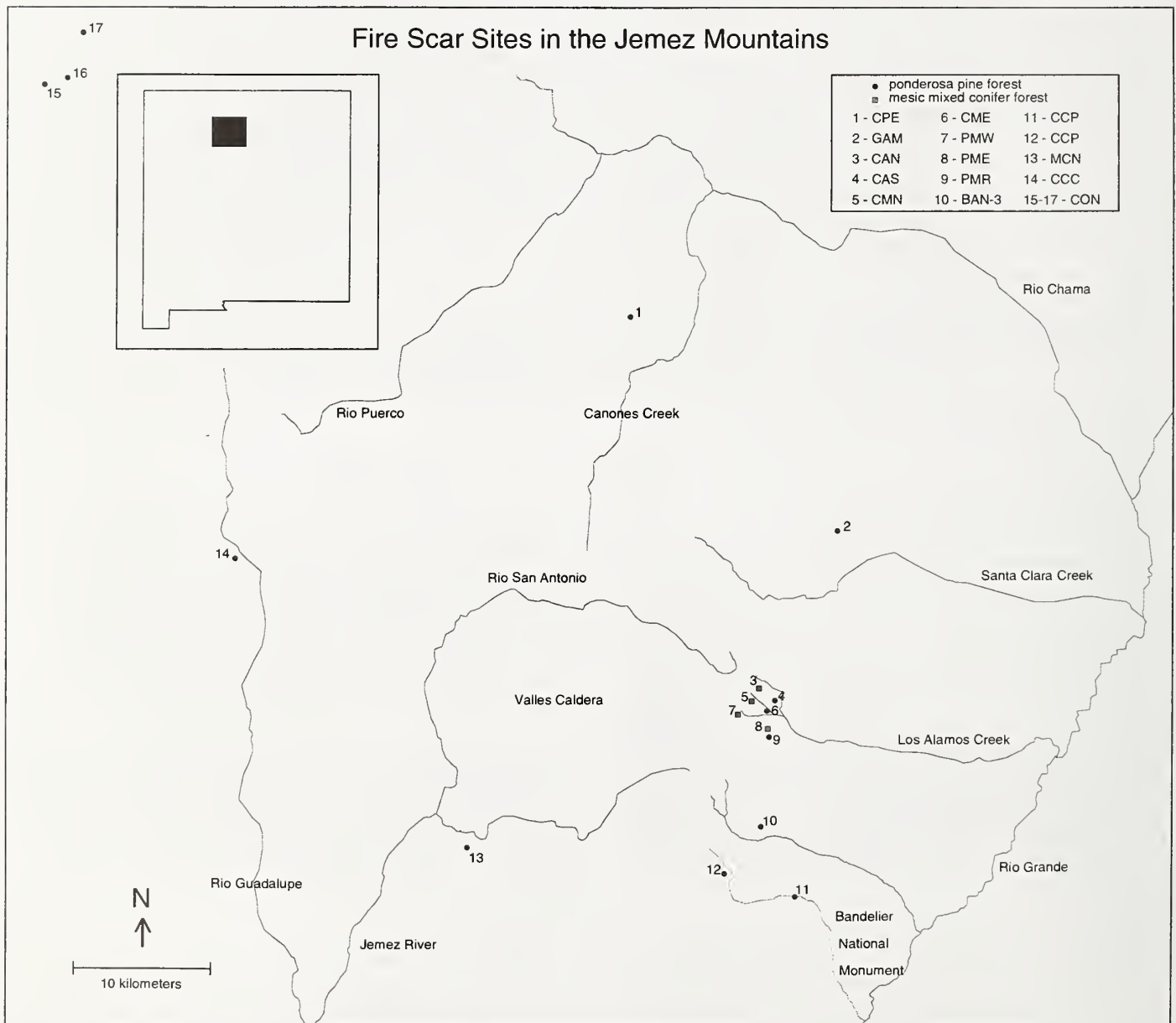


Figure 1. Locations of fire history study sites in the Jemez Mountains, northern New Mexico.

Alamos, with a mean temperature of 28° C, and January is the coldest month, with a mean temperature of -1.6° C. Annual precipitation ranges from about 30 cm at the lower elevations to about 90 cm at higher elevations. Yearly precipitation is bimodal, with maxima in winter (December-January) and summer (July-August). Winter precipitation falls primarily as snow, with average accumulations of about 130 cm. This moisture has its origin in eastern-moving storms coming from the Pacific Ocean. Summer precipitation results from a southeasterly wind pattern that typically transports moisture from the Gulf of Mexico to New Mexico. This moisture, combined with strong heating, produces an unstable atmosphere that leads to convective storms. Forty percent of the total annual precipitation falls in July and August during the height of the summer rainy season.

In a summary of forest fire statistics for the period 1960 to 1975, Barrows (1978) found that 80% of New Mexico fires were ignited by lightning, and about 20% were anthropogenic fires. Foxx and Potter (1978) and Allen (1984) found that 86% of the fires recorded at Bandelier were ignited by lightning, with a peak in July and smaller peaks in June

and August. Generally all local fires occurred between April and September. Barrows (1978) found that this seasonal pattern of ignitions occurred throughout the Southwest, but fires that start in June cause the greatest area burned. For example, approximately 72% of the area burned in New Mexico was due to lightning fires which started in June.

Sampled forests range from pure ponderosa pine (*Pinus ponderosa*) stands to high elevation, mesic, mixed-conifer forests (Table 1, Figure 1). Six of the sampled sites occur in ponderosa pine forests, including Monument Canyon Research Natural Area (MCN), Bandelier-Group 3 (Ban-GR3), Pajarito Mountain Ridge (PMR), Cerro Pedernal (CPE), Continental Divide (CON), and Clear Creek Campground (CCC). CON includes three adjacent subsites called Laguna Jaquez (LJA), Laguna Gurule (LGU), and Continental Divide (CON). The sampled mixed-conifer forests are dominated by Douglas-fir (*Pseudotsuga menziesii*), Englemann spruce (*Picea engelmannii*), and quaking aspen (*Populus tremuloides*), with Rocky Mountain maple (*Acer glabrum* var. *neomexicana*) and either white fir (*Abies concolor*) or corkbark fir (*Abies lasiocarpa* var.

Table 1. Jemez Mountains fire scar site locations. The area of each study site was estimated within a perimeter of an area defined by the sampled trees. Sites are listed by forest type (PIPO = ponderosa pine, PIPO/MC = ponderosa pine/mixed conifer, and MC = mixed conifer).

Name of site	Ranger District/Park	Latitude	Longitude	Veg. type	Area (ha)	Elevation (m)	No. of samples
Monument Canyon Natural Area	Jemez RD	35° 48' 12" N	106° 37' 3" W	PIPO	259	2,600	30
Ban-Group 3 (Apache Mesa)	Bandelier NM	35° 49' 20" N	106° 23' W	PIPO	110	2,510	18
Pajarito Mountain Ridge	Española RD	35°53'04"N	106° 22' 49" W	PIPO	3.5	2,985	26
Cerro Pedernal	Coyote RD	36°9'43"N	106°30'12"W	PIPO	16	2,865	26
Continental Divide	Cuba RD	36° 18' 42" N	106° 57' 30" W	PIPO	27	2,300	27
Clear Creek Campground	Cuba RD	36° N	106° 49' 4" W	PIPO	130	2,500	20
Capulin Canyon	Bandelier NM	35° 47' 12" N	106° 24' 2" W	PIPO/MC	103	2,250	23
Gallina Mesa	Espanola RD	36° 1' 26" N	106° 19' 42" W	PIPO/MC	285	2,700	25
Cañada Bonito South	Española RD	35°54'25"N	106°22'22"W	PIPO/MC	2	2,800	31
Camp May East	Española RD	35°54'N	106° 22' 57" W	PIPO/MC	1.3	2,710	6
Pajarito Mountain North East	Española RD	35° 53' 09" N	106° 22' 09" W	MC	7.6	2,925	14
Pajarito Mountain North West	Española RD	35°53'13"N	106°24'14"W	MC	7	3,000	11
Camp May North	Española RD	35°54'25"N	106°23'53"W	MC	8	3,000	20
Cañada Bonito North	Española RD	35°54'56"N	106°23'15"W	MC	4.8	2,980	28

arizonica) also present. The four mixed-conifer sample sites are Pajarito Mountain North (PMN), which includes two sub-sites called Pajarito Mountain East (PME) and Pajarito Mountain West (PMW), and Camp May North (CMN) and Cañada Bonito North (CAN). Four sites were sampled in transitional situations where mixed-conifer species like Douglas-fir and white fir were co-dominants with ponderosa pine: at Capulin Canyon (CCP), Gallina Mesa (GAM), Camp May East (CME), and Cañada Bonito South (CAS). At CME and CAS limber pine (*Pinus flexilis*) was also a dominant component of the forest. CCP includes two sub-sites, in the upper and middle reaches of the canyon, which are lumped in this treatment. These four PIPO/MC sites (Table 1) were analyzed as ponderosa pine sites.

METHODS

During 1988–1993, we collected fire-scarred samples from a total of 13 sites (including sub-sites) (Table 1). Full or partial cross-sections were cut with a chainsaw from fire-scarred boles of downed logs, snags, and stumps. Partial sections were also taken from living trees as described by Arno and Sneek 1977. The primary criterion for sample tree selection within study areas was the presence of a maximum number of well preserved scars showing evidence of fire by the number of healing ridges observed on the scarred surface ("cat face") (Dieterich and Swetnam 1984, Baisan and Swetnam 1990).

In addition to collecting fire-scarred samples in the mixed-conifer sites, we cored 202 quaking aspen since these trees often sprout abundantly after fire disturbance in mixed-conifer forests (Moir and Ludwig 1979). We sampled dominant and co-dominant aspen trees in aspen stands which were adjacent to the old-growth mixed-conifer stands which were sampled for fire scars. Hence, we determined both fire dates and tree recruitment dates to reconstruct fire and stand development histories.

In the laboratory, samples were fine-sanded and cross-dated using standard dendrochronological techniques (Stokes and Smiley 1968). In some cases, the aspen growth was very suppressed after 1979 because of a tent caterpillar outbreak that occurred in the early 1980's (Allen 1984). Because of this growth suppression the tree-rings on some cores were difficult or impossible to cross-date during this period. In these cases, the period from 1979 to 1993 was estimated by simple ring counts. If a particular core was near, but did not contain, the

pith, a pith locator (Applequist 1958) was used to estimate the pith dates.

All fire-scar dates from individual trees within each site were compiled into master chronologies in order to examine both temporal and spatial patterns of past fire occurrence. The FHX2 fire history analysis program was used to compute descriptive statistics (H. Grissino-Mayer - unpublished software documentation). These included fire frequency (number of fires per time period), fire-scar index ($[\text{number of trees scarred} / \text{Number of trees sampled}] \times 100$), Weibull median probability intervals (WMPI), maximum and minimum fire interval (Max. FI and Min. FI), and standard deviation (STD) of fire intervals. These statistics were computed separately for (1) all fire dates and (2) fires recorded by 10% or more of the sampled trees and (3) fires recorded by 25%. Because fire scarred trees are spatially dispersed within the sites, the =>10% and =>25% categories generally emphasize the relatively larger, more widespread fires within the sites.

The WMPI is calculated using the Weibull distribution, a very flexible distributional model that may be fitted to a variety of negatively and positively skewed distributions. The Weibull distribution often provides a superior fit to fire interval data than does the normal distribution (Johnson 1992; Baker 1992; Grissino-Mayer *et al.*, 1994). The WMPI is used here in addition to the Mean Fire Interval (MFI) because fire interval data are usually positively skewed (Baker 1992; Grissino-Mayer *et al.* 1994), Hence, simple averages (e.g. mean fire intervals) often provide a less robust estimate of the central tendency of the fire interval distribution. In this case, we report the fire interval associated with the 50% exceedance probability of the WMPI, which is the interval (in years) at which there was a 50% probability of fire intervals exceeding or being less than this interval (Grissino-Mayer *et al.* 1994).

Changes in fire frequency through time were graphically examined by computing and plotting moving-period fire frequencies. The moving periods were overlapping time periods of different lengths (51 and 21 years), during which the total number of recorded fires were summed. Each sequential value was the sum of fire events in the time period lagged one year forward from the previous period. The fire frequencies in these moving periods were plotted on the central-year of the period (i.e., 25th and 11th years respectively).

The computation of WMPI, Max. and Min. FI, and STD were based on a time span we termed the "period of reliability". This is the number that in-

cluded a minimum number of fire scar samples deemed sufficient to reliably estimate fire regime parameters. Generally this period included at least three to four samples recording the fire events (Table 2). This was a somewhat subjective determination, but given the degree of replication of fire dates among the sampled trees, and relatively small size of the study sites we are confident that these are reasonable time periods to confidently base our descriptive analyses.

Finally, we used superposed-epoch analyses (Baisan and Swetnam 1990; Swetnam and Betancourt 1990; Swetnam 1993) to compute the mean climate conditions before, during, and after sets of fire years in both the ponderosa pine and mixed-conifer forests. In this analysis, fire years were "superposed" on reconstructed precipitation. Precipitation values were obtained from a 333-year-long dendroclimatic reconstruction of December through June precipitation based on seven tree-ring width index chronologies developed from ponderosa pine that were collected from four dif-

ferent watersheds in northern New Mexico (Swetnam and Lynch 1993; Touchan and Swetnam, unpublished data). The winter-spring seasonal precipitation values used in this analyses are assigned to the calendar year corresponding with the spring months. Precipitation values (expressed as departures from the long term mean) are computed for the fire year and lagged years and then plotted. We conducted 1,000 Monte Carlo simulations to estimate confidence intervals for the mean departures at the 95% and 99% probability levels based on the normal approximation and percentile-rank methods (Mooney and Duval 1993).

RESULTS

Ponderosa Pine Fire Regimes

The fire-scarred samples in the ponderosa pine and transitional forests contained abundant and well preserved fire history records. We identified 1,858 fire events representing 221 separate fire

Table 2. Jemez Mountains fire scar dates. Period of reliability is the period when the number of samples was deemed sufficient to reliably estimate presuppression fire regime characteristics. Generally this was the period during which at least three or four samples recorded fire events. Sites are listed by forest types (PIPO = ponderosa pine, PIPO/MC = ponderosa pine/mixed conifer, and MC = mixed conifer).

Site name	Site code	Veg. type	Tree-ring date		Earliest fire-scar date	Latest fire-scar date	No. of fire-events (years)	Period of reliability	
			Earliest	Latest				Beginning date	Ending date
Monument Canyon Natural	MCN	PIPO	1408	1972	1493	1909	57	1648	1892
Ban-Group 3 (Apache Mesa)	BAN-GR3	PIPO	1459	1988	1480	1939	66	1614	1890
Pajarito Mountain Ridge	PMR	PIPO	1626	1993	1632	1912	39	1685	1875
Cerro Pedernal	CPE	PIPO	1380	1993	1522	1959	30	1598	1873
Continental Divide	CON	PIPO	1387	1979	1601	1899	54	1654	1870
Clear Creek Campground	CCC	PIPO	1538	1978	1548	1881	45	1664	1860
Capulin Canyon	CCP	PIPO/MC	1554	1990	1624	1955	44	1664	1893
Gallina Mesa	GAM	PIPO/MC	1531	1979	1558	1921	66	1663	1870
Cañada Bonito South	CAS	PIPO/MC	1378	1993	1480	1966	33	1672	1893
Camp May East	CME	PIPO/MC	1660	1993	1709	1880	11	1709	1879
Pajarito Mountain North-East	PME	MC	1702	1993	1773	1949	13	1801	1879
Pajarito Mountain North-West	PMW	MC	1617	1993	1669	1925	10	1841	1879
Camp May North	CMN	MC	1683	1993	1729	1880	7	1847	1879
Cañada Bonito North	CAN	MC	1655	1993	1685	1914	12	1801	1893

years (Figure 2, Table 2). The average, maximum, and minimum number of fire scars per tree was 8, 31, and 1 respectively. Long-lived specimens extended the record to more than 600 years before present in a few sites, but most of the samples began consistently recording fires after about AD 1600. Major fires ceased after the 1890's.

The pre-1900 WMPI varied at each site for the three different percentage scarred classes examined (Table 3). For example, the WMPI for major fire years (at least 10% of the trees scarred) ranged from 6.5 to 22.1 years. At CME and CAS the WMPI values for major fire years were much higher than at the other ponderosa pine sites.

Fire intervals varied considerably among the sites. The minimum fire intervals (Min. FI) for major fires ranged from 1 to 12 years (Table 3). The maximum fire intervals (Max. FI) for major fires ranged from 16 to 51 years. There were unusually long maximum fire intervals at CPE and CON.

The WMPI for all trees regardless of percentage scarred was lower in most cases than the MFI values derived from the arithmetic mean (Table 3). The MFI overestimate is due to a few longer fire intervals, which skew the distribution (Grissino-Mayer *et al.* 1994). During the pre-settlement period, the differences between the MFI and the WMPI for major fire events ranged from zero (i.e., no difference) at CAS to 3.9 years at CPE. Most of the differences were between 1 and 2 years. Thus, although WMPI is a more statistically robust estimation of central tendency, it only differs apprecia-

bly from MFI when the distributions are highly skewed.

Mixed-Conifer Fire Regimes

Samples collected from the mixed-conifer sites were not as well preserved as the samples from the ponderosa pine sites. For example, at the Cañada Bonito North (CAN) site, 33 fire-scarred samples were collected, but due to advanced decay only 28 samples could be dated. Many of these samples were fire scarred Douglas-fir and white fir, which are generally less resinous than ponderosa pine and seem to decay more rapidly following scarring. The composite of master fire chronologies for the four sites yielded a total of 113 individual fire scars representing 28 separate fire years (Figure 3).

The mixed-conifer sites presented a shorter tree-ring record than the ponderosa pine sites, extending to a maximum of 377 years before present *versus* over 600 years at some pine sites (Table 2). Note that the period of reliability was relatively short for all the mixed-conifer sites, ranging from only 38 years to 92 years, *versus* over 200 years for most ponderosa pine sites.

The pre-1900 WMPI for major fire events (at least 10% of trees scarred) ranged from 9.7 to 14 years (Table 3). The Max. FI and Min. FI for all percentage classes varied between sites. The Max. FI for major fire events ranged from 18 to 32 years. The Min. FI. for major fire events ranged from 4 to 6 years.

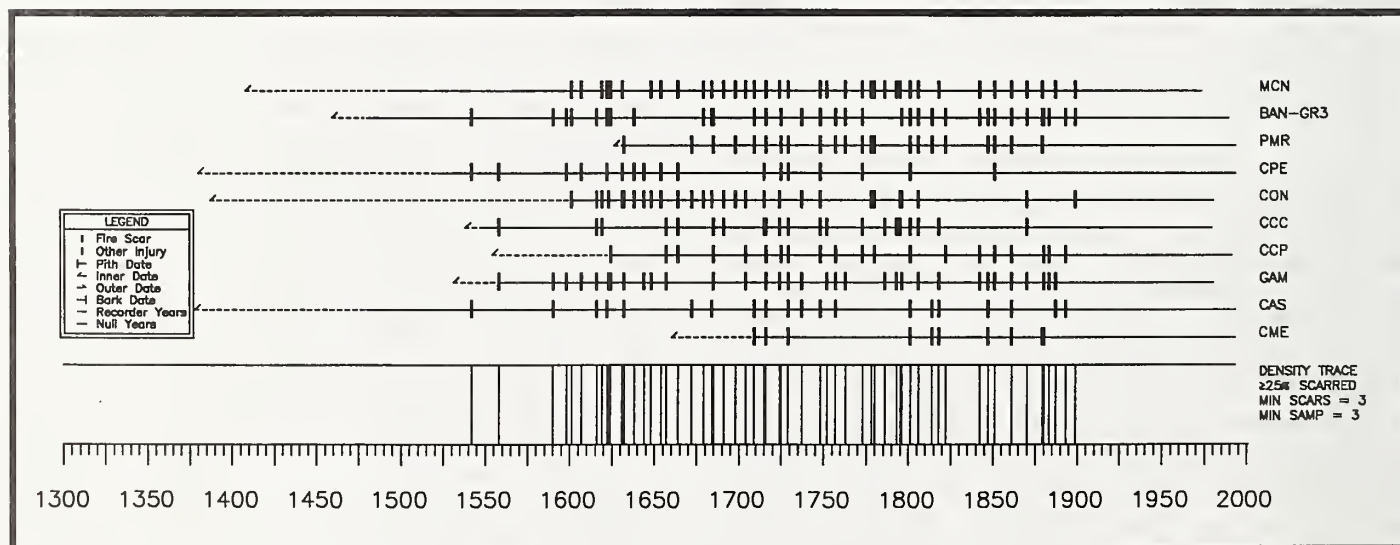


Figure 2. Composite of all fire chronologies for the ponderosa pine and transitional forests. Horizontal lines are maximum life span of trees within each site. Vertical lines are composite fire dates recorded by 25% or more of the trees within each site.

Aspen Age Distributions

The age distributions for the quaking aspen stands we sampled showed tree recruitment occurred sporadically from 1795 to 1918, but most of the regeneration concentrated in the period between 1850 to 1910 (Figure 4). Some of the fire scar dates obtained near the stands seem to correspond with the major recruitment episodes, but others do not. We hypothesize that most recruitment episodes in the late 1800's correspond to relatively intense, patchy, stand opening fires.

Precipitation-Fire Relations: Superposed-Epoch Analysis

The superposed epoch analysis revealed that both mixed-conifer and the ponderosa pine forest types exhibited significantly negative (dry) mean winter-spring precipitation departures during fire years (Figure 5). For example, in the mixed-conifer forests the mean precipitation departure during the fire years was -1.48 inches; in the ponderosa pine forests the mean precipitation departure during the fire year was -0.84 inches. In the ponderosa pine

Table 3. Summary of fire interval statistics for different sites in the Jemez Mountains for the period of reliability. Weibull median probability interval (WMPI), Mean Fire Interval (MFI), Standard deviation (STD), and maximum and minimum fire interval for all trees scarred and at least 10%, and 25% of all trees scarred. All values are expressed in years. Sites are listed by forest type (PIPO = ponderosa pine, PIPO/MC = ponderosa pine/mixed conifer, and MC = mixed conifer).

Site name (veg. type)	Site code	WMPI			MFI			STD			Maximum fire interval			Minimum fire interval		
		All fires	10% trees scarred	25% trees scarred	All fires	10% trees scarred	25% trees scarred	All fires	10% trees scarred	25% trees scarred	All fires	10% trees scarred	25% trees scarred	All fires	10% trees scarred	25% trees scarred
Monument Canyon Natural Area (PIPO)	MCN	5.4	6.5	8.1	5.5	6.6	8.4	2.5	2.9	4.3	12	16	18	1	2	3
Bandelier-Group 3 (PIPO)	BAN-GR3	5.2	6.7	9.8	6.1	7.7	9.5	4.4	5.1	6.8	21	23	24	1	1	1
Pajarito Mountain Ridge (PIPO)	PMR	5.6	7.0	13.0	6.1	7.6	13.6	4.0	4.7	6.9	21	21	27	1	1	5
Cerro Pedernal (PIPO)	CPE	8.8	12.3	20.1	11.5	16.2	22.9	11.5	15.2	17.8	51	51	53	1	1	9
Continental Divide (PIPO)	CON	4.7	6.9	11.3	6.2	9.8	15.4	6.8	12.7	18.0	28	48	64	1	2	2
Clear Creek Campground (PIPO)	CCC	4.3	7.2	12.6	5.6	8.2	13.1	5.5	5.6	6.5	24	24	25	1	1	5
Capulin Canyon (PIPO/MC)	CCP	5.4	6.8	10.6	6.5	8.2	11.5	5.3	6.2	6.4	21	21	23	1	1	2
Gallina Mesa (PIPO/MC)	GAM	4.6	7.5	11.5	5.0	8.0	11.5	3.4	4.2	4.0	16	16	19	1	1	5
Cañada Bonito South (PIPO/MC)	CAS	9.8	22.1	22.1	11.1	22.1	22.1	7.8	7.7	7.7	29	33	33	2	12	12
Camp May East (PIPO/MC)	CME	17.1	17.1	20.0	18.9	18.9	21.3	13.0	13.0	13.0	46	46	46	4	4	7
Pajarito Mountain North-East (MC)	PME	9.7	9.7	19.9	11.1	11.1	19.5	8.1	8.1	4.7	22	22	25	3	3	14
Pajarito Mountain North-West (MC)	PMW	12.6	12.6	10.0	12.7	12.7	10.0	6.1	6.1	5.7	18	18	14	6	6	6
Camp May North (MC)	CMN	10.2	10.2	16.0	10.7	10.7	16.0	7.0	7.0	2.8	18	18	18	4	4	14
Cañada Bonito North (MC)	CAN	14.0	14.0	20.4	15.3	15.3	20.0	10.1	10.1	5.6	32	32	25	4	4	14

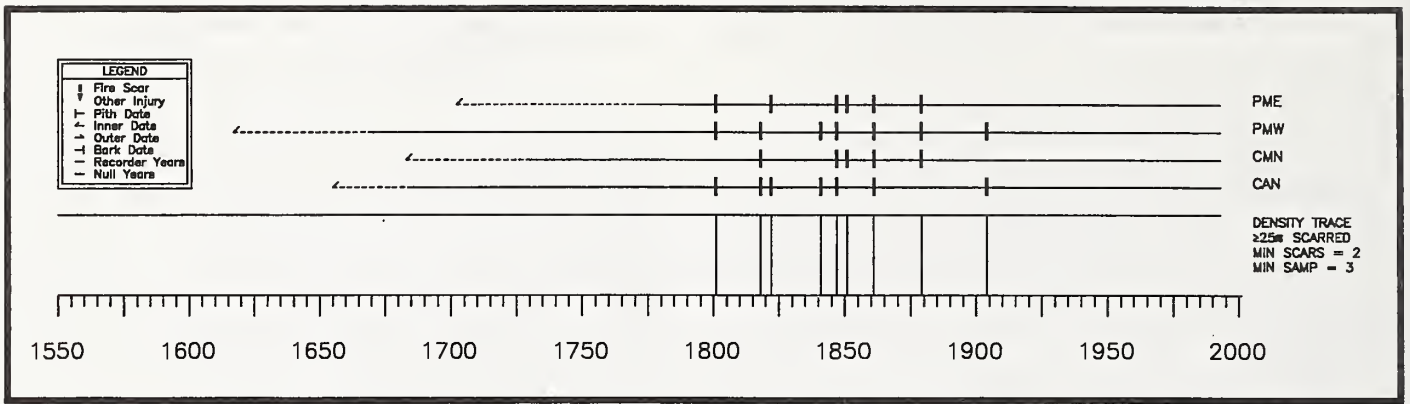


Figure 3. Composite of all fire chronologies from the mixed-conifer forests. Horizontal lines are maximum life span of trees within each site. Vertical lines are composite fire dates recorded by 25% or more of the trees within each site.

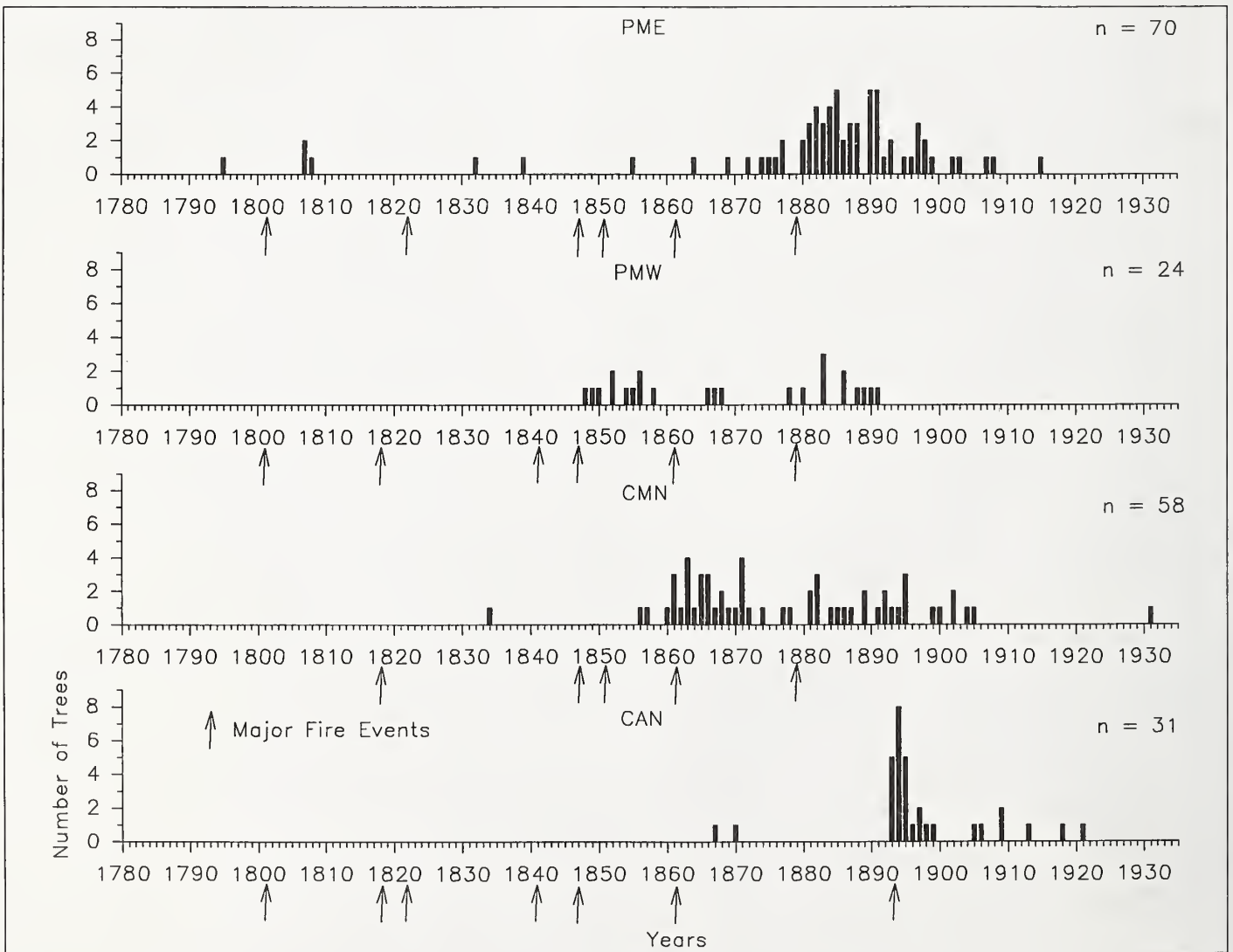


Figure 4. Aspen age structure and fire events (arrows) in the mixed-conifer forest sites. Graph shows inside tree-ring dates for sampled aspen stems, indicating establishment years.

forests, the first and the second years prior to the fire year were noticeably wet, with the second year significantly wetter than normal at the 95% confidence level.

DISCUSSION

Prior to 1900, fire regimes in ponderosa pine forests were characterized by high frequency, low intensity surface fires (Figures 6 and 7). At seven of the sites, the WMPI for major fire years (6.5 to 7.5 years, Table 3) falls within the range found in other Southwestern ponderosa pine forests. At three sites, CAS, CME, and CPE the WMPI values were greater (12.7 to 22.1 years) than for most other southwestern ponderosa pine forests (Swetnam and Baisan, This Volume). The MFI intervals for other southwestern ponderosa pine forests ranged between 4.9 to 10.2 years (Weaver 1951; Dieterich

1980; Swetnam and Dieterich 1985; Swetnam *et al.* 1989; Allen 1989; Baisan and Swetnam 1990; Grissino-Mayer and Swetnam 1992).

Variations in fire intervals between sites and through time were probably due to differences in topographic situation, site-specific histories of intensive livestock grazing, and climatic variability (Figures 2 and 3). Each of these factors are discussed below.

The CON sub-sites all show high fire frequency in the 1600's and early 1700's, with a clear reduction in fire frequency after 1752 and early cessation of major fires (Figure 2). These early reductions in fire frequency could be due to early sheep grazing by Navajo communities at CON (Touchan *et. al.* - in press). Intensive livestock grazing removes grasses and herbs necessary for fire spread in the high frequency fire regimes. Trails created by the herding of animals would also disrupt fuel continuity and hence fire spread patterns. Baydo (1970) and Bailey

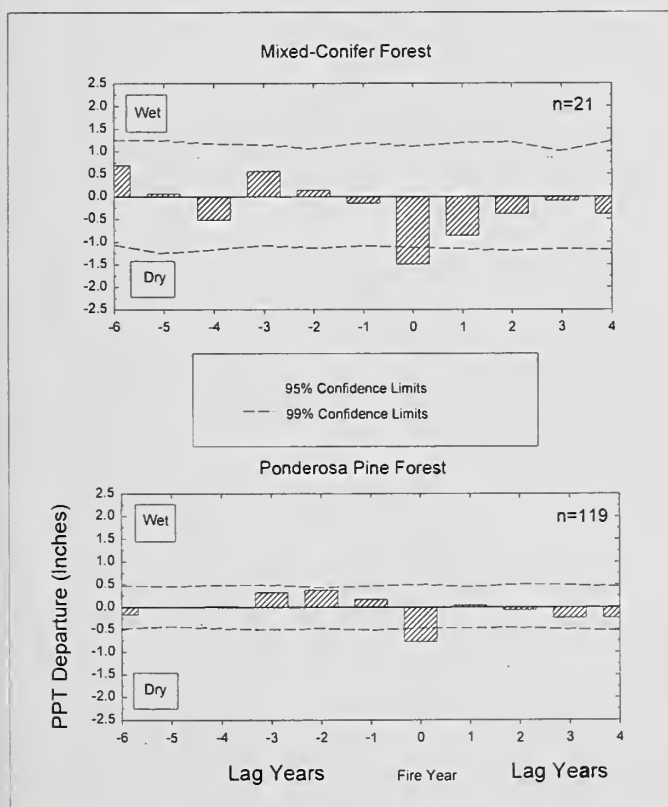


Figure 5. The superposed-epoch analysis for both the mixed-conifer (all fire dates) and the ponderosa pine forests (fire dates based on at least 10% trees scarred) for the period 1653–1986. The precipitation time series used was based on a tree-ring reconstruction of December–June precipitation. Departures were computed as the difference between the long-term mean precipitation level (1653–1986) and the observed mean precipitation during the fire years and lagged years. The “n” value is the number of lag years used in the calculations.

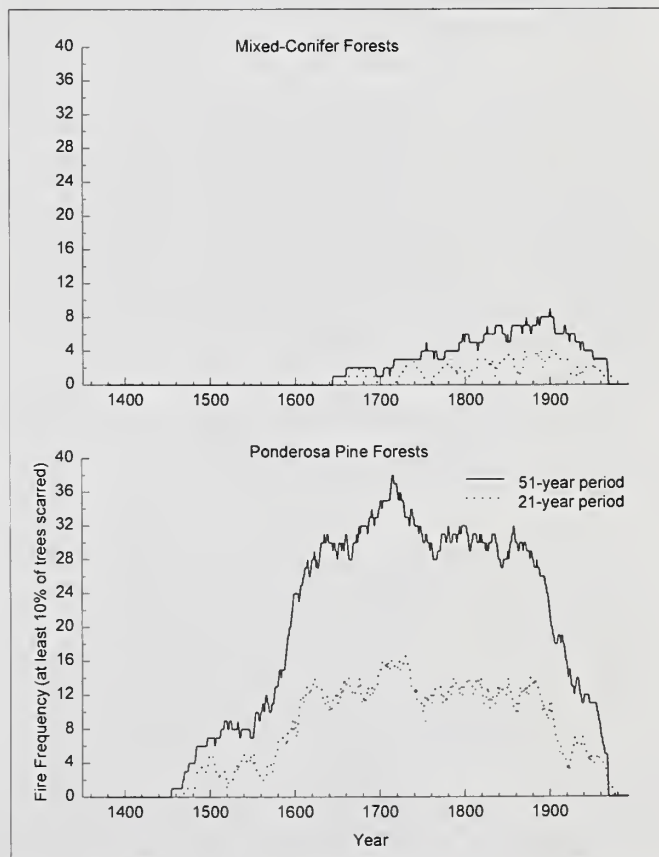


Figure 6. Fire frequency (number of fires/period, based on all fires date) for both mixed-conifer and ponderosa pine forests. Moving periods of 51 and 21-years length were used for computing the fire frequencies and are plotted on the central year of the moving period.

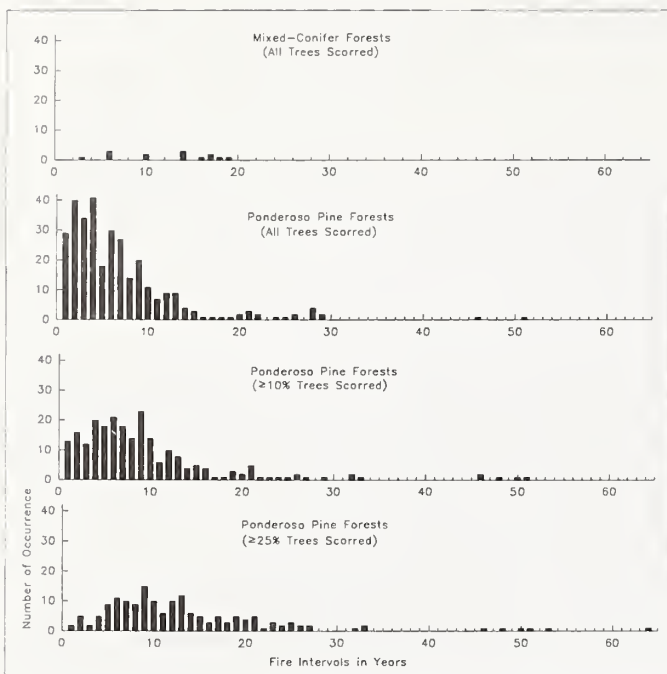


Figure 7. Distribution of fire intervals for mixed-conifer forests (all fires) and ponderosa pine forests (all fires and at least 10% and 25% of all trees scorred).

(1980) reported that early grazing of sheep and other livestock by the Navajo began in northern New Mexico in the mid 18th century. Savage and Swetnam (1991) documented an early decline in fire frequency beginning around the mid 1800s in ponderosa pine forests in the Chuska Mountains, and hypothesized that this change in fire regime was due to the rise of intensive sheep herding by the Navajo in this area.

The Cerro Pedernal site (CPE) also displays high frequency fire events during most of the 1600's and early 1700's, again with an obvious reduction in fire frequency after 1748 and early cessation of major fires by 1873 (Figure 2). Portions of the CPE area were grazed by Hispanic/genizaro peoples since the 1720s, and the initial Spanish land grant for Cañones (immediately northeast of CPE) was provided in 1731 (Van Ness 1987). These lines of evidence suggest Hispanic grazing practices might have caused the reduction in fire frequency which is apparent after 1748 in this area. In addition, CPE displays an unusually long, 51-year gap without any recorded fires between 1664 and 1715. This long fire interval may be due to utilization of the CPE area for livestock husbandry by Tewa Native Americans during the unsettled years immediately before and after the 1680 Pueblo Revolt, as indicated by Piedra Lumbre phase archeological sites

in the adjoining Chama River Valley (Wozniak 1992, Kemrer 1992) and historic documentation of Tewa Puebloans taking refuge from the Spanish reconquest in 1696–1697 “at the foot of the Cerro de los Pedernales” (Wozniak 1992:59–60). Potential explanations for this odd, long fire interval must remain speculative until additional historical information and comparative fire history data are gathered and analyzed for this locality.

The CAS and CME sites had much lower fire frequencies than the other ponderosa pine sites, and their Max. and Min. FI's were also relatively high (Table 3). Both stands are topographically isolated at relatively high elevations by unvegetated, steep, rocky cliffs in upper Los Alamos Canyon from fires which could otherwise have spread to these sites from the extensive ponderosa pine forests found on lower elevation uplands. Further, the adjoining north-facing slopes of these two mountains are quite mesic and are dominated by mixed-conifer forests which had somewhat lower fire frequencies than most ponderosa pine forests. Consequently, we suggest that topographic isolation from more extensive ponderosa pine stands (and their spreading fires), combined with the lower frequency of fire in the mixed-conifer forests on the adjoining north-facing slopes, led to lowered fire frequencies at these two sites.

There was a clear cessation in widespread fire occurrence at all sites after 1893 (Figure 2). The end of the frequent and extensive fires coincided with the onset of the documented period of intensive livestock grazing across northern New Mexico (Wooton 1908; Allen 1989:145–148), which reduced the continuity of herbaceous fine fuels (e.g., grasses) and hence the ability of fires to spread. Because the buildup of livestock numbers in the late 1800's was also a regional phenomenon, concurrent and similarly sharp declines in fire frequency are observed in most other southwestern fire scar studies (Weaver 1951; Dieterich 1980; Allen 1989; Swetnam 1990; Swetnam and Baisan, This Volume). However, fire histories show earlier cessation of fires at sites with earlier periods of intense grazing (e.g. Savage and Swetnam 1991; Touchan *et al.* 1993), and conversely fire regimes have continued little-changed well into the 20th Century at a few sites where grazing and fire suppression were limited (e.g., Dieterich 1983; Swetnam 1983; and Grissino-Mayer *et al.* 1994).

Our results indicate that fire during the pre-settlement period was less frequent in the mesic mixed-conifer forests in the Jemez Mountains than

in the ponderosa pine forests (Figure 6). Fire frequency is generally thought to decrease with increasing elevation in the southern and central Rockies (Wright and Bailey 1982), due to the cooler and wetter conditions that prevail at higher elevations. The fire frequencies for major fires in the Jemez mixed-conifer forests varied between sites, but they were similar to those found in other southwestern mixed-conifer forests where the MFI's were estimated to vary between about 7 and 22 years (Dieterich 1983; Ahlstrand 1980; Baisan and Swetnam 1990). However, our Jemez "mixed-conifer" stands are colder and more mesic than the other cited Southwestern sites, as PMN, CMN, and CAN all lack any pine species and include a significant Engelmann spruce component. Further, Grissino-Mayer *et al.* (1994) have recently reported high frequency fire regimes from upper-elevation, mixed-conifer forests on Mount Graham (3,267 m) in the Pinaleños Mountains of southeastern Arizona (the WMPI for at least 25% of all trees scarred was 7.9 years). This recent work indicates that great variability in past fire regimes existed among mixed-conifer forests in the Southwest, commensurate with the variability in species composition, stand structure, and landscape position of this forest "type". A linear model of changes in fire frequency as a function of elevation is too simplistic.

Our results for the age structure of aspen stands in Jemez Mountains mesic mixed-conifer forests indicates that aspen regeneration was the result of patchy crown fires. For example, at CAN the presence of a large aspen stand which displays a major pulse of aspen regeneration in the 1890's adjacent to the fire-scar-sampled conifer forest suggests that the widespread 1893 fire probably crowned across much of this slope (Figure 4). Other fire dates recorded on nearby conifer trees do not obviously correspond temporally with recruitment pulses. We conclude that a combination of surface and crown fires occurred in these mixed-conifer forests.

In the past century, both the ponderosa pine and mesic mixed-conifer forests sustained changes in species composition and stand structure. For example, changes in the ponderosa pine forest include the formation of dog-hair thickets, decreased understory cover, and increased fuel-loading (Covington and Moore 1994). Evidence of such changes are very obvious at the MCN site (Moir and Dieterich 1988). These changes are most likely a result of natural and anthropogenic factors such as grazing, good seed crop years, and fire suppression (deBuys 1985; Carlson 1969; Allen 1989; Touchan *et al.*, in press). In the mesic mixed-conifer

forests, these anthropogenic changes have favored the establishment of the shade tolerant, less fire resistant white fir within many portions of these stands (Allen 1984:70-75). As in ponderosa pine forests, fire suppression over the past century has allowed the development of a densely stocked, younger, understory ("doghair thickets") that would previously have been thinned by repeated surface fires (Harrington and Sackett 1990). These changes in forest structure and species composition have increased the probability of high intensity fires. In addition, these structural changes have probably resulted in other kinds of disturbance regime changes, such as increased synchrony and severity of regional spruce budworm outbreaks in mixed-conifer forests of the Southern Rockies (Swetnam and Lynch 1993).

Precipitation-Fire Relations: Superposed-Epoch Analysis

Climatic variation has an important influence on fire regimes in the Southwestern United States. On a regional basis fires are more likely to occur in years of below average moisture. For example, the regional drought years of 1748 and 1879 show up repeatedly as fire dates in fire history studies across the Southwest (Swetnam 1990; Swetnam and Betancourt 1990; Swetnam and Baisan, This Volume). Another factor that may play a role in regional fire occurrence is the influence of winter-spring precipitation on the accumulation and moisture content of the fuels. A dry spring may be followed by numerous lightning strikes at the onset of the summer precipitation season, which ignite the accumulated dry fuel (Baisan and Swetnam 1990). In contrast wet springs result in high fuel moisture which may persist into the early fire season inhibiting fire spread.

In our study, we found that the winter-spring season immediately preceding fire occurrence was significantly drier than normal in both the ponderosa pine and mixed-conifer forests (Figure 5). In the ponderosa pine forests, winter-spring seasons several years prior to fires were characterized by above average precipitation, but only the second year prior to the fire was significantly above average at the 95% confidence limit. This general pattern suggests that during wet years the build up of fine fuels is an important pre-condition for fire ignition and spread. Baisan and Swetnam (1990) documented a similar pattern in their study of pine forests in southeastern Arizona. They concluded that two unusually wet years prior to a fire season

increased fine fuel production and enhanced the probability of fire spread.

A consequence of the normally mesic, relatively productive conditions and lower fire frequencies on north facing slopes is that fuel is usually available in the mixed-conifer forests. Our analysis of climate/fire relationships in mixed-conifer forests of the Jemez Mountains suggests that the winter-spring season immediately preceding the fire season was much drier than normal, but found no significant relationships with preceding years (Figure 5). Therefore, we suggest that fuel moisture was the most important factor determining fire spread in these mesic forests. If fuels were dry enough, then there was a high probability of fire spread in this forest type. In contrast to ponderosa pine forests, fine fuel accumulation resulting from plant growth in preceding years was less important.

An unusually long fire-free interval in the 1820's and 1830's occurred at almost all of the Jemez sites (Figure 2). A similar decrease in fire occurrence during approximately the same period has been noted in several other southwestern fire history studies (Swetnam 1983; Swetnam and Dieterich 1985; Swetnam *et al.* 1989; Baisan and Swetnam 1990; Grissino-Mayer *et al.* 1994). Swetnam and Dieterich (1985) hypothesized that lack of fire during this period may have been due to regional climate changes. Fritts' (1991) regional precipitation reconstruction for the western US shows that the 1830's period was one of the wettest periods in the past two to three centuries. Our winter-spring reconstruction for the Jemez Mountains shows that 1824–1827 was very dry, followed by a wet period in the 1830's. Grissino-Mayer *et al.* (1994) also report that a severe drought occurred between 1817 to 1832 in southeastern Arizona; they hypothesize that this drought resulted in a decline in the herbaceous vegetation, and that the average to wet conditions that followed perhaps reduced both successful ignitions and the spread of fire. Hence, a combination of extreme drought and wetness is a plausible explanation of this regional scale, anomalously long fire-free interval. The extensiveness of this pattern across the Southwest also argues for a climatic, rather than an anthropogenic explanation.

CONCLUSIONS

Our data show that pre-1900 fire regimes in ponderosa pine forests were characterized by high frequency, low intensity fires. Fire regimes in the

mixed-conifer forests were characterized by somewhat lower fire frequencies than in the ponderosa pine forest. Patchy crown fires occurred during some years in the mixed-conifer forests. The variability of fire documented in both the mixed-conifer and the ponderosa pine forest was probably caused by three main factors.

First of all, anthropogenic factors, such as intense livestock grazing, reduced fine fuels necessary for the spread of fire in the high frequency fire regimes. Overall, one of the most important anthropogenic disturbances in the Jemez Mountains in the last century is fire suppression. Fire suppression has allowed changes in species composition and stand structure in both the ponderosa pine and the mixed-conifer forests. Fire suppression has caused both the build-up of woody and fine fuels and the increase in woody vegetation, such as the formation of densely overstocked understory thickets. These factors have also contributed to the decline of native grasses, due to the increased shading and accumulation of thick mats of pine needle litter. The current policy of fire suppression will result in further fuel buildups in both forest types, threatening modern forests with high-intensity conflagrations such as the La Mesa Fire of 1977 (Foxy and Potter 1978).

Second, on a local scale, topography and moist north facing slopes played an important role in lowering the frequency of fire at two ponderosa pine sites. Our study shows that forest type and elevation are sometimes less important than topographic situation in determining historic fire regimes.

Third, on a regional scale, climate played an important role in the fire regimes in both the ponderosa pine and the mixed-conifer forests. Major fire years in both forest types tended to be significantly drier than normal. Moreover, our analysis of climate/fire relationships suggests that the availability of fine-textured surface fuels was an important factor controlling the spread of fires in ponderosa pine forests. Similar patterns have been observed in modern fire occurrence patterns; e.g., the 1994 fire season has been particularly extensive in the southern portion of the Southwest, following three years of herbaceous and needle litter fuel buildups in the wet conditions of 1990, 1991, and 1992. In the sampled mixed-conifer forests fuel moisture is probably more important than fine fuel availability in determining fire occurrence. Usually, long intervals between fires in many sites across the Southwest could be important in synchronizing forest

structures, since these were concurrent periods when many trees may have established.

This study provides a baseline for planning and justifying ecosystem management programs. For example, an understanding of the pre-settlement fire regimes for specific areas can be used to design the appropriate prescribed burning plan to affect ecosystem dynamics in a fashion similar to the natural fire regime that existed before human disturbance (i.e., low-intensity surface fires). Such a management plan is not intended to strictly mimic the natural fire regime, but to meet ecological objectives by bringing the range of existing conditions in a landscape to within the historic "natural" range. This natural range of conditions, as defined by the pre-settlement, historical states, may not be the most desirable, or practical conditions for current forest ecosystems. On the other hand, in many cases the natural range of variability is the best template we have for longer-term sustainable conditions (Allen 1994).

In summary, this study demonstrates that the fire regimes in the Jemez Mountains are the result of complex interactions between combinations of anthropogenic and natural factors, and regional as well as local factors.

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Vegetation Succession After the La Mesa Fire at Bandelier National Monument

Teralene S. Foxx¹

Abstract.—In 1977 the La Mesa Fire burned over four areas of known fire history within Bandelier National Monument. All areas had been selected for study prior to the La Mesa Fire. Data was collected on two of the four plots in 1976 prior to the fire and provides pre-fire information. All four plots were examined post-fire in 1977, 1978, 1985 and 1993 (1 year, 2 years, 8 years and 16 years post-fire). Each plot was re-examined for density and cover of the understory and overstory component. Additionally, tree crown damage and recovery and growth of trees was also monitored.

INTRODUCTION

In 1975, after many years of fire suppression, the management of Bandelier National Monument began preparation for establishment of a controlled burn policy at the Monument. By introducing prescribed fires, the National Park Service (NPS) hoped to reduce fuel loads and thereby reduce the potential for wildfire in ponderosa pine and mixed conifer forests. Prior to establishing prescriptions for controlled burns they needed basic information concerning fire in the ecosystems of the Pajarito Plateau. Needed information included data on post-fire vegetation succession, previous fire history, and fuel loadings. In 1975, Loren Potter and I began a study to provide data on previous fire frequencies and information on plant succession after fire (Foxx and Potter 1978). Using historic records kept at the Monument, we located areas that had burned from the 1930s to the 1970s. We were most interested in areas of 10 acres or more that could be easily located. Such areas were found on Escobas, Frijoles, and Alamo Mesas. In each of the locations and in adjacent control sites, we sampled trees with evident fire scars and determined the pre-suppression fire frequencies by use of tree-ring analysis (Foxx and Potter 1978). We did vegetative analysis on each site obtaining information on tree density, size classes, and canopy cover.

Before the study was completed, the La Mesa Fire of 1977 burned over the previously studied plots, changing the nature and complexity of the project. This allowed us to compare sites of known

fire history and succession as related to the length of time since an area was burned by the La Mesa Fire. With the pre-La Mesa Fire data, a simple study of succession became a unique study of the influence of fire as related to fire history. The results of the study were reported at the 1981 *La Mesa Fire Symposium*. (Potter and Foxx 1981, Foxx & Potter 1981).

Subsequently, 5 of the more accessible sites were sampled in 1985 to provide a snapshot of the changes in the ecosystem (Potter and Foxx 1986). As the 15th anniversary of the La Mesa Fire approached, plans were made to conduct follow-up research that could be shared in another symposium. In the summers of 1992 and 1993, members of the Ecological Studies Team (ESH-20) of Los Alamos National Laboratory, returned to four of the original study sites known to have burned 84, 40, 17 years and 1 year prior to the La Mesa Fire. Using the same techniques employed in earlier studies, we measured the understory and overstory vegetation. This report compiles and compares some of the data and photographs collected in 1976, 1977, 1978, 1985, and 1993 at these four sites, providing quantitative and qualitative impressions of the changes that occurred since the 1977 La Mesa Fire. The changes are remarkable and are testimony to the complexity of post-fire succession. Additional follow-up data collected from 13

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plots established in 1977 after the fire will be reported elsewhere. Although this study developed serendipitously after an unfortunate event, rather than from a pre-designed study, the information reported here adds to our knowledge of the role of fire in ponderosa pine ecosystems.

METHODS

In 1975, two years prior to the La Mesa Fire, the NPS and the University of New Mexico commenced a study to determine the fire history and the fire frequency of forested areas within Bandelier National Monument. Using historic records and field examination, we sought areas of 10 acres or more that had burned during the time period of 1935 to 1975. The atlas maintained at the Monument headquarters from 1931 to 1969 revealed only five fires larger than 10 acres. The five study areas, indicated by irregularly shaped darkened areas in Figure 1, were Frijoles Canyon 1937, Upper Alamo Crossing 1945, Bear Mesa 1950, Boundary Peak 1955 and Frijoles Canyon 1960. Then in 1976, during the course of the study, a 14-acre fire burned on Escobas Mesa (Escobas Mesa 1976). A final area adjacent to the 1960 burn was determined by use of tree-ring analysis of fire scars not to have had a major fire since 1893 (in earlier reports this was described as the Frijoles Rim 1878 burn site). These 7 sites were to be used for determining fire history, frequency, and succession. Data were gathered from each of these sites on tree and shrub density and understory cover.

On June 16, 1977, the La Mesa Fire was ignited and eventually burned over 15,000 acres of Bandelier National Monument, Los Alamos National Laboratory, and US Forest Service lands. The course of the fire resulted in a re-burning of all previously studied sites except for the 1955 burn site (Figure 1). Immediately after the fire in 1977, and again in 1978, we returned to the field and examined the extent of damage that had occurred in each of the areas of known fire history ranging from the last burn being 84 years prior to the La Mesa Fire to an area burned 1 year prior to the La Mesa Fire. In addition to gathering the previously collected data, we examined each tree for the extent of foliar damage as related to the time since the area had burned.

We classified each tree into 6 classes according to the extent of crown remaining, from complete loss to no evidence of scorching (Figure 2). Each tree was numbered for future reference, the diameter

was measured at breast height (dbh). Additionally, we looked at the understory composition using a modification of Lindsey's (1955) line strip method (Foxy & Potter 1978). Soon after the fire, permanent photostations were established to provide long-term photographic records. From this re-examination with the plots of known fire histories, we concluded that if an area had not been burned within 25 years prior to the La Mesa Fire there had been complete loss of overstory trees (Figure 3).

Four sites were sampled two additional times—in 1985 and in 1992/93. The sample sites were Frijoles Rim 1893, Frijoles Rim 1937, Frijoles Rim 1960, and Escobas Mesa 1976. Because of their accessibility these four sites were the easiest to follow through time with limited resources. In 1985, trees were measured and mortality was determined giving an 8-year mortality rate. Then in 1992–93, we re-examined these 4 areas for tree survival, tree growth, shrub recovery, grass, and forb cover and species richness.

Each year of the analysis of the overstory vegetation (pre- and post-fire) was done similarly. Vegetation was measured using a modification of Lindsey's (1955) line intercept method. The sampling unit was a 1000-ft line with a 10-ft strip on each side of a metal tape, 20 ft wide in total. Within the 20-ft wide strip we relocated trees previously marked with metal tags, measured the diameter, and noted the health of each tree. In most plots we mapped the trees and shrubs within the strip and recorded all new reproductive stock (Figure 4). These maps provide additional successional information for future studies. We also recorded the percent cover of shrub layers over 3 ft tall. Trees less than 4 inches diameter and over 3 ft tall were considered reproductive stock.

The analysis for the understory vegetation was conducted somewhat differently on the various sampling years. This variability occurred because the intention of the original study was somewhat different than the post-fire study. Additionally, the lack of understory vegetation in 1977 made it necessary to increase the number of plots. The vegetation in the pre-fire study was measured every 50 ft using a quadrat, whereas post-fire the vegetation was measured every 20 ft using a Daubenmire quadrat. Also, in 1992–93 more categories of non-vegetation were recorded. Although data for the understory from pre-fire to post-fire are not strictly comparable, pre-fire data is included here as documentation of what existed prior to the La Mesa Fire.

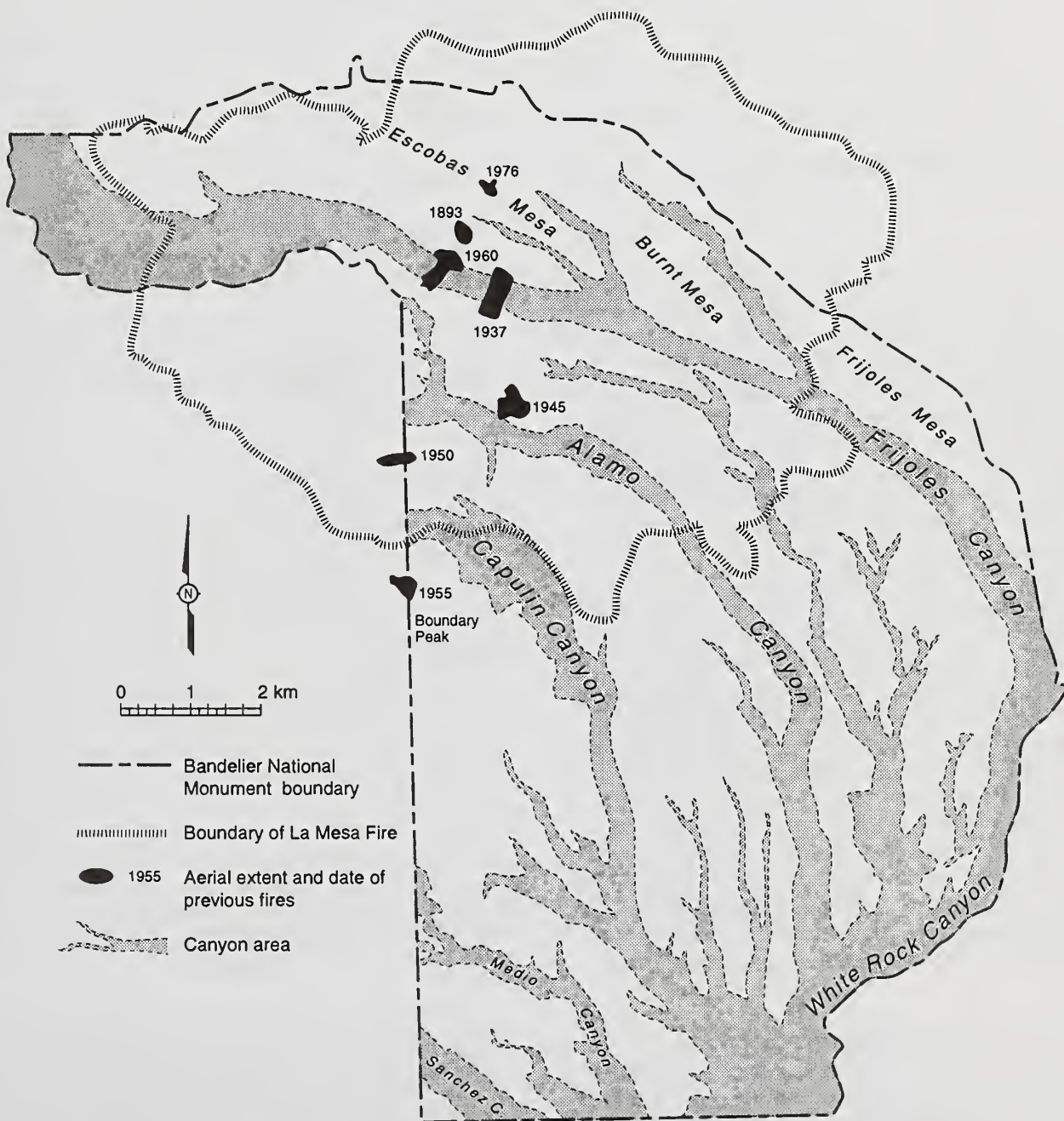


Figure 1. — Map of large historic fires in Bandelier National Monument. The 1893 fire was actually quite extensive (Allen 1989)—only the sampled area is shown here.

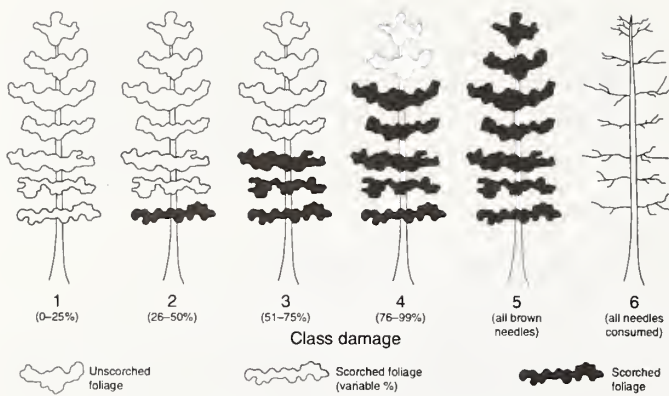


Figure 2. — Classification of foliar damage classes.

In addition to the fire history being of interest to the successional processes after the La Mesa Fire, the eventual reseeded of a number of grass species was important. One month after the fire, the burned areas of Bandelier were seeded with a mixture of native and non-native grass species (Foxy and Potter 1979b). The seeding operation was done to reduce erosion and subsequent damage to the numerous archaeological sites in the Monument. The seeded grasses included the native species sand dropseed (*Sporobolus cryptandrus*), spike muhly (*Muhlenbergia wrightii*), western wheatgrass (*Agropyron smithii*), slender wheatgrass (*Agropyron trachycaulum*), and blue grama (*Bouteloua gracilis*), as well as a Eurasian cultivar of sheep fescue (*Festuca ovina*). Within the first years after seeding only the slender wheatgrass and sheep fescue showed good germination. According to Flory and Marshall (1942), slender wheatgrass is a short-lived perennial bunchgrass, which is high in seed production and yields well up to 5 years, then declines. Sheep fescue, on the other hand, is a long-lived perennial with a spreading and shallow rooting system. Studies by Barnes (1981) and Foxy, Potter and Barnes (1981) indicated that sheep fescue, in particular, may compete with pine seedlings.

RESULTS

Frijoles Rim 1893 Burn

Pre-La Mesa Fire

The 1893 site is located north of the 1960 burn on the rim of Frijoles Canyon (Figure 1). The La Mesa Fire burned over this site before data could be col-

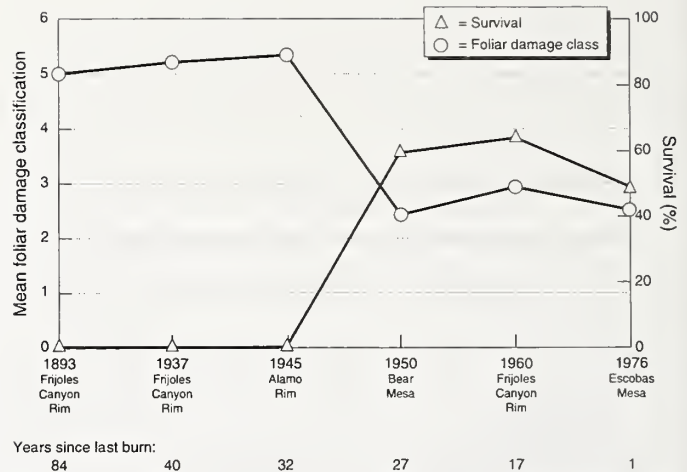


Figure 3. — Comparison of post-La Mesa Fire tree mortality and length of time since sampled areas had burned.

lected. As a result, there are no pre-fire cover, density or frequency data for this plot. However, adjacent areas were used as control sites for the Frijoles Rim Burn (1960).

Post-La Mesa Fire

1977 Conditions.—On the day the La Mesa Fire began, a tree was removed from the site to determine the fire history of a tree on an archaeological site within the area designated as the Frijoles Rim Burn 1893. Using dendrochronological methods, it was determined that the last fire to scar the tree was in 1878, or 99 years earlier. Subsequent analyses of a larger fire-scar data set (Allen 1989) indicate that the last significant fire likely burned through this area in 1893. Within hours of removal of the tree, the flame front of the fire reached the rim of Frijoles Canyon and consumed the trees in this location. The site was largely burned between 1430 hours and 2000 hours on June 17, 1977, during which time the predicted rate of spread was 24 chains (1584 ft) per hour. The photograph shown in Figure 5 was taken just one day before the area burned by the La Mesa Fire.

After the La Mesa Fire, the site was not examined until September, three months post-fire (Figure 6). However, the burning of the area had been so severe that little or no vegetation had come back with the exception of a few sprouting oaks (*Quercus* spp.). There was less than 1 percent cover of grasses, forbs, or shrubs. The area was devoid of any litter or duff and the mineral soil had been contracted and dried into polygons. Big bluestem (*Andropogon gerardii*) was the only grass species evident in the area.

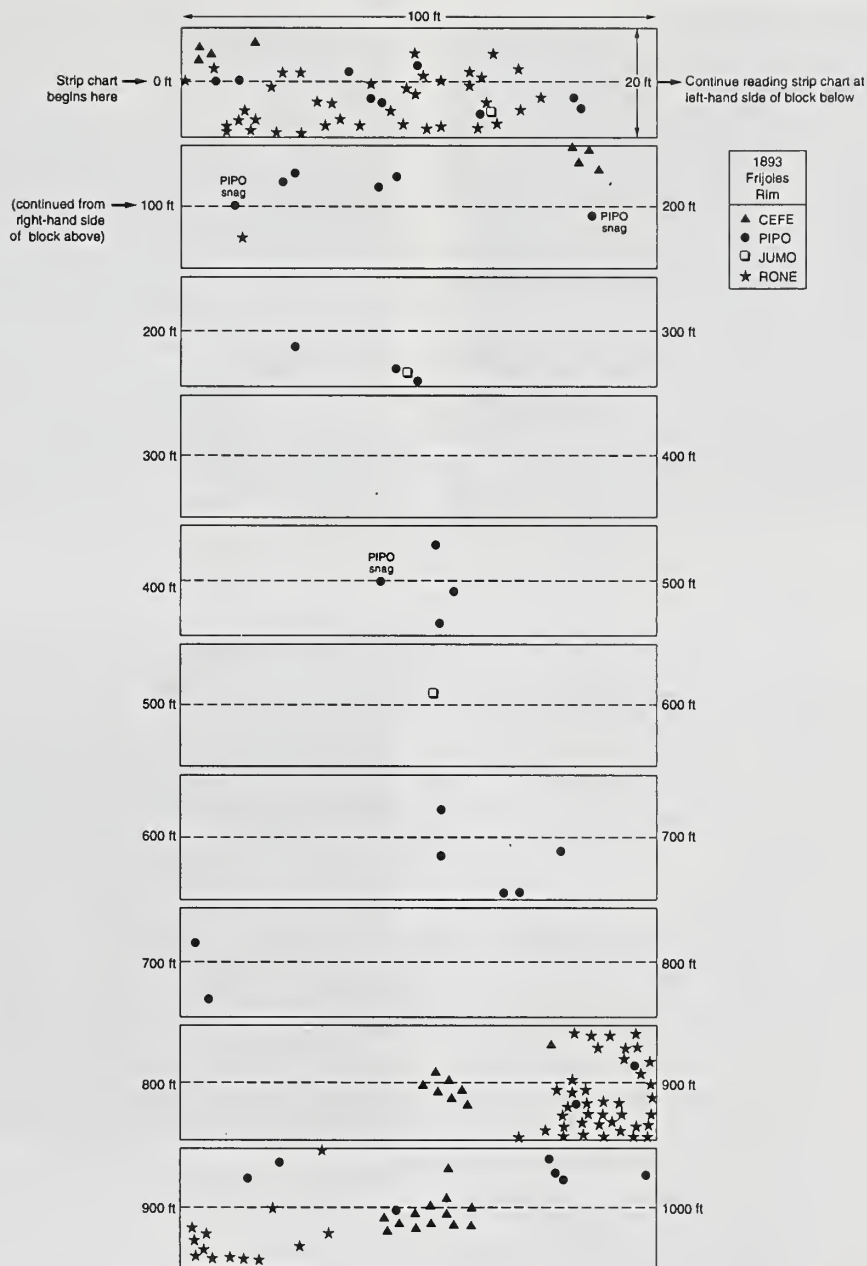


Figure 4. — Tree and shrub map for 1893 plot on Frijoles Rim, measured in 1913. The species codes are the first two letters of the genus and species combined (see Table 1).

Prior to the La Mesa Fire the site supported 342 trees per acre with an average diameter of 7 inches. After the fire all trees were in damage classes 5 (brown needles) and 6 (no needles) (99 percent in class 6), and considered dead when sampled (Figure 6).

1978 Conditions.—The site was examined again in September of 1978 (Figure 7, Table 1). In 1978, all trees were dead and there was a complete loss of

overstory canopy. However, the understory was dominated by a seeded grass, slender wheatgrass. Other seeded grasses, including sheep fescue, Wright's muhlenbergia (*Muhlenbergia wrightii*), and sand dropseed, were found less frequently. In 1978, grasses, forbs, and shrubs covered only 5 percent of the soil surface.

1985 Conditions.—By 1985, the total vegetation cover for the site had increased to 25.5 percent.



Figure 5. — The 1893 plot on June 16, 1977 prior to being burned by the La Mesa Fire. The rocks are part of the rubble mound of an archaeological site.

Seven species of grass were identified with the highest cover being slender wheatgrass. The cover of sheep fescue and big bluestem had both increased. Among the 14 forbs identified in the area, wormwood (*Artemisia carruthii*), goldenweed (*Chrysopsis foliosa*) and perky sue (*Hymenoxys argentea*) were most common.

1993 Conditions.—The site was examined in September of 1993. As can be seen in Figure 8, nearly all the snags that had been standing in 1978 were downed. Data analysis indicates only two snags remained standing and they were greater than 15 inches in diameter. A map of the study area (Figure 4) and data analysis (Table 2) shows pine regeneration was evident throughout the study area with a total of 218 seedlings/hectare. Most seedlings were less than 4 ft tall and 1 inch in diameter. Additionally, shrubs had increased over time (3.1 percent) with the highest cover being buckbrush (*Ceanothus fendleri*) and New Mexico locust (*Robinia neomexicana*) (Table 1). The understory cover increased from little or no vegetation immediately after the fire in 1977 to 37.74 percent in 1993 (Figure 9).

Twelve species of grass were identified within the study over the 17 years. However, the types and percent distribution of the grasses had changed from 1978 to 1993. The dominant grass, until 1985, was slender wheatgrass (Figure 10). By 1993, slender wheatgrass had disappeared from the ecosystem and the dominant grasses were big bluestem, Wright's muhlenbergia, western wheatgrass and sheep fescue (Figure 10). One of the more striking aspects of the area was the large and ap-



Figure 6. — The 1893 plot on September 1977, 3 months post-fire. Note the barren nature of this site.



Figure 7. — The 1893 plot on September 1978, 1 year post-fire. Slender wheat grass is the prominent grass.

parently spreading patches of big bluestem standing over 5 ft tall (Figure 11). Through time the native grasses increased in cover while the overall cover of seeded grasses decreased with the loss of the slender wheatgrass. Although the overall percent cover of seeded grasses decreased through time, sheep fescue and Wright's muhlenbergia increased (Figure 10).

Other changes were apparent (Figure 9). Non-vegetated soil surface decreased continuously from 99% in 1977, to 62% in 1993. Whereas there was initially little organic litter present after the fire, tree fall and increased vegetation cover had built up a litter layer that covered 42 percent of the soil

Table 1. Comparison of actual percent cover and relative cover of grasses, forbs and shrubs for the 1893 plot through time.

Category or species	1978		1985		1993	
	Total cover	Relative cover	Total cover	Relative cover	Total cover	Relative cover
Non-Vegetation (Bare Soil and Litter)	95.04		74.5		62.26	
Bare Soil					20.64	
Litter				41.62		
Soil Crusts					3.50	9.27
Vegetation	4.96		25.50		37.74	
Grass (and Graminoides)						
<i>Andropogon gerardii</i>			0.07	4.20	1.60	4.24
<i>Agropyron smithii</i>			0.03	0.10	2.92	7.74
<i>Agropyron trachycaulum</i>	2.01	41.37	16.17	63.40		
<i>Bouteloua gracilis</i>	0.01	0.29	0.54	2.10	0.20	0.53
<i>Blepharoneuron tricholepis</i>					0.60	1.59
<i>Bromus tectorum</i>					0.03	0.10
<i>Carex</i> spp.			0.03	0.10	0.40	1.06
<i>Festuca ovina</i>	0.20	4.19	1.30	5.10	5.04	13.35
<i>Muhlenbergia asperifolia</i>					3.37	13.20
<i>Muhlenbergia montanus</i>			0.23	0.90	1.90	5.03
<i>Muhlenbergia wrightii</i>	0.21	4.24			4.10	10.86
<i>Sporobolus</i> spp.	0.11	2.31				
Total Grass	2.54		18.37		20.16	
Forbs						
<i>Achillea lanulosa</i>					0.20	0.53
<i>Agastache wrightii</i>	0.20	4.11				
<i>Allium cernuum</i>					0.02	0.05
<i>Artemisia carruthii</i>	T	0.04	0.74	T 2.90	3.92	10.39
<i>Artemisia dracunculoides</i>			T	T		
<i>Bahia dissecta</i>			0.13	0.50	0.06	0.16
<i>Castilleja integra</i>					0.02	0.05
<i>Chenopodium fremontii</i>	T	0.04				
<i>Chenopodium graveolans</i>	1.11	22.74				
<i>Chrysopsis foliosa</i>	T	T	0.41	1.60	2.72	7.21
<i>Cirsium</i> spp.					0.12	0.32
<i>Commelina</i> spp.			T	T		
Compositae					0.10	0.26
<i>Conyza canadensis</i>					0.26	0.69
<i>Erigeron divergens</i>	0.30	6.17	0.15	0.60	0.10	0.27
<i>Erigeron flagellaris</i>					0.60	1.59
<i>Erigeron philadelphicus</i>					1.10	2.91
<i>Helianthus petiolaris</i>					0.20	0.53
<i>Hymenoxys argentea</i>			0.69	2.70		
<i>Hymenoxys richardsonii</i>			0.05	0.20	0.02	0.05
<i>Liatris punctata</i>			0.03	0.10	0.02	0.05
<i>Lotus wrightii</i>	0.50	10.32			3.54	9.38
<i>Lupinus</i> spp.	0.10	2.14				
<i>Penstemon</i> spp.					0.04	0.11
<i>Petalostemum candidum</i>					1.10	2.91
<i>Potentilla</i> spp.			0.20	0.80	T	T
<i>Taraxacum officinale</i>			T	T		
<i>Tragopogon dubius</i>			0.05	0.20	0.02	0.06
<i>Verbascum thapsus</i>	0.10	2.06	0.03	0.10	0.02	0.05
Unknown			0.20	0.52		
Total Forbs	2.31		2.48		14.38	
Shrubs						
<i>Ceanothus fendleri</i>					3.00	7.95
<i>Quercus gambelii</i>	T	T	0.28	1.10		
<i>Robinia neomexicana</i>					0.10	0.26
Total Shrubs	0.1		0.28		3.10	8.21
Total Species	15		14		23	



Figure 8. — The 1893 plot on September 1993, 16 years after being burned by the La Mesa Fire. The clump of locust and oak at left covers the archaeological site shown in Figure 5.

surface by 1993. Some of the soil surface not covered with vegetation or litter had a layer of soil crusts (3 percent) in 1993 (Table 1).

In 1978, the forb cover was dominated by goosefoot (*Chenopodium graveolans*) and small percentages of 9 other forbs (Table 1). Goosefoot dominated only the first year (1978). In 1993, three forbs were dominant: goldenweed, wormwood (*Artemisia carruthii*), and deervetch (*Lotus species wrightii*). Forb species richness increased continuously from 9 species in 1978 to 14 species in 1985 and 21 species in 1993 (Table 1).

Frijoles Rim 1937 Burn

Pre-La Mesa Fire

This site was scheduled to be examined the summer of 1977, but the La Mesa Fire burned over the site before data could be collected. This area had not burned for 40 years prior to the La Mesa Fire. This area was located near the rim of Frijoles Canyon (Figure 1)

1977 Conditions.—The area was burned on June 17, 1977, during which time the predicted rate of spread was 24 chains per hour. The study area was in the immediate vicinity where the fire jumped across Frijoles Canyon from the south. Although the area burned was somewhat more open than the 1893 site, damage to mature and reproductive trees was severe, with all trees in class 5 (brown needles) and 6 (no needles). Total foliage cover for herba-

Table 2. The density and percent canopy cover of trees within the four plots through time.

Plot	Year	Trees/ hectare <4"	Trees/ hectare >4"	Percent cover tree canopy
1893	1977	0	0	0
	1978	0	0	0
	1985	0	0	—
	1993	218	0	<1%
1937	1977	0	0	0
	1978	0	0	0
	1985	209.9	0	0
	1993	318	0	<1%
1960	1976	—	—	—
	1977	—	133.4	—
	1978	—	—	—
	1985	49.4	123.5	15
	1993	75.35 (14)	177.5 (33)	22
1976	1976	0	0	0
	1977	0	0	0
	1978	128.5	382.9	21
	1985	74.1	370.5	31
	1993	—	—	—

ceous plants was 2.9 percent (Table 3) compared with the adjacent 1960 burn of 16 percent and the 1893 burn of 1 percent. Perennial grasses and herbs were regenerating. Like the 1893 plot, patches of big bluestem were noted in the area.

1978 Conditions.—In 1978, no trees were alive (Figure 12) and total vegetation cover was 9.6 percent (Table 3). Ten different grass species were found in the area, the most common being the seeded slender wheatgrass. Sixteen species of forbs were identified. Four species had the highest cover: goosefoot, puccoon (*Lithospermum* spp.), perky sue (*Hymenoxys argentea*) and goldenweed. Two species of shrub (buckbrush and wild rose (*Rosa* spp.)) were found in small amounts (Table 3).

1985 Conditions.—In 1985 the area was still devoid of trees. We did not specifically sample the area for the seedling density, so we have no indication of the number of seedlings/hectare at this site. Plant species richness had increased further, with 14 species of grasses and 26 species of forbs present (Table 3). Total grass cover was up 20.1%. Although slender wheatgrass was still present, other species had increased in cover including big bluestem, mountain muhly (*Muhlenbergia montana*) and sheep fescue. Four species of shrub were found including oak, New Mexico locust, wild rose and buckbrush. Buckbrush had the highest percent cover with 5.4 percent.

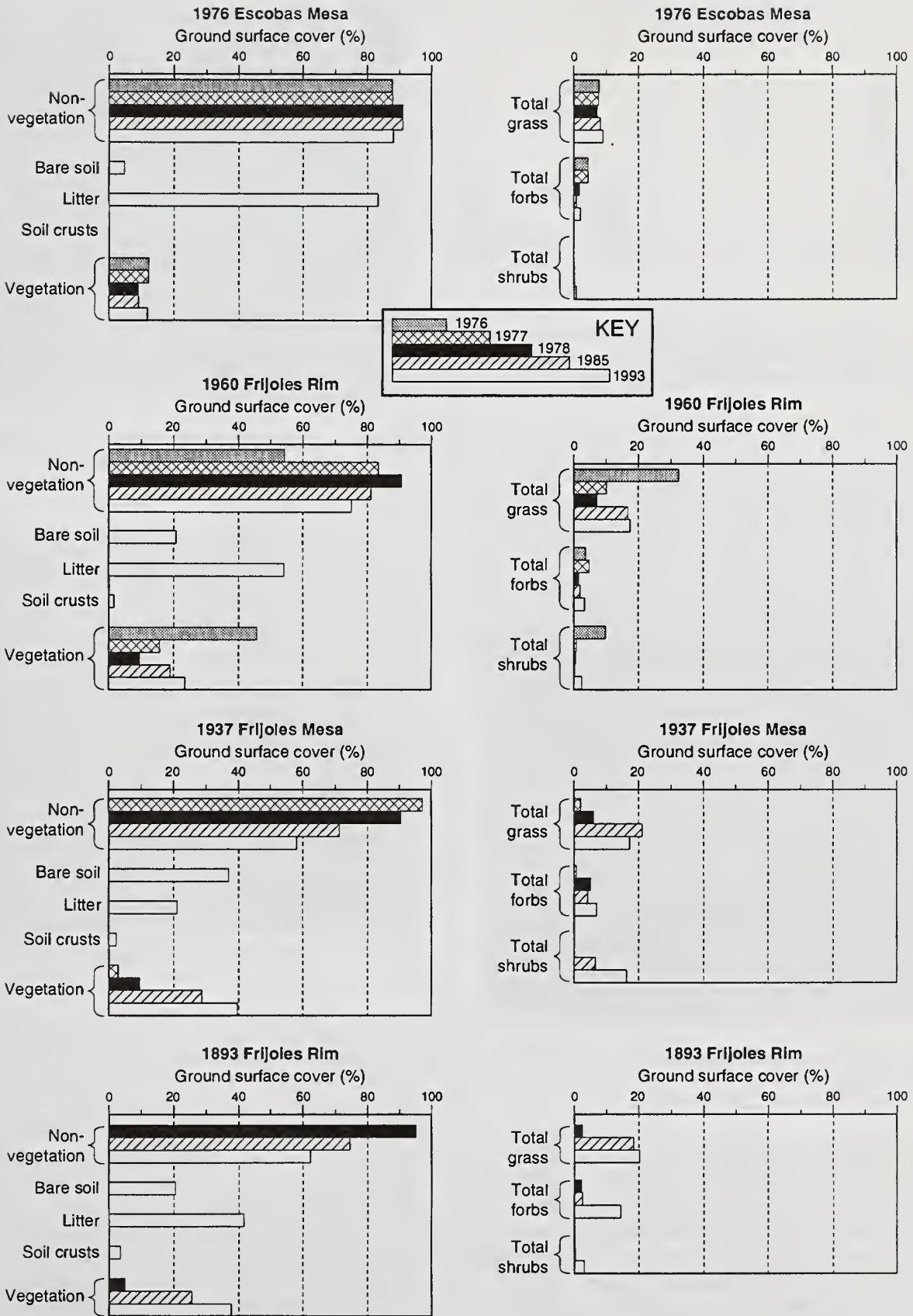


Figure 9. — Changes in ground surface cover through time at all four sites.

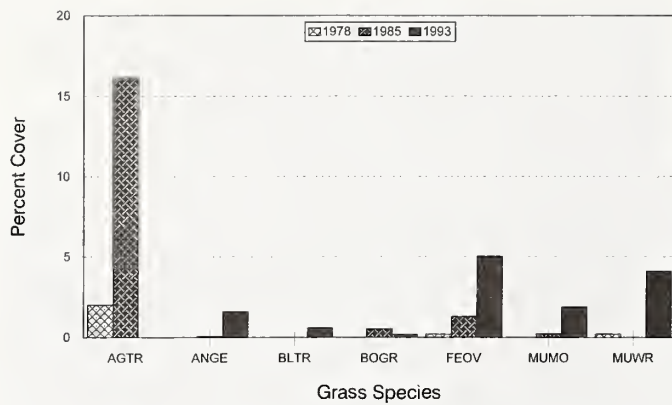


Figure 10. — Percent cover of dominant grass species found in the 1893 plot through time. The species codes are the first two letters of the genus and species combined (see Table 1).



Figure 11. — Patches of big bluestem in the 1893 plot in 1993. The person is 5'3" tall.

1993 Conditions.—When we revisited the site in September, 1993, all of the trees that had been standing in 1978 were down (Figure 13). The litter component of the soil cover had increased to 21 percent. Interspaces were commonly covered with soil crusts (2.3 percent) (Table 3). Figure 9 shows the increase in grasses, forbs and shrubs seen in this plot over time. As in the 1878 plot, the slender wheatgrass was no longer part of the grass compo-



Figure 12. — The 1937 plot on September 1978, 15 months post-fire. Note the presence of some needle litter.



Figure 13. — The 1937 plot on September 1993, 16 years post-fire.

nent and had been replaced by little bluestem (*Andropogon scoparius*), mountain muhly, big bluestem, and pine dropseed (*Blepharoneuron tricholepsis*) (Figure 14). The dominant forb species were purple prairie clover (*Petalostemum purpureum*), goldenweed, and pinque (*Hymenoxys richardsonii*) (Table 3). Total shrub cover was up to 16.3%—buckbrush, covering 14% of this area's surface, was particularly striking. Total vegetation cover had increased from less than 3 percent in 1977 to greater than 39 percent in 1993. As in the 1893 plot, we saw a great increase in the total cover of native unseeded grass species and a modest overall decrease in the total cover of seeded spe-

Table 3. Comparison of actual percent cover and relative cover of grasses, forbs and shrubs for 1937 plot through time.

Category or species	1977		1978		1985		1993	
	Total cover	Relative cover	Total cover	Relative cover	Total cover	Relative cover	Total cover	Relative cover
Non-Vegetation (Bare Soil and Litter)	97.14		90.45		71.35		58.06	
Bare Soil							37.02	
Litter							21.04	
Soil Crusts							2.30	5.48
Vegetation	2.9		9.55		28.65		39.64	
Grass (and Graminoides)								
<i>Agropyron gerardii</i>					2.04	7.1	3.40	8.4
<i>Agropyron smithii</i>					0.10	0.35	0.40	1.0
<i>Agropyron trachycaulum</i>			2.65	27.77	2.65	12.7		
<i>Andropogon scoparius</i>	1.1	37.9	0.59	6.22	0.68	2.4	3.3	7.9
<i>Aristida</i> spp.			0.09	1.0	0.36	1.3		
<i>Blepharoneuron tricholepis</i>			0.4	4.5	0.25	0.9	2.1	5.0
<i>Bouteloua curtipendula</i>							0.1	.24
<i>Bouteloua gracilis</i>			0.01	0.10	0.54	1.9	1.0	2.4
<i>Carex</i> spp.	0.04	1.4	0.08	0.08	0.35	1.2		
<i>Festuca ovina</i>			0.4	4.35	1.47	5.1	2.6	6.2
<i>Koeleria cristata</i>					0.09	0.3	0.3	0.7
<i>Muhlenberia asperifolia</i>					1.28	4.5		
<i>Muhlenberia montana</i>	0.9	32.2	1.6	16.8	6.74	23.5	3.60	8.58
<i>Muhlenberia wrightii</i>					0.18	0.62	0.60	1.43
<i>Sitanion hystrix</i>			.196	2.05	0.12	0.42		
<i>Sporobolus cryptandrus</i>			0.07	0.68				
Total Grass	2.06		6.07		20.1		17.14	
Forbs								
<i>Achillea lanulosa</i>					0.04	0.14		
<i>Antennaria parviflora</i>					0.02			
<i>Artemisia carruthii</i>	0.04	1.4			0.07	0.26		
<i>Artemisia frigida</i>			0.10	1.05	0.01	0.03	0.02	0.05
<i>Bahia dissecta</i>			0.1	1.1	0.01	0.03	0.02	0.05
Boraginaceae							0.12	0.29
<i>Castilleja</i> spp.				0.08	0.01	0.04	0.92	2.19
<i>Chenopodium album</i>			T	0.02	0.01	T	0.01	
<i>Chenopodium graveolans</i>	0.1	3.5	0.20	2.12				
<i>Chrysopsis foliosa</i>			0.59	6.18	1.09	3.82	1.62	3.86
<i>Cirsium</i> spp.					0.06	0.20	0.52	1.24
<i>Commelina</i> spp.					T	0.01		
<i>Erigeron divergens</i>				0.03	0.93	3.25	0.10	0.24
<i>Erigeron flagellaris</i>							0.10	
<i>Erigeron philadelphicus</i>							0.10	0.24
<i>Euphorbia</i> spp.			T	0.02				
<i>Geranium caespitosum</i>					0.04	0.14		
<i>Gutierrezia</i> spp.			0.20	2.05	0.06	0.21		
<i>Helianthus petiolaris</i>							0.1	0.24
<i>Hymenoxys argentea</i>			0.76	7.97	0.65	2.25	0.42	1.00
<i>Hymenoxys richardsonii</i>					0.60	2.11	0.50	1.19
<i>Hymenopappus filifolius</i>			T	0.02	0.02	0.05		
<i>Liatris punctata</i>			T	0.04			0.04	0.10
<i>Lithospermum</i> sp.			1.25	13.19	0.02	0.06		
<i>Lotus wrightii</i>							0.20	0.48
<i>Melilotus</i> spp.	0.02	0.70						
<i>Mentzelia pumila</i>							0.02	0.05
<i>Mirabilis linearis</i>	0.04	1.4						
<i>Penstemon</i> spp.	0.04	1.4			0.03	0.09		
<i>Petalosemum candidum</i>			T	0.02			0.10	0.24
<i>Petalostemum purpureum</i>					0.02			

continued

Table 3 (continued). Comparison of actual percent cover and relative cover of grasses, forbs and shrubs for 1937 plot through time.

Category or species	1977		1978		1985		1993	
	Total cover	Relative cover	Total cover	Relative cover	Total cover	Relative cover	Total cover	Relative cover
Forbs (continued)								
<i>Petalostemum</i> spp.	0.10	3.5			0.02	0.07	0.80	1.91
<i>Potentilla</i> spp.	0.02	0.06	0.10	0.24				
<i>Pseudocymopterus montanus</i>					T	T		
<i>Senecio</i> spp.	0.02	0.70			0.44	1.52		
<i>Sonchus</i> spp.					0.01	0.03		
<i>Solidago</i> spp.			1.00	1.03			0.04	0.10
<i>Taraxacum officinale</i>							0.22	0.52
<i>Thermopsis pinetorum</i>					0.01	0.03		
<i>Tragopogon dubius</i>					0.02	0.05		
<i>Verbascum thapsus</i>							0.90	2.15
Unknown			0.10	1.05				
Total Forbs	0.7		5.21		4.17		6.94	
Shrubs								
<i>Berberis fendleri</i>							0.5	1.19
<i>Ceanothus fendleri</i>	0.10	3.50	0.06	0.62	5.41	18.89	14.20	33.86
<i>Cercocarpus montanus</i>					0.34	1.2	1.19	
<i>Quercus undulata</i>					0.84	9.92		
<i>Robinia neomexicana</i>					0.07	0.23	0.30	0.72
<i>Rosa</i> spp.			T	0.02			0.10	0.24
Total Shrub	0.1		0.08		6.6		16.29	
<i>Pipo</i> seedlings								
							0.20	0.48
Total Species	10		28		44		38	

cies. While the seeded sheep fescue and Wright's muhlenbergia had increased through time, slender wheatgrass had disappeared from the ecosystem.

The mapping (Figure 16) and data analysis (Table 2) indicate that there are an increasing number of pine seedlings within the area. The area sup-

ports 318 seedlings/hectare with an average diameter at breast height of .1 inch. Seventy-five percent of the plots had one or more seedlings. Total tree cover was less than one percent.

Frijoles Rim 1960 Burn

Pre-La Mesa Fire

This area had not burned for 17 years prior to the La Mesa Fire. The area burned during the period 1430 to 2000 hours on June 17, 1977, during which time the predicted rate of spread was 24 chains per hour. The site is located on the rim of Frijoles Canyon where the fire jumped across the canyon.

1976 Conditions.—Prior to the La Mesa Fire, this area had been examined, including both the overstory and understory components (Table 4). Total understory cover was 45.7 percent. Because of the nature of the pre-fire study the grasses were not identified by species but represented 32 percent of the total cover. Common forbs in 1976 were goldenweed, estafiata (*Artemisia frigida*), and lupine (*Lupinus caudatus*).

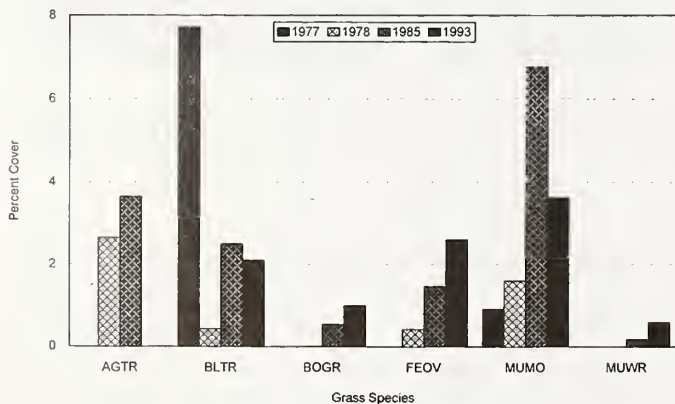


Figure 14. — Percent cover of dominant grass species found in the 1937 plot through time. The species codes are the first two letters of the genus and species combined (see Table 3).

The overstory was composed of ponderosa pine (*Pinus ponderosa*), juniper (*Juniperus monosperma*), oak and (Table 2). Trees ranged from a diameter of 4 inches to greater than 18 inches.

Post-La Mesa Fire

1977 Conditions.—After the La Mesa Fire most trees in the 1960 study area were in damage classes 1 to 4, ranging from no leaves singed to 75 percent

of the crown being damaged. Only a few trees were within classes 5 and 6 (Figures 2, 16).

The total understory vegetation cover was reduced from 45.7 percent in 1976 to 15.6 percent. Six species of grass were identified with the highest cover represented by pine dropseed, big bluestem, and little bluestem. Ten forb species were found and goosefoot represented the most dominant species (Table 4).

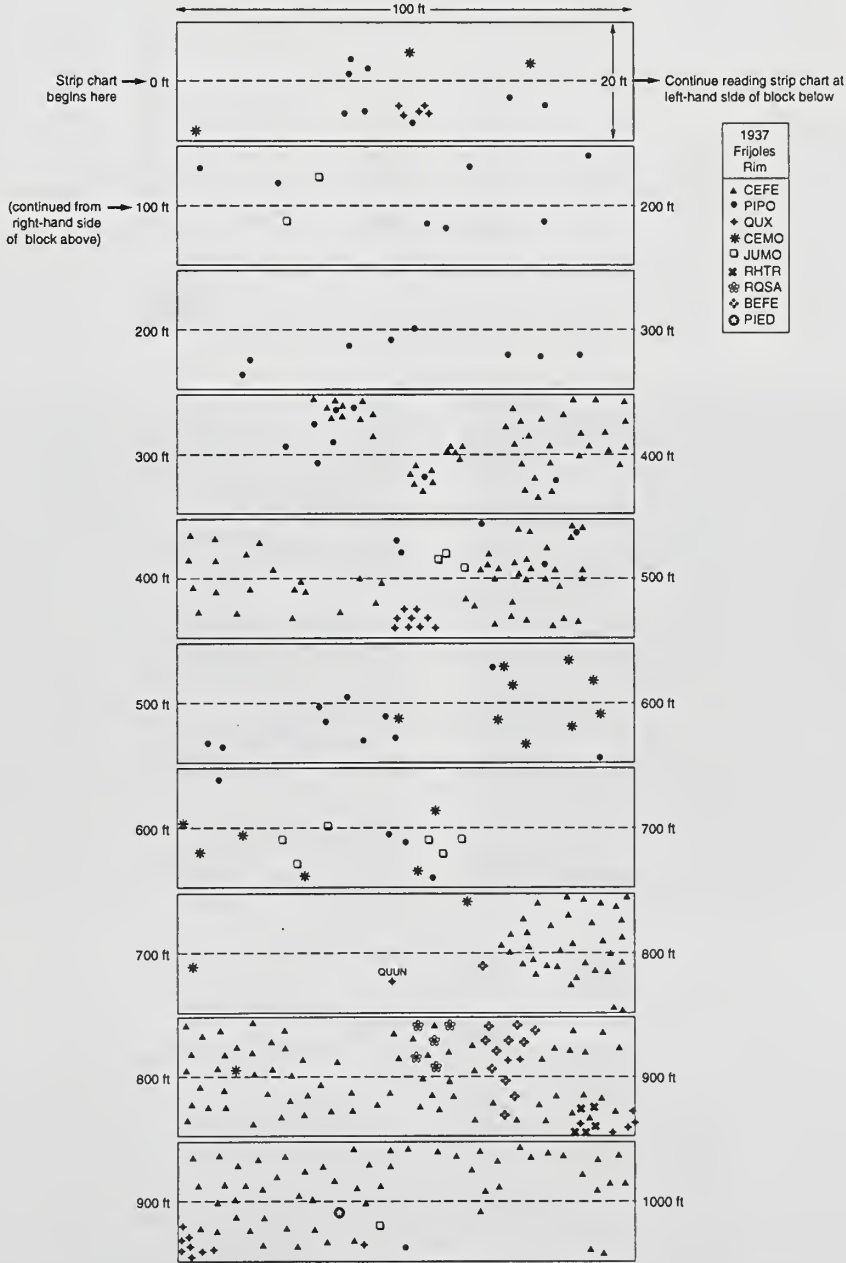


Figure 15. — Map for 1937 plot on Frijoles Rim measured August 25, 1993. Line strip beginning at post near rim. The species codes are the first two letters of the genus and species combined (see Table 3).

Table 4. Comparison of actual percent cover and relative percent cover of grasses, forbs and shrubs for the 1960 plot through time.

Category or Species	1976		1977		1978		1985		1993	
	Total cover	Relative cover	Total cover	Relative cover	Total cover	Relative cover	Total cover	Relative cover	Total cover	Relative cover
Non-Vegetation (Bare Soil & Litter)	54.29		84.37		90.63		81.10		75.04	
Bare Soil									20.86	
Litter									54.18	
Soil Crusts									1.60	6.41
Vegetation	45.71		15.63		9.37		18.90		23.37	
Grass (and Graminoides)										
Grass (undistinguished)	31.93	70.3							0.20	0.80
<i>Agropyron smithii</i>					0.70	7.50	0.82	4.36		
<i>Agropyron trachycaulum</i>					0.20	2.14	0.59	3.11		
<i>Andropogon gerardii</i>			2.40	15.32			1.13	5.96	3.70	14.82
<i>Andropogon scoparius</i>			0.74	4.75	1.10	11.77	2.53	13.36	3.80	15.22
<i>Aristida</i> spp.			0.30	1.92	0.10	1.07	0.10	0.40		
<i>Blepharoneuron tricholepis</i>			6.57	42.03	1.71	18.24	2.00	10.60	3.42	13.70
<i>Bouteloua gracilis</i>	0.45	1.0	0.05	0.34	0.20	2.14	0.03	0.13		
<i>Carex</i> spp.			0.05	0.34	0.30	3.25	0.13	0.69	0.40	1.60
<i>Festuca ovina</i>					0.10	1.09	0.11	0.56	0.60	2.40
<i>Koeleria cristata</i>							0.06	0.30	0.52	2.08
<i>Muhlenbergia montana</i>					2.51	26.78	8.83	46.73	4.10	16.42
<i>Muhlenbergia wrightii</i>					0.1	1.07				
<i>Poa</i> spp.							0.21	1.11		
<i>Sitanion hystrix</i>					0.20	2.18	0.28	1.49	0.82	3.28
Total Grass	32.38		10.11		7.22		16.72		17.46	
Forbs										
<i>Artemesia</i> spp.					T	0.04				
<i>Allium cernuum</i>					0.01	0.06	0.18	0.95	0.06	0.24
<i>Antennaria parviflora</i>							0.06	0.32	0.10	0.40
<i>Artemesia carruthii</i>							0.31	1.64	0.60	2.40
<i>Artemesia frigida</i>	1.02	2.25								
<i>Artemesia dracunculul</i>	0.14	0.30								
<i>Aster</i> spp.					0.10	1.07				
<i>Bahia dissecta</i>			0.10	0.67	0.12	1.26	0.06	0.30	T	0.01
<i>Boraginaceae</i>									0.52	2.09
<i>Castilleja integra</i> .			0.04	0.24			0.31	1.64		
<i>Castilleja</i> spp.									0.12	0.48
<i>Chenopodium graveolans</i>			3.62	23.18						
<i>Chrysopsis foliosa</i>	0.84	1.85	0.54	3.47	0.31	3.27	0.43	2.30	0.84	3.36
<i>Cirsium</i> spp.			0.05	0.34	0.10	1.09	0.03	0.14	0.10	0.40
<i>Commelina</i> spp.							T	0.02		
<i>Erigeron divergens</i>	0.24	0.53	0.05	0.30	0.20	2.14	0.10	0.53	0.02	0.08
<i>Erigeron philadelphicus</i>									0.02	0.08
<i>Euphorbia</i> spp.									0.04	0.27
<i>Geranium caespitosum</i>	T	0.02	0.04	0.17						
<i>Hymenoxys argentea</i>	0.40	0.88	0.05	0.34	0.06	0.68	0.06	0.32		
<i>Ipomopsis aggregata</i>							T	0.02		
<i>Lithospermum multiflorum</i>			0.05	0.30	0.26	2.80	0.16	0.83		
<i>Lotus wrightii</i>					T	0.02			0.44	1.76
<i>Lupinus caudatus</i>	0.45	1.0								
<i>Mertensia</i> spp.							0.01	0.03		
<i>Medicago</i> spp.	0.10	0.21								
<i>Opuntia</i> spp.	0.11	0.25								
<i>Penstemon</i> spp.							0.04	0.21		
<i>Petalostemum candidum</i>					0.10	1.07			0.10	0.40
<i>Petalostemum</i> spp.	0.09	0.20								
<i>Potentilla</i> spp.					T	0.02	0.04	0.21	0.20	0.80
<i>Townsendia</i> spp.									0.04	0.16

continued

Table 4. Comparison of actual percent cover and relative percent cover of grasses, forbs and shrubs for the 1960 plot through time (continued).

Category or species	1976		1977		1978		1985		1993	
	Total cover	Relative cover	Total cover	Relative cover	Total cover	Relative cover	Total cover	Relative cover	Total cover	Relative cover
Forbs (continued)										
<i>Pseudocymopterus montanus</i>							0.07	0.38		
<i>Senecio</i> spp.			0.05	0.34			0.05	0.26		
<i>Solidago</i> spp.					0.10	1.07				
Unknown	0.15	0.34	0.10	0.64	0.15	1.56	0.01	0.05		
Total Forb	3.54		4.69		1.51		1.92		3.24	
Shrubs										
<i>Ceanothus fendleri</i>					0.50	5.34	0.06	0.32	1.0	4.01
<i>Cercocarpus montanus</i>	3.40	7.49								
<i>Quercus undulata</i>	6.39	14.07	0.52	3.35			0.19	1.02		
<i>Robinia neomexicana</i>			0.24	1.52	0.10	1.07			1.40	5.61
Total Shrub	9.79		0.76		0.60		0.25		2.40	
<i>Pipo Seedling</i>			0.05	0.34	T	0.02	0.02	0.13	0.10	0.40
Total Species	14		19		29		33		28	



Figure 16. — The 1960 plot, September 1977, 3 months post-fire.



Figure 17. — The 1960 plot, September 1978, 1 year post-fire.

Over 35 trees were marked and measured in 1977. Table 5 represents only a subset of the trees marked and measured and the crown damage for each tree. These trees were the ones we were able to successfully follow through to 1993. Because the line strip was not precisely marked previously, the accuracy of the placement in 1993 may have accounted for some of the discrepancy. Additionally by 1993 some of the trees had lost tags. There were 133 mature trees/hectare at the time of the La Mesa Fire (Table 2).

1978 Conditions.—The area was revisited in 1978 and the total understory cover showed a slight decrease (9.4 percent). The photographic record indicated that trees in class 4 had shown remarkable recovery (Figure 17). Eleven species of grass were identified. Various species including big bluestem and little bluestem (Table 4) had increased in cover. Seeded grasses, sheep fescue and slender wheatgrass had increased in cover, but not as extensively as in the 1893 and 1937 plots. Those

Table 5. The diameter at breast height (inches) and growth rates (dbh increment/time period) through time of 19 ponderosa pine trees located on the 1960 plot.

Tree no.	1977	1985	1993	1993-1977	1993-1985	1985-1977	Damage class
221	7	7.6	8.8	1.8	1.2	0.6	4
222	11.5	12	13.8	2.3	1.8	0.5	3
223	5.3	4	6.9	1.6	2.9	-1.3	4
232	21.8	22.3	23.4	1.6	1.1	0.5	1
233	8.3	10.9	13.5	5.2	2.6	2.6	1
234	24.3	23.9	26.1	1.8	2.2	-0.4	1
235	19	18.8	19.5	0.5	0.7	-0.2	1
237	17.1	17.4	18.1	1	0.7	0.3	1
238	13.2	13.6	15.3	2.1	1.7	0.4	1
239	15.4	16.2	16.7	1.3	0.5	0.8	1
240	14.6	15	14.6	0	-0.4	0.4	1
241	11.5	11.8	12.6	1.1	0.8	0.3	1
242	10.3	10.5	10.8	0.5	0.3	0.2	1
247	12.6	13.5	14.7	2.1	1.2	0.9	3
248	8.7	8.7	6.7	-2	-2	0	3
249	7.2	7.6	8.7	1.5	1.1	0.4	3
250	8.2	9.4	10.9	2.7	1.5	1.2	1
251	19.3	19.5	20.6	1.3	1.1	0.2	4
Total	235.3	242.7	261.7	26.4	19	7.4	35
Total							
Av. DBH	12.38	12.77	13.77				
Av. Growth				1.39	1.00	0.39	

species with the highest percent cover were native grasses including mountain muhly, pine dropseed, and little bluestem (Table 4).

1985 Conditions.—In 1985 the trees within these plots were examined to determine survival rates after 8 years. Table 5 indicates the number of trees remaining alive and their growth. Most of the trees were relocated in 1985.

The understory cover in 1985 had increased to 19 percent (Table 4). Grasses made up the largest part of that percentage with 16.7 percent. Twelve grass species were identified. As in 1978, the native species had a higher cover than the seeded grasses (Table 4). Nineteen forb species were identified within the plot. The dominant species included wormwood, Indian paintbrush (*Castilleja integra*) and goldenweed.

By 1985, only a couple of trees had died. Table 5 represents the trees and growth rates of only those trees tracked through 1993. The average diameter was 13.77 and growth rates from 1977 to 1985 were 0.39 inches. The total overstory cover was 15 percent (Table 2).

1993 Conditions.—There was very little apparent visual change in the trees from 1978 to 1993 (Figure 18). By 1993, the total vegetation cover had increased to 23.4 percent from a low of 9.4 percent in

1978 (Figure 9). One substantial change was the increase in litter cover from the needle fall (personal observation). The litter component had increased to 54 percent and the interspaces were covered by soil crusts (1.6 percent). Nine species of grass were identified. Slender wheatgrass dropped out of the ecosystem, replaced by increasing cover of big bluestem, little bluestem, pine dropseed and mountain muhly (Figure 19). The most substantial



Figure 18. — The 1960 plot, September 1993, 16 year post-fire.

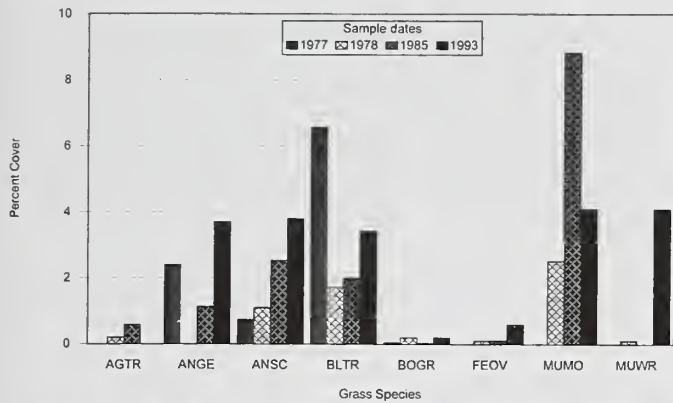


Figure 19. — Percent cover of dominant grasses found in 1960 plot through time. The species codes are the first two letters of the genus and species combined (see Table 4).

change in soil surface cover was the increase of litter from needle fall. Native grasses increased from 1977 to 1993, while the seeded grasses decreased. Fifteen forb species were identified, with the highest cover represented by wormwood, deervetch and goldenweed (Table 4).

In 1993, we attempted to locate as many of the tagged trees as possible and mapped the area (Figure 20), however, approximately 19 trees were not found. Table 5 describes the 19 relocated trees including their average diameter and growth rates. Because of the uncertainty of the location of the transect, I have calculated trees/hectare based on the 1993 transect and have not compared it to the 1985 data. Whether the trees not found were dead or the tags had been dislodged by birds and other animals is uncertain, thus these data do not represent a perfect comparison with the 1976–1985 overstory data. By 1993 the average diameter was 13.77 inches and the average growth increment from 1977 was 1.39 inches.

Escobas Mesa 1976 burn.

Pre-La Mesa Fire

This area had not burned for 1 year prior to the La Mesa Fire. The 1976 Escobas Mesa fire burned during the 1976 field season. The area, like the other 3 sites, had apparently been logged in the late 1890's and 1930's.

1976 Conditions.—After the 1976 Escobas Mesa fire, we examined the area. We took both vegetation data and litter data. Fuel loads were measured at 1.3 tons per acre. After the fire the total understory vegetation cover was 12.3 percent. Three species of grass were present with pine dropseed as dominant (Table

6). Eight species of forb were identified, with the dominant species being wormwood.

Post-La Mesa Fire

1977 Conditions.—This site burned June 18, 1977, between 1100 and 2200 hours, during which time the predicted rate of spread was 38 chains per hour. The area was sampled July 7, 1977. The boundaries of the 1976 fire were easy to locate because the narrow, barren 1976 hand lines were still evident. The area burned by the La Mesa Fire differed little from 1976 conditions. Most of the damage was from a bulldozer developing a fireline (Figure 21). The trees within the 1976 burn were all in classes 1–4 from the crown only slightly singed to 75 percent of the crown burned and 25 percent remaining alive (Figure 17). The total percent understory vegetation cover was approximately the same as after the 1976 Escobas Mesa fire (12.2 percent) (Table 6). Only two graminoides were found in the 1977 field study and they were pine dropseed and a sedge. The six forbs included goldenweed and pussytoes (*Antennaria parvifolia*).

Over 70 trees were measured and tagged and the amount of crown damage was determined. Table 7 provides diameter and basal area information on those trees that we were able to relocate in 1993. The total overstory cover was 21% (Table 2).

1978 Conditions.—When the area was re-examined in 1978 the understory cover had decreased slightly from 12.2 percent to 9 percent. Although not measured in 1978 there was considerable needle fall from the trees singed by the fire. Eight species of grass were found to be present including the seeded slender wheatgrass and sheep fescue. However, native grasses, especially mountain muhly and pine dropseed, had a higher percent cover than did the seeded grasses.

1985 Conditions.—In 1985, eight species of grass were found within the study plot. Although slender wheatgrass persisted, the total percent cover represented by this species had decreased. There was an increase in the percent cover of sheep fescue and some native grass species, such as little bluestem.

In 1985, the trees within the plot were remeasured and the mortality examined. Table 7 indicates the condition of the trees in 1985.

1993 Conditions.—The area was photographically compared with the condition in 1977 (Figure 22). Figure 9 indicates that there was a rebound in forb cover after a decrease from 1977 to 1978 through 1985. Five

species of grass were found within this plot. Slender wheatgrass had dropped out of the system and mountain muhly and sheep fescue were dominant along with little bluestem (Figure 23). Fourteen forbs were identified. Species with the highest percent cover were goldenweed and wormwood. There was an increase in the native species and a decrease in the seeded species as previously seen in other plots.

In 1993 we attempted to relocate the trees along the transect. A number of trees could not be relocated either because of a different alignment of the transect or because trees had died in the past 8 years and the tags were no longer visible. Only 35 trees were relocated in 1993 and the average dbh was 8.56 inches and the growth rate from 1977 was 1.59 inches (Table 7).

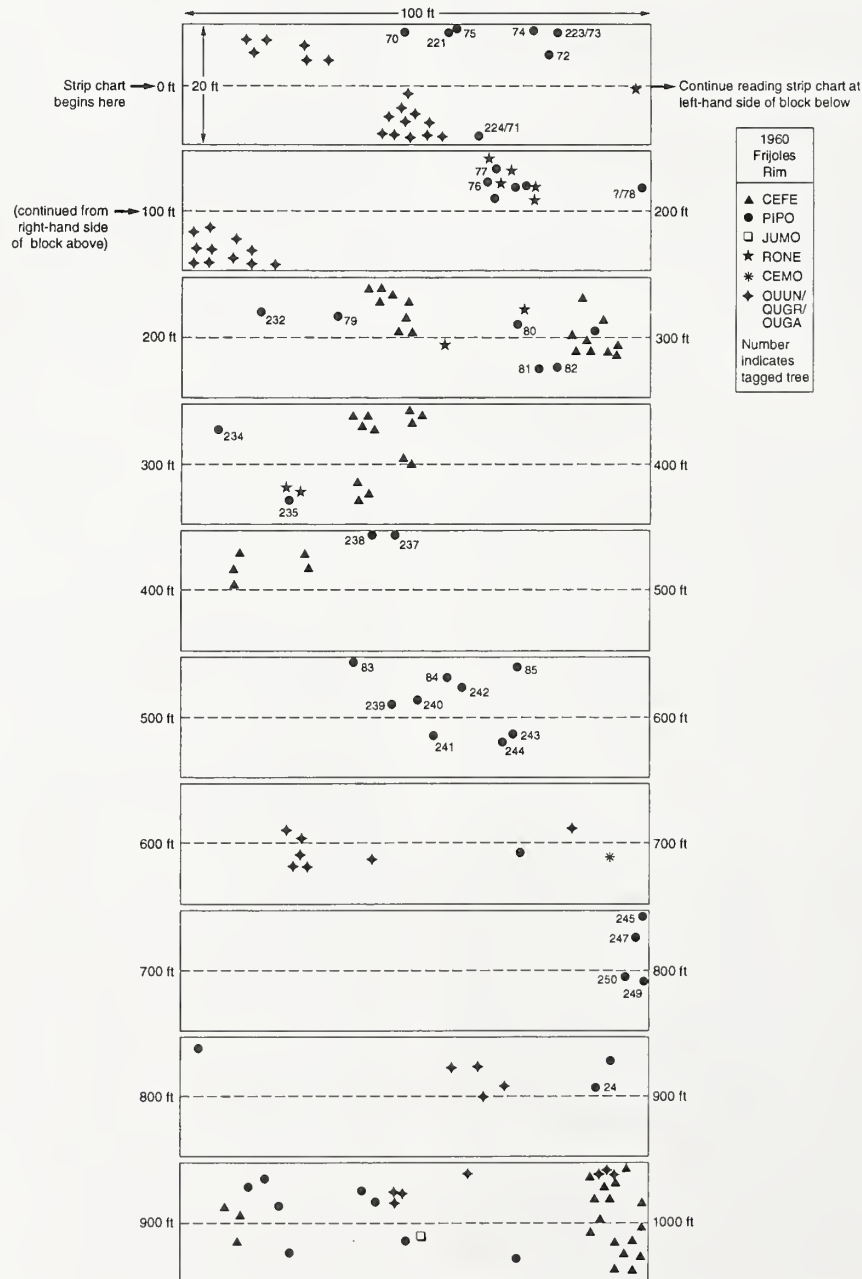


Figure 20. — Tree and shrub map for 1960 plot, measured in 1993. The species codes are the first two letters of the genus and species combined (see Table 4).

Comparisons Between Plots

Total Understory Cover

I compared the four plots for patterns of post-fire vegetative recovery. Figure 9 shows that the 1893 and the 1937 plots had similar patterns of recovery

for understory cover, as did the 1960 and 1976 plots. Those plots with no post-fire overstory cover (the 1893 and 1937 plots) had a linear recovery from low vegetation cover (2 to 4 percent) to higher vegetation cover from 1977 to 1993. However, those plots with surviving overstory tree cover (the 1960

Table 6. Comparison of actual percent cover and relative percent cover of grasses, forbs, and shrubs for the 1976 plot through time.

Category or species	1976		1977		1978		1985		1993	
	Total cover	Relative cover	Total cover	Relative cover	Total cover	Relative cover	Total cover	Relative cover	Total cover	Relative cover
Non-Vegetation (Bare Soil and Litter)	87.75		87.83		91.05		90.95		88.04	
Bare Soil									4.78	
Litter									83.26	
Soil Crusts									0.14	1.17
Vegetation	12.25		12.17		8.95		9.05		11.83	
Grass and Graminoides										
<i>Agropyron trachycaulum</i>					1.30	14.55	0.07	0.72		
<i>Andropogon scoparius</i>	0.25	2.04			0.30	3.35	0.85	9.39	1.0	8.36
<i>Aristida</i> spp.					0.20	2.26				
<i>Blepharoneuron tricholepis</i>	7.45	60.82	7.70	63.27	0.70	7.85	0.24	2.62	0.22	1.84
<i>Carex</i> spp.	0.08	0.61	0.01	0.04	0.27	3.00	1.80	19.85		
<i>Festuca octoflora</i>							0.18	2.02		
<i>Festuca ovina</i>					0.51	5.66	2.08	23.01	2.34	19.56
<i>Muhlenberia montana</i>					3.71	41.47	2.60	28.67	5.26	43.97
<i>Sitanion hystrix</i>					0.30	3.40	0.41	4.47	0.24	2.01
Total Grass	7.78		7.71		7.29		8.23		9.06	
Forbs										
<i>Allium cernuum</i>	0.10	0.82	0.01	0.04	T	0.04	0.01	0.08	0.02	0.18
<i>Antennaria parviflora</i>	0.05	0.41	1.31	10.72						
<i>Artemisia carruthii</i>	1.25	10.20					0.03		0.30	2.51
<i>Bahia dissecta</i>					0.20	2.28		0.33		
<i>Castilleja</i> spp.					0.27	3.00			0.02	0.17
<i>Chenopodium album</i>					0.20	2.26	T	0.01		
<i>Chrysopsis foliosa</i>	0.83	6.73	1.26	10.31	0.20	2.24	0.25	2.71	0.40	3.34
Compositae			1.50	12.33	0.30	3.35				
<i>Erigeron divergens</i>					0.33	3.67			0.12	1.02
<i>Erigeron philadelphicus</i>									0.40	3.34
<i>Helianthus petiolaris</i>							0.24	2.60	0.36	3.01
<i>Hymenoxys argentea</i>		0.6					0.05	0.51	0.22	1.84
<i>Liatris punctata</i>									0.02	0.17
<i>Lotus wrightii</i>									0.04	0.33
<i>Lupinus caudatus</i>		0.9								
<i>Penstemon</i> spp.	0.15	1.22	0.05	0.41						
<i>Petalostemum purpureum</i>									0.02	0.17
<i>Potentilla</i> spp.					0.10	1.16	0.21	2.32	0.08	0.67
<i>Pseudocymopterus montanus</i>	0.25	2.04	0.25	2.05	T	0.02				
<i>Senecio</i> spp.	0.05	0.41	0.05	0.41			0.03	0.28	0.02	0.17
<i>Solidago</i> spp.					0.20	2.26			0.04	0.33
Unknown	1.70	14.29								
Total Forb	4.38		4.43		1.8		0.82		2.06	
Shrubs										
<i>Robinia neomexicana</i>					T	0.02			0.70	5.85
<i>Rosa</i> spp.	0.05	0.41	0.05	0.41	0.10	1.16				
Total Shrubs	0.05		0.05		0.10				0.70	
<i>Pipo</i> Seedling							0.04	0.40		
Total Species	11		10		20		17		20	



Figure 21. — The 1976 plot, July 1977, 1 month post-fire.



Figure 22. — The 1976 plot, August 1993, 16 month post-fire.

Table 7. The diameter at breast height (inches) and growth rates (dbh increment/time period) through time of 34 ponderosa pine trees located on the 1976 plot.

Tree no.	1977	1985	1993	1993-1977	1993-1985	1985-1977	Damage class
221	7	7.6	8.8	1.8	1.2	0.6	4
156	9.1	10.1	11.4	2.3	1.3	1.5	1
157	4.4	5.8	7.7	3.3	1.9	1.4	1
158	4.8	6	7.4	2.6	1.4	1.2	1
159	10.7	12.2	14.5	3.8	2.3	1.5	1
161	9.5	11	12.6	3.1	1.6	1.5	1
165	18.1	18.8	19.5	1.4	0.7	0.7	1
166	16	16.8	17.7	1.7	0.9	0.8	1
185	7.4	8.2	9.8	2.4	1.6	0.8	1
186	5	6	6.6	1.6	0.6	1	1
187	4.9	5.3	5.6	0.7	0.3	0.4	4
189	4.4	4.7	5.1	0.7	0.4	0.3	4
190	5.6	5.6	6.2	0.6	0.6	0	2
191	5.5	6	6.4	0.9	0.4	0.5	4
192	5.7	6.2	7	1.3	0.8	0.5	4
193	4.5	4.2	4.5	0	0.3	-0.3	4
194	5.4	5.4	6.8	1.4	1.4	0	4
196	3.6	3.7	4.2	0.6	0.5	0.1	4
198	12	14	15.2	3.2	1.2	2	
200	6.8	7.1	7.6	0.8	0.5	0.3	3
201	8.6	9.2	10	1.4	0.8	0.6	1
202	8.2	9.1	10.7	2.5	1.6	0.9	2
204	6.9	7.8	9.1	2.2	1.3	0.9	1
206	5.5	5.7	6.2	0.7	0.5	0.2	1
207	6.5	6.7	6.9	0.4	0.2	0.2	1
208	5.6	6.2	6.4	0.8	0.2	0.6	1
209	4.9	5	9.1	4.2	4.1	0.1	
212	7.4	8.3	8.1	0.7	-0.2	0.9	3
213	6.4	7.9	8.6	2.2	0.7	1.5	
214	6.9	7.6	8.1	1.2	0.5	0.7	3
216	8.2	9.4	10.4	2.2	1	1.2	4
218	5.2	5.7	6.2	1	0.5	0.5	4
219	5.5	6.1	6.7	1.2	0.6	0.6	3
220	7.8	8.3	8.9	1.1	0.6	0.5	4
Total	237	260.1	291.2	54.2	31.1	23.1	70
Av. DBH	6.97	7.65	8.56				
Growth Rate				1.59	0.91	0.69	

and 1976 plots) had higher ground vegetation cover values in 1977, which then decreased in 1978 before recovering in later years. This could be a result of increased litter fall from dead needles or the effect of the nutrient flush that may have begun to dissipate in the second year after the fire. Plots lacking tree cover now have greater herbaceous and shrub cover than forested sites.

Soil Crusts

In the early data collections we did not collect understory information other than vegetative cover. In 1993, we took the data in 4 different elements—bare soil, litter, vegetation, and soil crusts. Since we did not record the soil crust cover from 1976 to 1985, we have no successional information. However, the areas that were most severely burned and devoid of trees had the highest cover of soil crusts (2.3 to 3.5 percent), while those areas that had lots of needle litter in 1993 had lower cover of soil crusts (0.14 to 1.6 percent).

Comparison of Planted Tree Sites with Natural Regeneration Sites

We compared four sites for pine regeneration (Table 8). Two of the sites were planted. Areas on the south rim of Water Canyon and on the north side of State Route 4, within the boundaries of Los Alamos National Laboratory (LANL), were planted with 2.0 stock in 1978. These areas now have a cover of 14.9 percent and a density of 1217 trees/hectare. An area directly south, on the south side of State Route 4, was planted with germinants (Foxy 1983). Seeds were germinated in containers and then the germinated seeds were planted. Perhaps 1000 pine seedlings of nursery origin were also planted in this area in 1986 (planting records on file at Bandelier National Monument). That area has a cover of 1.9 percent with 975 trees/hectare. Areas with only natural regeneration, exemplified by the 1937 and 1893 plots, have less than one percent cover and around 200 to 300 trees per acre. These

plots are adjacent to the 1960 plot which has living trees and have provided a seed source.

Growth of Trees

We compared the growth of trees that we were able to relocate in 1993 through time. The growth was compared in relationship to the amount of crown damage recorded in 1977 and by size class. Trees with lower degrees of crown damage (0 to 25 percent crown singed, classes 1 and 2) grew more during the past 17 years than those in the classes with more intense crown damage (with 50 to 75 percent of the crown singed, classes 3 and 4) (Figure 24). There did not appear to be any significant difference in recovery rate of trees by size class (Figure 25).

Grass Cover

When comparing between sites we saw a dramatic shift in the grass species from 1985 to 1993. The seeded grass, slender wheatgrass disappeared from the ecosystem sometime after 1985. In every plot that had slender wheatgrass as a dominant species within one year after the fire, this seeded

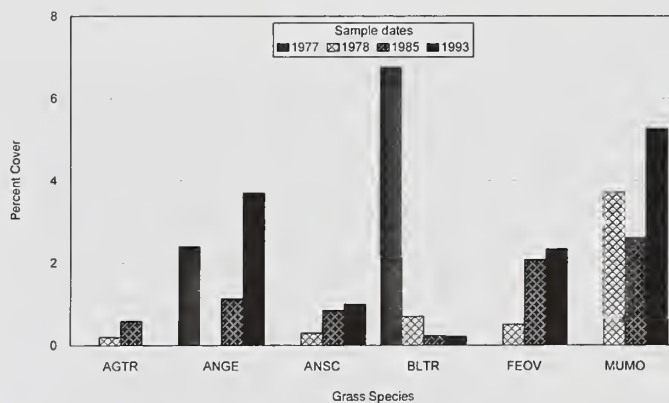


Figure 23. — Percent cover of dominant grass species in the 1976 plot through time. The species codes are the first two letters of the genus and species combined (see Table 6).

Table 8. Comparison of post-fire regeneration tree numbers, size and recovery as of 1993 in the sites planted with trees as compared to natural regeneration.

Location	Type of planting	Average diameter	Percent cover	Trees/hectare	Relative frequency
LANL, TA-26	2.0 Stock	1.9	14.9	1217	100
BNM, Ponderosa Campground Area	Germinants and someseedlings	1.1	1.9	975	100
1937 Burn Plot	None	.1	<1	318	75
1893	None	.6	<1	218	60

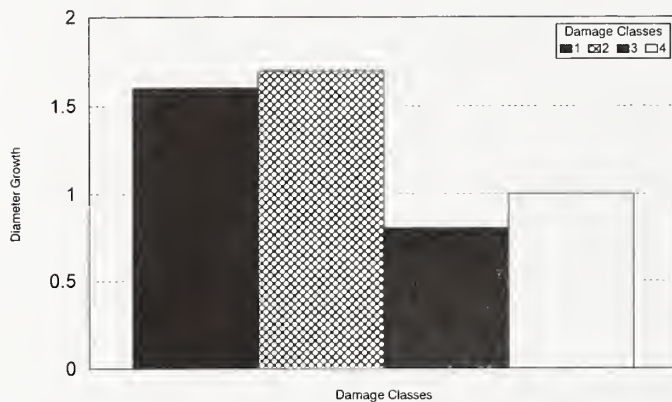


Figure 24. — Average diameter growth (inches of ponderosa from 1977 to 1993 by damage class.

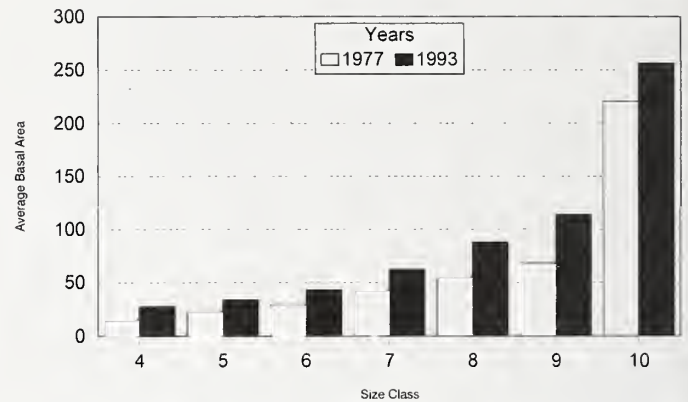


Figure 25. — Comparison of change in ponderosa pine basal area (square inches) from 1977 to 1993 by size class.

species disappeared from the study plots by 1993. This is consistent with the information in Flory and Marshall (1942). On the other hand, sheep fescue increased continuously through time on all plots, particularly in the areas where the tree canopy had been destroyed and there was little competition from tree canopy and native grasses. Native grasses also increased in cover from 1978 to 1993, with mountain muhly being the dominant species.

Species richness

The most interesting observation relative to species richness is that the areas which had burned severely were dominated early on by forbs, but as succession progressed the number of forb species then decreased through time. If the area had a good tree canopy, the change in forbs through time did not change as drastically. Note that this forb response was entirely due to the natural seed bank and resprouting, as no forb seed was applied by people after the fire. There were no set species patterns of forb dominance found in the early successional stages, with the exception of the prominence of goosefoot. This weedy species, which was found in abundance in the early years after the fire, soon disappeared as grasses and other forbs filled in the intensely burned areas. Also, buckbrush and big bluestem are two prominent species which were found in greater abundance by 1993 than prior to, or immediately after, the fire.

CONCLUSIONS

When comparing the four sites, there are several general summary observations that may be stated:

1) In areas where the tree canopy was destroyed, the successional recovery of understory cover is

linear. However, in areas where there was tree canopy, there was a reduced cover the second year and then a continued increased in cover percent from 1978 through 1993.

2) Soil crusts appear to be more extensive on sites that burned more intensely and which have less tree canopy and ground litter cover.

3) The seeded grass, slender wheatgrass, was a dominant species early in the post-fire succession but dropped out of the ecosystem after 1985.

4) Where there was little tree canopy cover, the seeded grass sheep fescue became more dominant than in the areas with more canopy cover. The grass does not seem to have markedly inhibited tree reproduction.

5) Certain plant species appear to be fire related, although post-fire successional patterns vary. For example, goosefoot was abundant after the fire through 1978, but disappeared from the ecosystem by 1985, whereas big bluestem has increased markedly through time since the fire at several sites.

6) Trees which sustained less fire damage to their crowns grew faster than trees which suffered more severe crown damage, but there seems to be little correlation between tree size and post-fire growth rate.

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Avifaunal Response to the 1977 La Mesa Fire

Terrell H. Johnson¹ and Roland H. Wauer²

Abstract.—Three of 4 breeding bird transects in habitats ranging from mixed conifer to pinyon-juniper were burned by the 1977 La Mesa Fire. Large portions (25–80 percent) of the 3 burned transects suffered forest loss from crown fire or scorching, but the pinyon-juniper transect did not burn. The transects were surveyed during the breeding season before the fire and 1, 2, 4, 6, and 14 years afterwards.

Species diversity increased after the fire, but breeding populations generally declined for several years before increasing above prefire levels. This temporary population decline was more pronounced and lasted longer on the more severely burned transects. Conversely, the population on the unburned pinyon-juniper transect temporarily increased after the fire. After 14 years, avian diversity and populations in the burn remained well above prefire levels, except on the transect with 80% forest loss, where the population was 22% lower due to a reduction in insectivores. Populations of seed-eating birds and raptors were consistently higher than before the fire. All 3 burned transects experienced both immediate and successional changes in species composition.

Even an uncontrolled crown fire such as the La Mesa Fire can increase the diversity and population of breeding birds. High fire intensity appears to delay recovery of avian populations from short-term postfire declines, and extensive crown fire appears to reduce populations after most snags have fallen, but even the most severely burned areas of the La Mesa Fire generally retained some live trees and snags and supported diverse, substantial populations of breeding birds after the fire. Application of moderate intensity prescribed fire to relatively dense stands such as those burned by the La Mesa Fire can enhance avian diversity and populations without the disadvantages of high intensity crown fires.

INTRODUCTION

In May and June, 1977, before the La Mesa Fire, Wauer began to survey 7 avian population transects in different habitats in Bandelier National Monument. In mid-June, 1977, the La Mesa Fire burned 3 transects (near Apache Spring, on Escobas Mesa, and on Burnt Mesa) and burned to within 400 m of a fourth (on Frijoles Mesa). These 4 transects are all located on the mesas between Frijoles Canyon and State Highway 4, ranging from higher to lower elevations in the order of Apache, Escobas, Burnt, and Frijoles. The major vegetation types range along the gradient from mixed conifer to pinyon-juniper (Table 1). Wauer and Johnson (1984) described vegetation on the 3

burned transects in more detail, as did Wauer and Dennis (1980) for the unburned Frijoles Mesa transect.

These 4 transects were again surveyed for breeding birds in 1978, 1979, 1981, 1983, and 1991—1, 2, 4, 6, and 14 years after the fire—except for Frijoles, which was not surveyed in 1983. Analysis of the short-term effects of the fire on avifauna, based on 1977–79 data for the 3 burned transects, was presented at the 1981 La Mesa Fire Symposium

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Table 1. Percent coverage of major vegetation types on four 40 ha bird transects before the La Mesa Fire. Data were derived from GIS analysis of Koehler (1974) and Potter and Foxx (1981) maps of prefire vegetation. Average transect elevations are in parentheses.

Vegetation type	Apache (2540 m.)	Escobas (2250 m.)	Burnt (2210 m.)	Frijoles (2030 m.)
Montane meadow	1			
Mixed conifer	51			
Ponderosa/mixed conifer	38	70		
Ponderosa pine	10	30	56	
Ponderosa/pinyon-juniper			44	41
Pinyon-juniper				59
Total	100	100	100	100

(Wauer and Johnson 1984). These included increased species diversity, marked increases in woodpeckers, and declines in total population. Subsequent surveys recorded long-term trends and succession after the fire. These data also highlight some differences among the transects, which can provide guidance for fire management.

METHODS

All transects were permanently marked fixed lines, each 1 mile long. Fifty-two 31 m intervals along the center line and four 31 m intervals on each side defined 416 cells that totaled 40 ha (Emlen 1971). Transects were surveyed during the first 2–3 hours after sunrise by slowly walking the transect line and recording all birds heard or seen on a gridded field form (Wauer and Johnson 1984). The species, type of detection (song, note, or sight), breeding activities, and movements were also recorded, making the field form a complete record of observations during the survey. Occasional excursions from the center line were made to aid identification and detection. All transects were surveyed during the height of the breeding season, on dates ranging from May 13 to June 17 for Frijoles, and May 16 to June 20 for Apache. Wauer initiated the study and did all the fieldwork in 1977, Johnson and Wauer each did half in 1978, Johnson did all the fieldwork in 1979, 1981 and 1983, and Wauer returned to do it all in 1991.

Each field form is essentially a map of the distribution of birds that were detected during that survey. For analysis, each survey was summarized by the counts of each species in each of the 4 lateral distance intervals, on either side of the center line. Breeding species were assumed to be paired and

counted in pairs, i.e., counting 2 for a singing male, an isolated individual, or 2 birds together. Conversely, non-breeding species were counted singly. Species were classified as breeding if they could breed in the habitat of each transect (whether or not firm evidence of breeding was recorded) or non-breeding if they were known not to breed in that habitat. Classification was based on personal observations and a local breeding bird atlas (Travis 1992). Birds were counted in the cell where they were first detected, and recorded movements were used to avoid double counting.

Rather than using coefficients of detectability to estimate population densities (Emlen 1977), an effective survey area was determined for each species, its population was estimated in that area, and the result was normalized to the density of birds per 40 ha. For each species, counts in each interval were totaled for all years and transects to judge the lateral range of intervals in which birds of that species were regularly detected, which was never less than 2 intervals. A regular detection range of 2, 3, or 4 intervals corresponded with an effective survey area of 20, 30, or 40 ha, and only birds counted within the detection range of each species were used to estimate its population (see Appendix 1). For 20% of the species (mainly the smaller flycatchers, nuthatches, and warblers), prefire and postfire detection ranges differed due to the loss of forest cover, and the smaller prefire ranges were used both before and after the fire.

Compared to mapping census techniques, transect surveys cover more ground and attempt to compensate for less precision with better statistics. The essential premise in estimating populations of breeding birds from survey counts is that they are paired and resident during the breeding season. Actually, some birds may not be paired, some may be moving through the area, and double counts are possible, all of which would exaggerate pair counts, but more birds are likely to be paired but sometimes undetected. Wauer and Johnson (1984) used the maximum count for each species as a reasonable estimator of population, because most breeding birds probably do meet the premise of being paired residents, and in that case the counts could not exceed the population. However, the maximum count is a statistically biased estimator because it tends to increase the more times a transect is surveyed, which varied from 3 to 6 times in our study (Table 2).

We refined this approach with the conjecture that the average maximum count should approach a

Table 2. Number of breeding species detected on each transect from 1977–1991. The number of surveys is listed in parentheses.

Transect	1977	1978	1979	1981	1983	1991
Apache	29 (1)	39 (5)	34 (3)	40 (5)	39 (6)	41 (3)
Escobas	32 (3)	31 (4)	30 (3)	34 (5)	39 (6)	36 (3)
Burnt	32 (4)	36 (5)	30 (3)	38 (4)	39 (5)	37 (3)
Frijoles	31 (5)	29 (3)	29 (4)	31 (3)	(0)	30 (3)
Average (total)	31 (13)	34 (17)	31 (13)	36 (17)	39 (17)	36 (12)

limit as the number of surveys increases, and that this limit is a better estimator of population. The actual maximum in any particular sample is likely to be less but may be more than the expected value of the maximum. The standard deviation of transect survey counts was low for highly detectable species such as solitary vireos, and high for less consistently detected species such as western bluebird. Nonetheless, the average maximum count, expressed as a number of standard deviations above the mean, was similar for all species. Combining all species in all years, the average maximum count exponentially approached a value of 1.58 standard deviations above the mean (Figure 1).

Assuming a normal distribution, the mean, standard deviation, and the variances of the sampling distributions of survey counts can be estimated (Bulmer 1979). From unbiased estimators of these values, the population of each breeding species on each transect each year was estimated as the mean plus 1.58 times the estimated standard deviation of its survey counts, and a standard error was calculated to represent the statistical uncertainty in this estimate. The variance provided an estimate of the standard error of the population estimate, which is a measure of the statistical variability of the data, and not necessarily of the uncertainty in the true population. True population uncertainty may also include a number of unquantifiable potential biases related to methods of gathering and analyzing data, which should not primarily affect comparisons between years or transects.

In cases where birds were readily detected and counts were consistent, e.g., 10–12 birds, the standard deviation was small and the population estimate was not far above the mean count, but in cases where birds were not as easily detected and the counts varied considerably, e.g., 0–12 birds, the standard deviation was large, and the estimate was well above the mean. In both cases, the estimate was generally similar to the maximum count. The

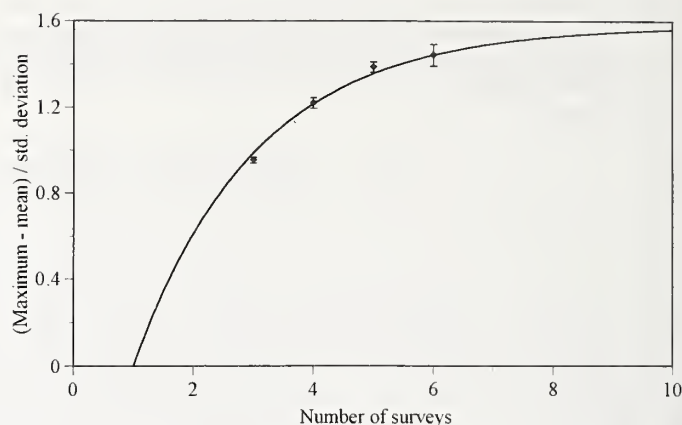


Figure 1. Average dependence of the maximum count on the number of surveys performed. The maximum count was measured by the number of standard deviations by which it exceeded the mean, which was similar for all species. Combining all species and transects, this plot shows the average value of the maximum count for 3 surveys ($n = 373$), 4 surveys ($n = 151$), 5 surveys ($n = 242$), and 6 surveys ($n = 82$). Error brackets display a range of plus or minus 1 standard error. An exponential approach to a limit was assumed, and the population of each breeding species was estimated as the mean plus 1.58 standard deviations of the sample count, which is unbiased by the number of surveys.

1977 data on Apache were limited to a single survey before the fire, so neither the standard deviation nor population can be estimated for that year.

The species diversity index was calculated as $H' = -\sum P_i \log(P_i)$, where P_i is the proportion of the total population filled by each species (Shannon and Weaver 1963). This number is higher the more species are present and the more equal the populations of each, but does not depend on the total population. No attempt was made to compensate for the tendency of the known number of species to increase with the number of surveys, which affects the species diversity index, or to estimate uncertainty in these results. Observer differences might also affect species totals through the ability of a more experienced observer to identify uncommon species quickly. However, the data do not manifest any obvious variations due to survey effort or observers. Biomass estimates were derived from population estimates and published average individual weights of each species (Bock and Lynch 1970; Salt 1957; Wauer and Dennis 1980; Terres 1980).

Classification of each species into nesting and foraging guilds (Appendix 1) was determined by observations and known behavior (Ehrlich et al. 1988; Terres 1980). Four nesting guilds were distinguished: ground, cavity, foliage, and parasitic. Spe-

cies were assigned to foraging guilds (Table 3) similar to those developed by Salt (1957), except that omnivores were placed in the category that best represents their primary consumption during the breeding season. These guilds represent both a kind of food gathered and a method of gathering it. Many species consume a variety of foods, e.g., both seeds and insects, and some gather it in a variety of ways, but each species was assigned to a single guild for purposes of comparison. Western and mountain bluebirds and Townsend's solitaires (all of which habitually swoop from perches to insects near the ground) and house wrens (which often glean insects from downed wood) were moved from the foliage insect guild (Wauer and Johnson 1984) to the ground insect guild to better distinguish their foraging habits from the more arboreal habits of warblers and vireos. Foraging guilds were grouped into those of primary consumers (seed and nectar), insectivores (including crustaceans and other invertebrates gathered in a variety of ways), and predators.

Habitat use by non-breeding species is not comparable to use by breeding species, but may be significant. For non-breeding species, which do not nest but may forage on a transect, the mean survey count was used instead of the maximum as a reasonable estimate of presence, and hence foraging use. Only breeding species were included in analyses of species richness and diversity, population, biomass, and nesting guilds, but foraging use esti-

mates for non-breeding species were combined with population estimates of breeding species in analysis of foraging guilds.

Potter and Foxx (1984) mapped foliar damage of trees in the La Mesa Fire area, and we used that information to assess the intensity and extent of the fire on and around each transect. Nearly all trees died in areas of crown fire (all needles consumed) or scorching fire (all needles browned), but many survived in areas of less intense ground fire (foliar damage classes 1–4). Browned needles, which subsequently fell to the ground and reduced erosion, indicate somewhat lower fire temperatures than consumed needles. The Escobas transect had the largest area of crown fire (one third). Combining areas of crown fire and scorching fire, Apache lost about one quarter of its forest, Escobas lost one third, and Burnt lost four fifths (Figure 2). Forest loss was proportionately greater on both the Apache and Burnt transects than in the surrounding areas, but it was similar in the case of Escobas.

Although the habitats on the 3 burned transects ranged from mixed conifer and ponderosa pine at higher elevations to ponderosa pine with pinyon-juniper at lower elevations (Table 1), and characteristics of the burn were different on each transect, their data were averaged. In a broad sense, all burned transects were forested with a component of ponderosa pine, and were burned by an intense, uncontrolled fire. They were also examined individually for information on response of avifauna in the specific habitats to different burn characteristics. The only unburned transect was pinyon-juni-

Table 3. Foraging guilds, modified from Salt (1957).

Consumer Category	Foraging guild	Abbreviation	Example
Primary	Ground seed	GS	Mourning dove
	Foliage seed	FS	Red crossbill
	Foliage nectar	FN	Broad-tailed hummingbird
Insectivore	Ground insect	GI	American robin
	Timber drilling insect	TDI	Hairy woodpecker
	Timber searching insect	TSI	White-breasted nuthatch
	Foliage insect	FI	Yellow-rumped warbler
	Air perching insect	API	Western wood-pewee
	Air soaring insect	ASI	Violet-green swallow
	Predator	Ground predator	GP

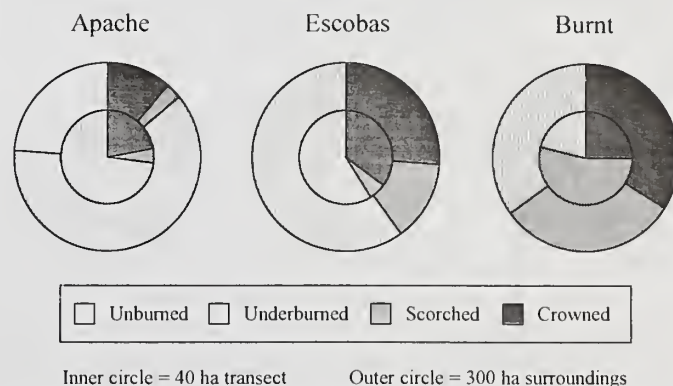


Figure 2. Relative extent and intensity of the La Mesa Fire on the 3 burned 40 ha transects and on 300 ha surrounding and including the transects. Nearly all trees died on both scorched and crowned areas, but the fire consumed all needles in the crowned areas. Data were derived from GIS analysis of the Potter and Foxx (1984) map of foliar damage.

per with ponderosa pine and we compared that to the 3 burned transects primarily as a check on methods, weather variations, and large scale trends. Finally, we have assumed orderly change to represent periods when transects were not surveyed. This is displayed graphically by straight lines connecting data of surveyed years.

RESULTS

Species Richness and Diversity

Overall, 85 species of birds were detected on a total of 89 transect surveys, including 71 breeding species, with 51 on Apache, 50 on Escobas, 51 on Burnt, and 38 on Frijoles. The average number of breeding species (richness) on the 3 burned transects temporarily increased the year after the fire, decreased the second year, increased from 2–6 years after the fire, and remained high thereafter. It followed the same pattern on each of the burned transects (Table 2), except that it did not increase the year after the fire on Escobas. The study period concluded with more breeding species on each burned transect than before the fire, increasing from 29 (only 1 survey) to 41 on Apache, 32 to 36 on Escobas, and from 32 to 37 on Burnt. In contrast, species richness on unburned Frijoles changed little, ranging from 29–31 throughout the study period.

Before the fire, the average breeding species diversity (H') on the 3 burned transects (Figure 3) was lower than on unburned Frijoles. Similar to

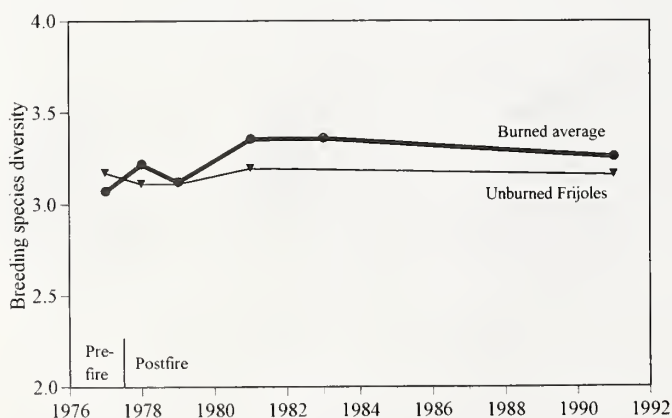


Figure 3. Shannon diversity index for populations of breeding birds on the 3 burned transects (Apache, Escobas, and Burnt) and the unburned Frijoles transect from 1977-1991. Dependence of diversity on species richness and hence the number of surveys performed (Table 2) precludes calculating standard errors for these data.

changes in the number of breeding species, species diversity on the 3 burned transects temporarily increased the year after the fire, increased from 2–4 years after the fire, and remained high thereafter. Species diversity on the unburned Frijoles transect changed little. Each of the 3 burned transects had similar species diversities before the fire and from 6–14 years after the fire, but differed during the period from 1–4 years after the fire, especially on Escobas, where diversity increased more slowly.

Population and Biomass

The average population of breeding birds on the 3 burned transects (Figure 4) dropped during the first 2 years after the fire, but recovered by the fourth year and remained high at the end of the study. In contrast, the population on unburned Frijoles was higher 1–4 years after the fire than before it, but thereafter declined to below its prefire level. Population trends on the 3 burned transects differed.

The Apache breeding bird population increased for 1–4 years after the fire (Figure 5), and declined slightly thereafter, but remained higher than immediately after the fire (the prefire population is uncertain). Some species, such as pygmy nuthatch and pine siskin, declined then recovered, while others, such as violet-green swallow and house wren, simply increased. Some species, such as mourning dove and several woodpeckers, were most common from 1–4 years after the fire.

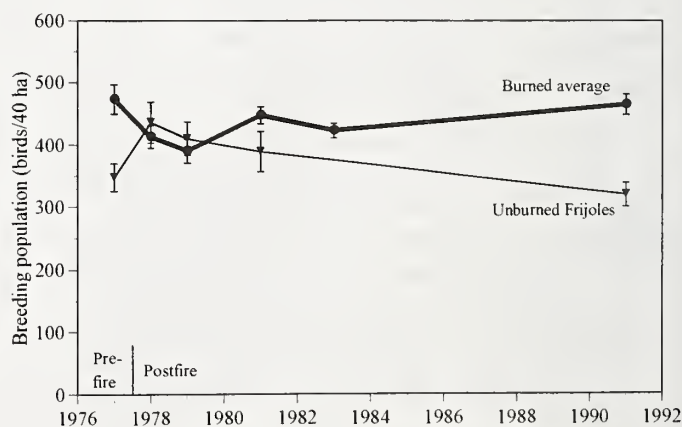


Figure 4. Population of breeding birds on the 3 burned transects (Apache, Escobas, and Burnt) and the unburned Frijoles transect from 1977-1991. Error bars display a range of plus or minus 1 standard error in the population estimates.

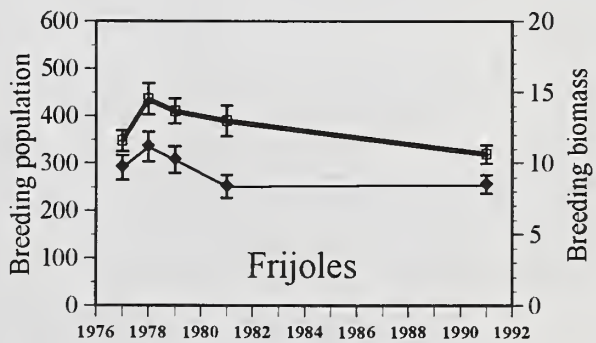
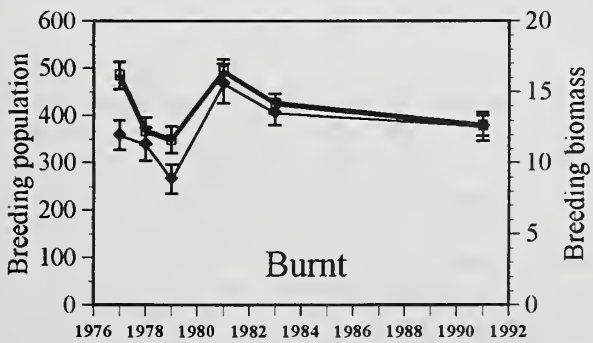
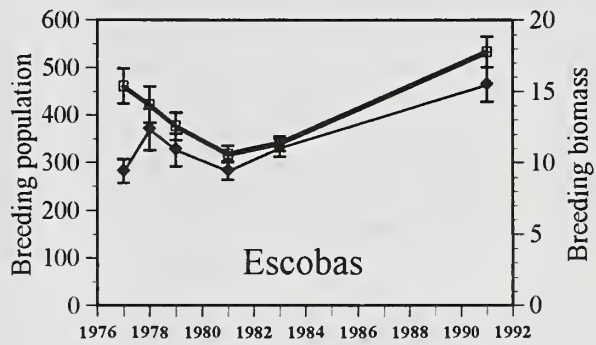
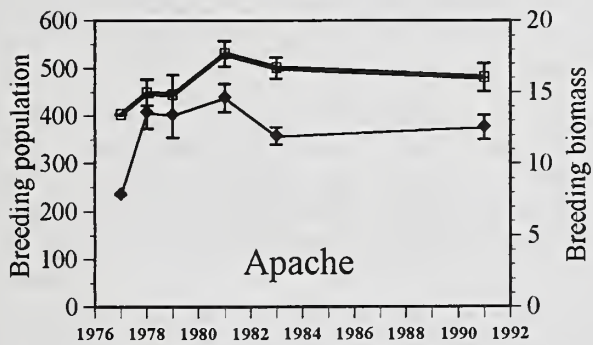
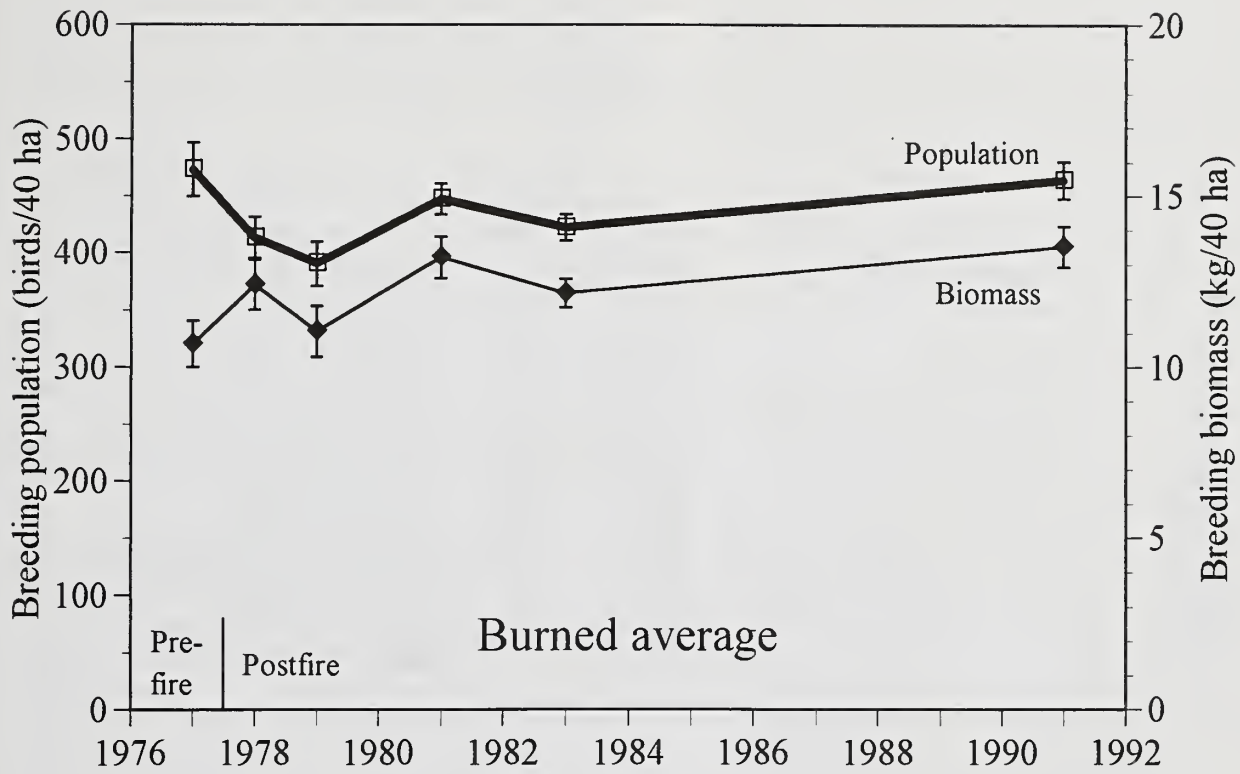


Figure 5. Population and biomass for populations of breeding birds on the 3 burned transects (Apache, Escobas, and Burnt) and each individual transect from 1977-1991. Error bars display a range of plus or minus 1 standard error in the population and biomass estimates. Apache data for 1977 were based on only 1 survey, and underestimate prefire values.

The Escobas breeding bird population declined to a minimum 4 years after the fire, then increased to its highest level at the end of the study (Figure 5). Some species, such as hermit thrush and Virginia's warbler were immediately reduced by the fire, while others, such as solitary vireo and yellow-rumped warbler, experienced slower declines. Some species, such as violet-green swallow and western bluebird, increased fairly steadily. Others, such as acorn woodpecker and rufous-sided towhee, did not appear until 6 years after the fire, and then increased markedly.

The Burnt breeding bird population decreased for 1–2 years, increased markedly the fourth year, but declined thereafter, ending lower than before the fire (Figure 5). Some species, such as Hammond's flycatcher and Grace's warbler, were initially reduced by the fire, and remained low, while others, such as mountain bluebird and black-headed grosbeak, increased from 2–4 years after the fire, then declined.

The average standing crop biomass of breeding birds on the 3 burned transects and unburned Frijoles were similar before and for the first 2 years after the fire, both with a temporary increase in total biomass the year after the fire (Figure 5). However, the burned average biomass increased 4 years after the fire and remained higher than before the fire, while the unburned Frijoles biomass decreased and remained lower than at the beginning of the study. As with population, the burned average biomass was compiled from broadly similar changes on Apache and Burnt and markedly different changes on Escobas.

Comparison of population and total biomass (Figure 5) reveals average bird biomass (biomass/population) in the relative position of the two graphs. At the chosen scales, when the biomass graph falls on top of the population graph, average bird mass is 33 g, and when the biomass graph is lower than the population graph, average bird mass is lower. Average bird mass on the 3 burned transects increased from about 23 g before the fire to 30 g after, and has remained higher than before. This increase was greatest and persisted throughout the study period on Escobas and Burnt, but lasted only 2–4 years on Apache. On unburned Frijoles, the average bird size decreased from 1–4 years after the fire.

Nesting guilds

Overall, average populations in the nesting guilds on the 3 burned transects (Figure 6) were

fairly steady except for a decreased number of foliage nesters the year after the fire and a temporary decrease in the number of cavity nesters 2 years after the fire. Parasitic nesters (solely the brown-headed cowbird) generally increased after the fire.

On Apache, where prefire data were not reliable, the population of ground nesters declined after the first postfire year, which was primarily due to a decline in dark-eyed juncos. Cavity nesters increased slightly but fairly steadily after the fire, due first to temporary increases in populations of several species of woodpeckers, then violet-green swallows, western bluebirds, and house wrens. Foliage nesters peaked 4 years after the fire, when populations of species such as warbling vireo and western tanager were highest.

On Escobas, changes in nesting guild populations were more dramatic. Populations of ground nesters, especially dark-eyed juncos, and cavity nesters, especially pygmy nuthatches and western bluebirds, were lowest 2 years after the fire, but foliage nesters were lowest 4 years after. Foliage nesters such as Hammond's flycatchers and Grace's warblers were still declining then, and increases in species such as broad-tailed hummingbird and Virginia's warbler had not yet overtaken those declines. The decline and recovery of foliage nesters took longest here, as some species were gradually replaced by others.

On Burnt, a dip in the population of cavity nesters occurred 2 years after the fire, as pygmy nuthatches suffered a delayed decline. Cavity nesters recovered from 2–4 years after the fire, led by western bluebirds and house wrens, but declined from 4–14 years after the fire, due to decreases in mountain bluebirds, black-headed grosbeaks and others. Foliage nesters also reached a low point 2 years after the fire, but increased from 2–4 years after the fire, led by rufous-sided towhees and lesser goldfinches.

On unburned Frijoles, ground nesters, especially Virginia's warblers, temporarily increased 2 years after the fire. Cavity nesters, such as western bluebirds, were actually less numerous 2–4 years after the fire than earlier or later, which is when they increased on Burnt. Foliage nesters, such as rufous-sided towhees and lesser goldfinches, were more numerous for 1–4 years after the fire. The parasitic nesting brown-headed cowbird increased more on this transect than on any other. Sometime from 4–14 years after the fire, ground and foliage nesting guilds declined to below their prefire populations, while cavity nesters maintained their numbers.

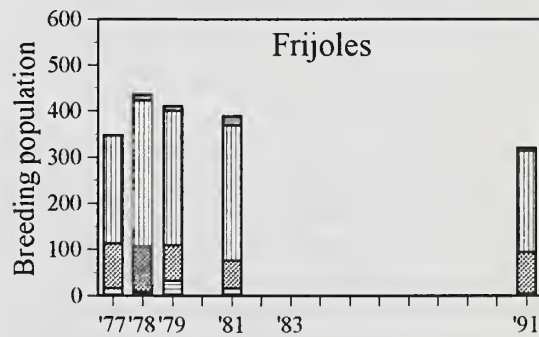
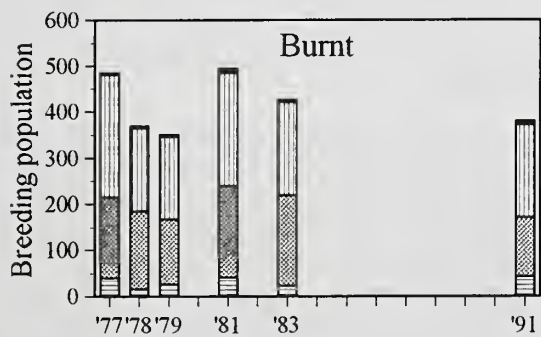
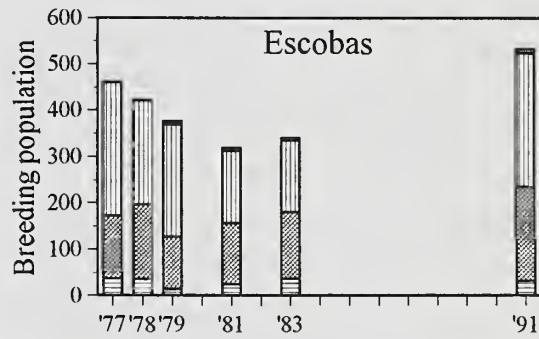
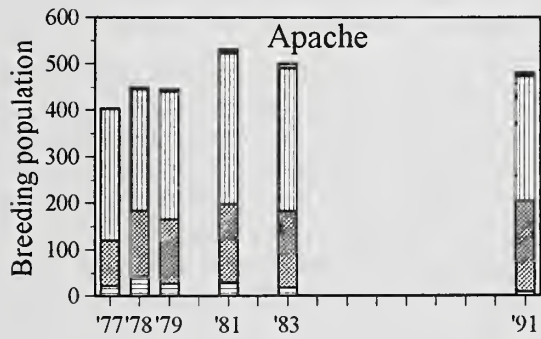
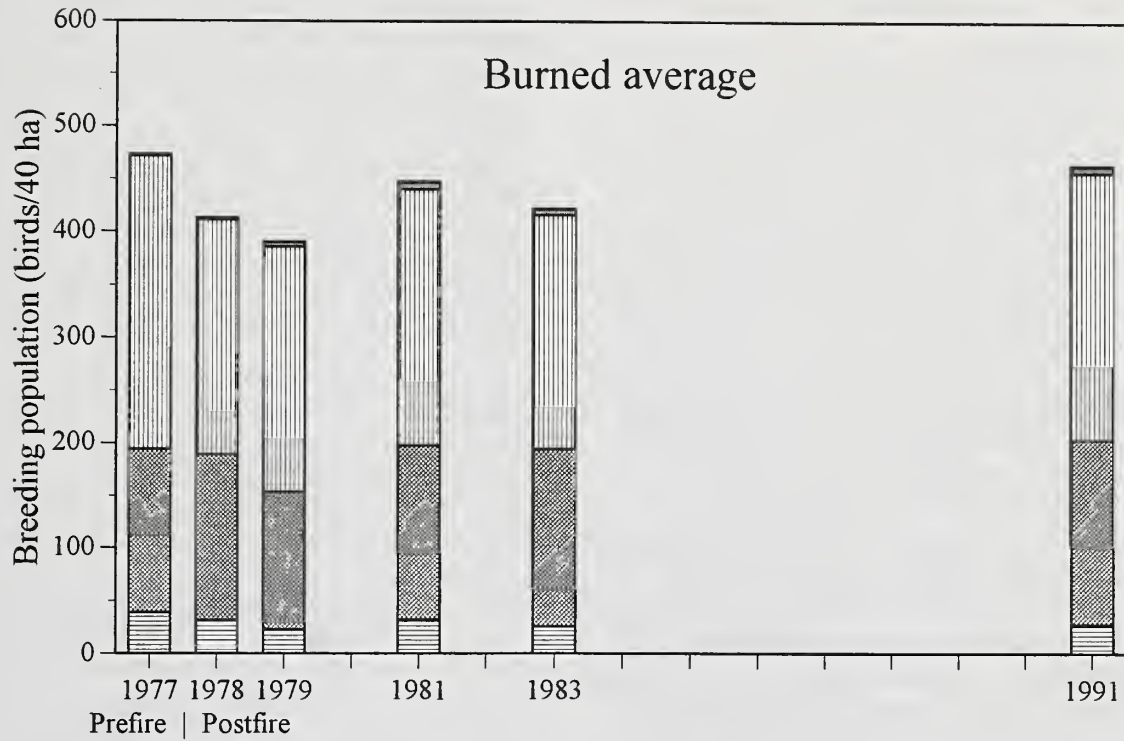


Figure 6. Populations of breeding bird nesting guilds on the 3 burned transects (Apache, Escobas, and Burnt) and each individual transect from 1977-1991. Apache data for 1977 were based on only 1 survey, and underestimate prefire values.

Foraging guilds

Primary consumers

Overall, populations of all primary consumers (ground seed, foliage seed, and foliage nectar guilds) on the 3 burned transects increased fairly steadily after the fire, except for a temporary decline in 1979 (Figure 7). The same pattern held on each of the 3 burned transects. By the end of the study, each of the guilds of primary consumers had increased well above prefire levels. The decline in population 2 years after the fire and recovery 4 years afterward occurred mainly in the foliage seed guild on all 3 burned transects, especially among Steller's jays and pine siskins. The foliage nectar guild, solely the broad-tailed hummingbird, increased markedly on all 3 burned transects.

On Apache, where prefire data were not reliable, population of the ground seed guild decreased somewhat from the year after the fire until the end of the study, but still remained higher than the single count before the fire. Long-term growth in the foliage seed guild was led by red crossbills and pine siskins, which overcame a decline in evening grosbeaks.

On Escobas, population of the ground seed guild was slightly higher the year after the fire, but fell back and did not increase significantly until near the end of the study, due to marked increases in rufous-sided towhees and mourning doves. Long-term growth in the foliage seed guild was led by red crossbills.

On Burnt, population of the ground seed guild was lower the first 2 years after the fire, but increased by the fourth year, led by rufous-sided towhees and dark-eyed juncos. The dark-eyed junco had declined by the end of the study, but the mourning dove and rufous-sided and green-tailed towhee had increased more. Population of the foliage seed guild did not change much, and ended the study near its prefire level.

On unburned Frijoles, primary consumers temporarily increased for 1–4 years after the fire. Population of the ground seed guild, led by rufous-sided towhees, was higher for 2 years after the fire than before, but returned to its prefire level by the end of the study. The foliage seed guild was higher for 4 years after the fire, due primarily to higher numbers of lesser goldfinches. The foliage nectar guild was slightly higher during the whole period after the fire than before.

Insectivores

Overall, total populations of all insectivores (ground insect, timber drilling insect, timber

searching insect, foliage insect, air perching insect, and air soaring insect guilds) on the 3 burned transects decreased the year after the fire, but changed little thereafter (Figure 8). However, only the timber drilling and timber searching insect guilds responded similarly on all 3 transects. Average timber drilling insect guild (woodpecker) populations increased during the first year after the fire, especially hairy and three-toed woodpeckers. At the same time, the timber searching insect guild (nuthatches) decreased for the first 2 years after the fire, and never recovered to prefire levels.

Overall, populations of the ground insect guild increased, as increases in western bluebirds and house wrens overwhelmed dramatic losses of hermit thrushes, but details differed among transects. The foliage insect guild decreased after the fire, due to loss of warbler habitat, but responses were different on the 3 burned transects. The air perching insect guild includes all the flycatchers and changed little, except for being lower the year after the fire, due primarily to decreases in Empidonax flycatchers, but that response was not universal. The air soaring insect guild is dominated by the violet-green swallow, and generally increased after the fire, but this did not occur everywhere either.

On Apache, where prefire data were not reliable, population of the ground insect guild appeared to decrease initially, then gradually increased, driven by a steady increase in western bluebirds. The foliage insect guild remained steady after the fire, but fell back at the end of the study, when warbling vireos and Grace's warblers decreased. The air perching insect guild remained fairly steady except for the year after the fire, but populations of Hammond's flycatchers and western wood-pewees varied and tended to compensate for each other. The air soaring insect guild increased fairly steadily.

On Escobas, population of the ground insect guild changed little before increasing in the final year of the study, due to a marked increase in western bluebirds. The foliage insect guild decreased initially, and again after 2 years, due to similar trends in yellow-rumped and Grace's warblers. Virginia's warblers, which were not found here for 2 years after the fire, increased toward the end of the study, as the habitat became more shrubby. Unlike the other transects, the air perching insect guild did not decrease on Escobas the year after the fire, but it was lower 4–6 years later, due to decreases in Hammond's flycatchers. The air soaring insect guild increased slowly but steadily.

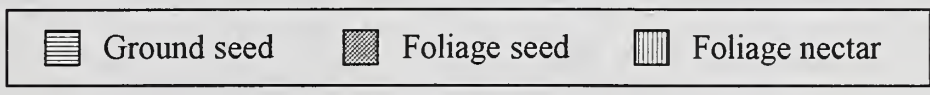
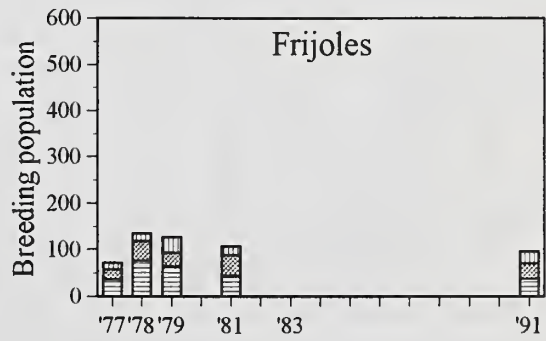
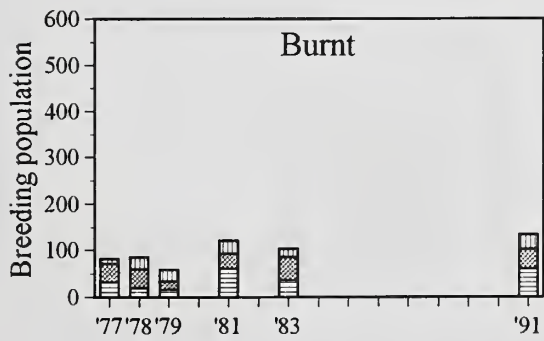
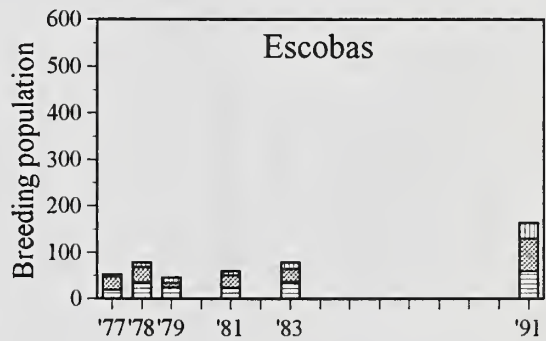
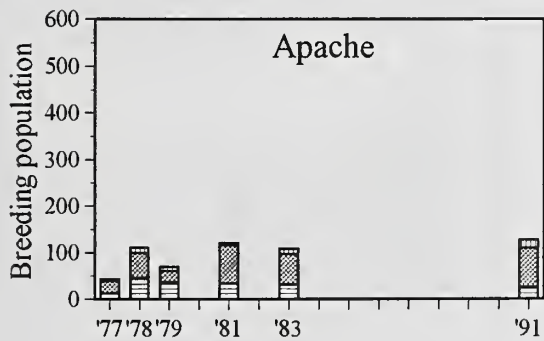
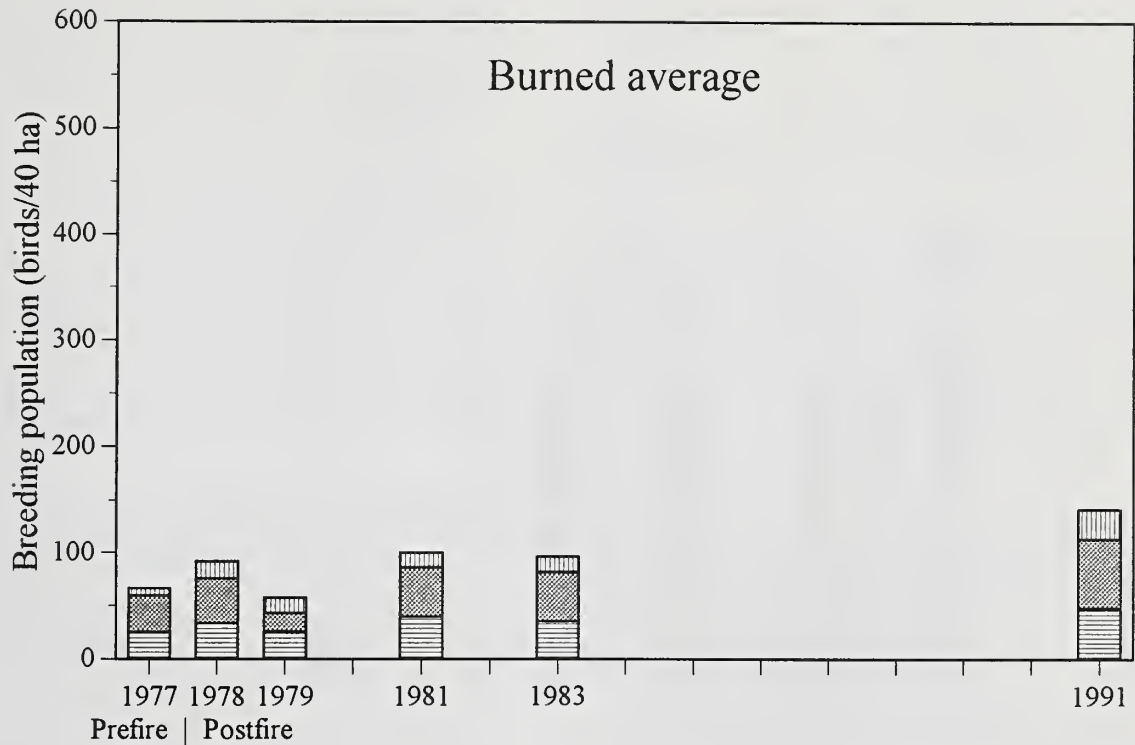


Figure 7. Populations of 3 avian primary foraging guilds on the 3 burned transects (Apache, Escobas, and Burnt) and each individual transect from 1977-1991. Apache data for 1977 were based on only 1 survey, and underestimate prefire values.

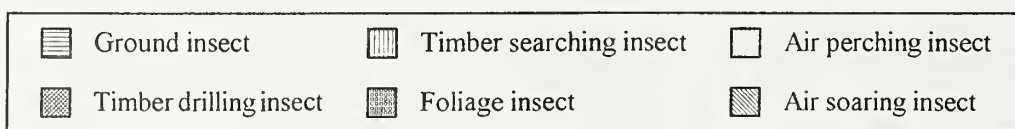
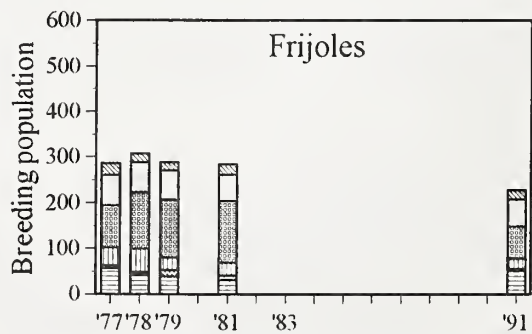
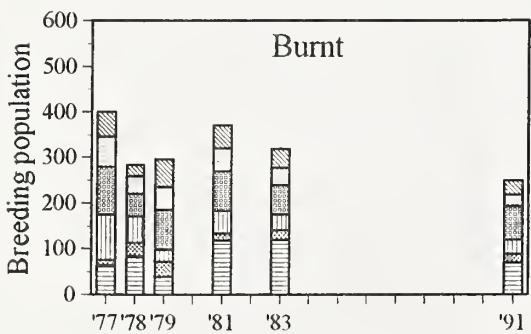
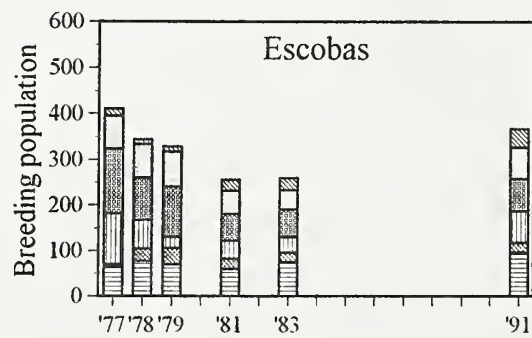
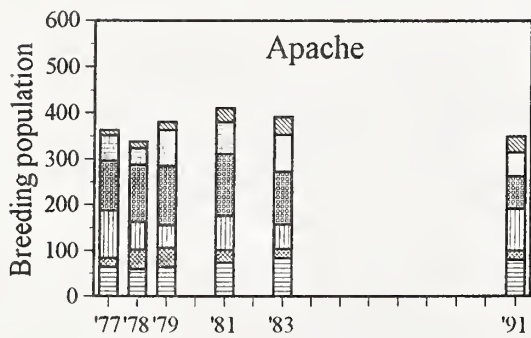
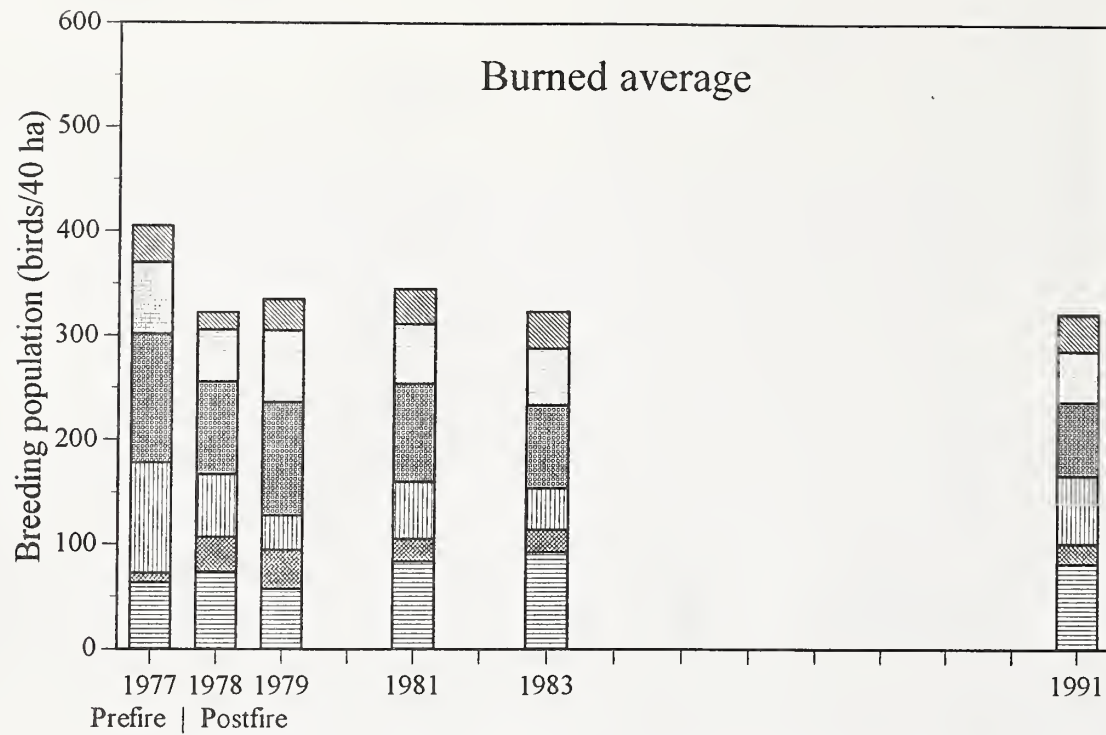


Figure 8. Populations of 6 avian insect foraging guilds on the 3 burned transects (Apache, Escobas, and Burnt) and each individual transect from 1977-1991. Apache data for 1977 were based on only 1 survey, and underestimate prefire values.

On Burnt, population of the ground insect guild was variable after the fire, except for being markedly higher from 4–6 years after the fire, due to the temporary appearance of many mountain bluebirds and lasting increases in house wrens and western bluebirds. The foliage insect guild was lowest the year after the fire, but fairly steady after that, as solitary vireos and Virginia's warblers increased the second year. The air perching insect guild not only declined temporarily the year after the fire, but declined again toward the end of the study, due to a decline in western wood-pewees. The air soaring insect guild decreased the year after the fire, rebounded, and subsequently declined slowly.

On unburned Frijoles, population of the ground insect guild decreased gradually through most of the study, but recovered at the end of the study, due to a marked increase in western bluebirds. The timber drilling insect guild was higher from 2–4 years after the fire. The foliage insect guild population was slightly higher for 1–4 years after the fire, especially plain titmice and black-throated gray warblers, neither of which occurred in the fire area. The air perching and air soaring insect guilds remained steady throughout the study.

Predators

The ground predator guild includes all raptors, even those that take their prey in the air. Population density estimates for these species are variable, as their territories are much larger than the transects, and a nest may be located on the transect one year and elsewhere the next. Nonetheless, enough species were involved that predator guild totals consistently increased on each of the 3 burned transects (Appendix 4). Raptor foraging populations did not change on unburned Frijoles. American kestrels were the most consistently found nesting raptor on each burned transect, and they increased especially 4–14 years after the fire.

DISCUSSION

Fire Effects

Apache was the least intensely burned transect, where about one quarter of the mainly mixed conifer forest was lost. This extent of burn seems to have resulted in increased diversity, with a relatively quick recovery of forest species. Although Burnt suffered much more extensive forest loss than Apache, about 80% compared to 25%, both

transects experienced about the same amount of crown fire (Figure 2). The population on Burnt peaked during a window of time when snags were falling but still plentiful, and the ground was still open, and then declined as the snags disappeared and the habitat became more brushy.

Escobas experienced more forest loss than Apache and less than Burnt, and is located midway between the elevations of Apache and Burnt, but it had the largest area of crown fire. We found no other feature that separated Escobas from Apache and Burnt, and assume that this greater extent of crown fire accounts for the longer decline and slower recovery of the population on Escobas than on Apache or Burnt.

Bird biomass data indicate that, on average, more large and fewer small birds were found after the fire. The strength of the effect seems to be related to the extent of forest loss, as average mass increase was smallest and temporary on Apache, but continued through the end of the study on Burnt. Birds that are more suited to the more open habitat found after extensive forest loss, such as Lewis' woodpecker, tend to be larger, and birds that are suited to living among the branches of trees, such as Grace's warbler and pygmy nuthatch, tend to be smaller. While fewer small birds occupied the burned transects after the fire, more small birds occupied Frijoles for 1–4 years after the fire. However, this is evidently not directly related to the fire, as the only species that increased significantly on Frijoles while decreasing significantly on Burnt was the rufous-sided towhee, a larger than average bird. Two species that were not even present on the burned transects, black-throated gray warbler and plain titmouse also increased significantly on unburned Frijoles. It is possible that weather conditions or deposition of airborne ash temporarily increased the biological productivity of the Frijoles transect.

Experience with Frijoles and other transects where the habitat was not changing suggests that annual population variations of as much as 20% are possible due to weather and other causes. Weather may cause some species to shift their breeding to higher or lower elevations in warmer and drier or colder and wetter seasons. For example, 1979 was a cold, wet season, and was the only year of our study that the ruby-crowned kinglet or orange-crowned warbler were found on Escobas or the warbling vireo or dark-eyed junco were found on Frijoles. Also, higher or lower productivity one year may affect breeding populations

the next year. Pygmy nuthatches generally took 2 years to reach their lowest level on the 3 burned transects, while woodpecker populations took the same time to peak. The increase in numbers of woodpeckers on Frijoles from 2–4 years after the fire, seems like an overflow from the earlier and larger increase of woodpeckers on the burned transects.

A note of caution should be sounded concerning the possibility that long-term effects other than fire succession might be operating on the avifauna over the 14 years of this study. In particular, large scale trends in populations of neotropical migrants are in question. From 1981–1991, populations on Apache, Burnt, and Frijoles all declined, and only the population on Escobas increased. Because the transects were surveyed only 1 year after 1983, more data are needed to determine if any declines in neotropical migrants could be account for some of the population changes observed here.

Ecological relationships

The most obvious effect of a high intensity fire such as the La Mesa Fire is to kill trees, creating more open habitat and initiating a series of successional events. It is important to realize that none of the fire-killed trees were removed in Bandelier, and the presence of snags and downed logs benefited the avifauna (Moeur and Guthrie 1984). While site-specific ecological succession after the La Mesa Fire was to a large extent a function of the different habitat of each transect and the different intensities and extents of forest loss each transect sustained, some generalities are apparent. These are summarized in Table 4.

Successional events began with the establishment of more herbaceous growth in the first 1–2 years, in both more open forested areas and in deforested areas with abundant snags. The year after the fire, perennial or annual grasses and forbs seeded artificially or naturally the year before often

Table 4. Ecological succession after the La Mesa Fire.

Period	Environmental change	Favored species	Disfavored species
1-2 yrs	Forest and foliage loss		Pygmy nuthatch Mountain chickadee Ruby-crowned kinglet Orange-crowned warbler Grace's warbler Pine siskin
	Abundant snags, wood insects	Hairy woodpecker Three-toed woodpecker	
	Open understory	Western bluebird	Hermit thrush Virginia's warbler Rufous-sided towhee
2-4 yrs	Abundant nutrients, vigorous herbaceous growth, seed production	Broad-tailed hummingbird Dark-eyed Junco	
	Increasing ground debris	House wren	
	Falling snags, declining wood insects	Mountain bluebird Violet green swallow Olive-sided flycatcher	Hairy woodpecker Three-toed woodpecker
4-14 yrs	Mature herbaceous layer, seed production	Mourning dove	
	Shrubs developing	Virginia's warbler	
	Shrubs, aspen maturing, most snags fallen	Dusky flycatcher Rufous-sided towhee Green-tailed towhee	Mountain bluebird
	Tree foliage recovering	Pygmy nuthatch Grace's warbler	
	Acorn production	Acorn woodpecker Lewis' woodpecker	

grew to gigantic proportions, fertilized by nutrients released by the fire. This may account for increased avian populations that year, which took place among primary consumers (Figure 7), but not among insectivores (Figure 8). Mortality of so many trees provided a short term benefit to woodpeckers, as insects proliferated within fire-killed trees, but evidently reduced the availability of insects on the bark, as nuthatches declined dramatically (Figure 8).

From 2–4 years after the fire, many snags fell, more structure was added to the ground, and the herbaceous layer became more fully developed. Bluebirds and house wrens benefited from these changes. Finally (in our study period), from 4–14 years after the fire, some snags persisted, understory shrubs grew in surviving forest patches, and brush developed in deforested areas. Primary consumers, such as towhees and hummingbirds, continued to increase, and species that utilize acorns, such as acorn woodpecker, appeared. Species associated with shrubs, such as Virginia's warbler and the towhees multiplied.

Not a single species of bird detected before the fire failed to be detected afterwards. On the other hand, by creating diversity in the physical habitat, the La Mesa Fire created openings for species that were not found there before the fire. Not counting rarely detected species, which are not adequately represented by just 1 year of prefire data, fully 11 breeding species that had not been found on the 3 burned transects before the fire were found there afterwards. These include the northern goshawk, American kestrel, Lewis' and acorn woodpecker, olive-sided flycatcher, rock, canyon and house wren, mountain bluebird, green-tailed towhee, and Cassin's finch. Populations of some species, such as Steller's jay, Townsend's solitaire, and American robin were generally little changed by the fire.

Habitat preferences of each species dictate where it will be found. Several examples illustrate this. The three-toed woodpecker prefers, and is able to find, recent burns. Before the fire, it was only found in a recent (1976) burn on one transect, whereas it was found on all 3 burned transects for 1–6 years after the fire. It was not detected on any transect 14 years afterwards. The mountain bluebird prefers open grassland situations, and was not found before the fire. Unlike the western bluebird, which increased the year after the fire, the mountain bluebird did not appear in numbers until 4–6 years afterwards, when snag fall had resulted in more open habitat. Like the three-toed wood-

pecker, it had disappeared by the end of the study, as brush had encroached on the grassland habitat. The green-tailed towhee, acorn and Lewis' woodpecker did not appear until 4–6 years after the fire, when some of the habitat became brushy, oaks became productive, and many old cavities became available in snags.

Predators increased, probably due to increased prey availability, as the northern goshawk, for example, nested near the Burnt transect 4 years after the fire, which was well below its normal nesting elevation. The spotted owl, which is generally viewed as an inhabitant of dense, old growth forests, was not detected in this daytime study but was known throughout the study period to inhabit canyons within the fire area where most of the forest was underburned. Spotted owls have also been heard at night in areas of adjacent mesas that were deforested by the fire, which still provide both hunting perches and abundant prey.

CONCLUSIONS

The avifauna adapted well to the changing conditions brought about by the 1977 La Mesa Fire. On each of the 3 burned transects, species richness and diversity increased. Prefire conditions generally included fairly uniform stands of dense, second-growth forest, which were variously replaced by more open forests or complete loss of forest. Species that lacked habitat before the fire found it in these new, varied conditions, while all of the species present before the fire continued to find some habitat afterwards.

The effect of the fire on the total avian breeding population depended on the severity of the burn. On Apache, where the burn was least severe and about one quarter of the forest was lost, the population increased. On Escobas, where the intensity of the fire was greatest (the most crown fire), and about one third of the forest was lost, the population declined for 4 years, then increased above its prefire level. On Burnt, where the fire intensity was not as great as on Escobas, but four fifths of the forest was lost, the population declined for 2 years, increased to peak after 4 years, then declined to a lower level than before the fire. By comparison, the population on unburned Frijoles was temporarily higher after the fire.

Several management lessons are apparent. Fire has beneficial effects on avian diversity, and moderate fire can increase populations. Up to 25% forest loss in a 40 ha transect (Apache) does not seem

to affect total breeding bird populations, and provides habitat for a diverse avifauna, at least when fire-killed trees are left standing. Therefore, managers who are attempting to restore fire to the ecosystem should not be too concerned if 10 ha pockets of tree mortality occur during the process. However, intense crown fire (Escobas) appears to depress and delay recovery of bird populations, and extensive forest loss (Burnt) appears to result in a long-term lower population. In both cases, the resulting habitat still supports diverse bird populations, but crown fire and extensive forest loss should be avoided by implementing prescribed and natural fire plans to restore the role of fire as a natural ecosystem process.

ACKNOWLEDGMENTS

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Appendices

Appendix 1. Avifauna species data. Foraging guild abbreviations are listed in Table 3. Area is the effective survey area, which depends on the detectability of each species.

Common name	Latin name	Weight (g)	Nesting Guild	Foraging Guild	Area (ha)
Turkey Vulture	<i>Cathartus aura</i>	2030.0	Ground	GP	40
Sharp-shinned Hawk	<i>Accipiter striatus</i>	177.0	Foliage	GP	40
Cooper's Hawk	<i>Accipiter cooperii</i>	428.5	Foliage	GP	40
Northern Goshawk	<i>Accipiter gentilis</i>	937.5	Foliage	GP	40
Red-tailed Hawk	<i>Buteo jamaicensis</i>	1105.0	Foliage	GP	40
American Kestrel	<i>Falco sparverius</i>	113.5	Cavity	GP	40
Peregrine Falcon	<i>Falco peregrinus</i>	699.0	Cavity	GP	40
Band-tailed Pigeon	<i>Columba fasciata</i>	406.0	Foliage	GS	40
Mourning Dove	<i>Zenaida macroura</i>	137.5	Foliage	GS	40
Great Horned Owl	<i>Bubo virginianus</i>	1971.0	Cavity	GP	20
Northern Pygmy-Owl	<i>Glaucidium gnoma</i>	52.5	Cavity	GP	30
Common Nighthawk	<i>Chordeiles minor</i>	80.0	Ground	ASI	30
Common Poorwill	<i>Phalaenotilus nuttallii</i>	47.3	Ground	GI	20
White-throated swift	<i>Aeronautes saxatalis</i>	14.5	Cavity	ASI	30
Black-chinned Hummingbird	<i>Archilochus alexandri</i>	2.5	Foliage	FN	20
Broad-tailed Hummingbird	<i>Selasphorus platycercus</i>	4.0	Foliage	FN	20
Lewis' Woodpecker	<i>Melanerpes lewis</i>	138.0	Cavity	TDI	30
Red-headed Woodpecker	<i>Melanerpes erythrocephalus</i>	73.2	Cavity	TDI	40
Acorn Woodpecker	<i>Melanerpes formicivorus</i>	67.4	Cavity	TDI	40
Red-naped Sapsucker	<i>Sphyrapicus nuchalis</i>	45.0	Cavity	TDI	40
Williamson's Sapsucker	<i>Sphyrapicus thyroides</i>	61.5	Cavity	TDI	40
Downy Woodpecker	<i>Picoides pubescens</i>	26.5	Cavity	TDI	30
Hairy Woodpecker	<i>Picoides villosus</i>	69.8	Cavity	TDI	30
Three-toed Woodpecker	<i>Picoides tridactylus</i>	62.0	Cavity	TDI	30
Northern Flicker	<i>Colaptes auratus</i>	145.0	Cavity	GI	40
Olive-sided Flycatcher	<i>Contopus borealis</i>	31.5	Foliage	API	40
Western Wood-Pewee	<i>Contopus sordidulus</i>	14.0	Foliage	API	30
Hammond's Flycatcher	<i>Empidonax hammondii</i>	12.1	Foliage	API	20
Dusky Flycatcher	<i>Empidonax oberholseri</i>	12.5	Foliage	API	20
Gray Flycatcher	<i>Empidonax wrightii</i>	12.6	Foliage	API	30
Cordilleran Flycatcher	<i>Empidonax occidentalis</i>	12.5	Cavity	API	30
Say's Phoebe	<i>Sayornis saya</i>	18.8	Cavity	API	40
Ash-throated Flycatcher	<i>Myiarchus cinerascens</i>	27.6	Cavity	API	30
Cassin's Kingbird	<i>Tyrannus vociferans</i>	45.4	Foliage	ASI	40
Violet-green Swallow	<i>Tachycineta thalassina</i>	10.6	Cavity	ASI	20
Cliff Swallow	<i>Hirundo pyrrhonota</i>	12.5	Cavity	ASI	30
Steller's Jay	<i>Cyanocitta stelleri</i>	106.5	Foliage	FS	40
Scrub Jay	<i>Aphelocoma coerulescens</i>	72.0	Foliage	FS	40
Pinyon Jay	<i>Gymnorhinus cyanocephalus</i>	108.0	Foliage	FS	40
Clark's Nutcracker	<i>Nucifraga columbiana</i>	130.0	Foliage	FS	40
Common Raven	<i>Corvus corax</i>	1027.0	Cavity	GP	40
Mountain Chickadee	<i>Parus gambeli</i>	11.5	Foliage	TSI	20
Plain Titmouse	<i>Parus inornatus</i>	15.0	Foliage	FI	30
Bushtit	<i>Psaltriparus minimus</i>	5.8	Foliage	FI	20
Red-breasted Nuthatch	<i>Sitta canadensis</i>	10.1	Cavity	TSI	30
White-breasted Nuthatch	<i>Sitta carolinensis</i>	18.0	Cavity	TSI	30
Pygmy Nuthatch	<i>Sitta pygmaea</i>	10.0	Cavity	TSI	20
Brown Creeper	<i>Cethia americana</i>	7.7	Cavity	TSI	20
Rock Wren	<i>Salpinctes obsoletus</i>	16.4	Ground	GI	30
Canyon Wren	<i>Catherpes mexicanus</i>	16.0	Ground	GI	30
Bewick's Wren	<i>Thryomanes bewickii</i>	10.1	Cavity	FI	30
House Wren	<i>Troglodytes aedon</i>	10.0	Cavity	GI	40
Golden-crowned Kinglet	<i>Regulus satrapa</i>	5.1	Foliage	FI	20

continued

Appendix 1. Avifauna species data. Foraging guild abbreviations are listed in Table 3. Area is the effective survey area, which depends on the detectability of each species (continued).

Common name	Latin name	Weight (g)	Nesting Guild	Foraging Guild	Area (ha)
Ruby-crowned Kinglet	<i>Regulus calendula</i>	6.1	Foliage	FI	30
Blue-gray Gnatcatcher	<i>Poliptila caerulea</i>	5.0	Foliage	FI	20
Western Bluebird	<i>Sialia mexicana</i>	24.6	Cavity	GI	30
Mountain Bluebird	<i>Sialia currucoides</i>	26.6	Cavity	GI	30
Townsend's Solitaire	<i>Myadestes townsendi</i>	32.0	Cavity	GI	30
Hermit Thrush	<i>Catharus guttatus</i>	25.6	Foliage	GI	30
American Robin	<i>Turdus migratorius</i>	88.0	Foliage	GI	40
Solitary Vireo	<i>Vireo solitarius</i>	15.3	Foliage	FI	30
Warbling Vireo	<i>Vireo gilvus</i>	11.3	Foliage	FI	30
Orange-crowned Warbler	<i>Vermivora celata</i>	9.6	Foliage	FI	30
Virginia's Warbler	<i>Vermivora virginiae</i>	8.4	Ground	FI	20
Yellow Warbler	<i>Dendroica petechia</i>	9.3	Foliage	FI	30
Yellow-rumped Warbler	<i>Dendroica coronata</i>	13.1	Foliage	FI	30
Black-throated Gray Warbler	<i>Dendroica nigrescens</i>	7.5	Foliage	FI	30
Grace's Warbler	<i>Dendroica graciae</i>	7.5	Foliage	FI	20
MacGillivray's Warbler	<i>Oporornis tolmiei</i>	10.8	Foliage	FI	30
Hepatic Tanager	<i>Piranga flava</i>	40.0	Foliage	FI	40
Western Tanager	<i>Piranga ludoviciana</i>	29.0	Foliage	FI	30
Black-headed Grosbeak	<i>Pheucticus melanocephalus</i>	46.0	Foliage	FI	40
Green-tailed Towhee	<i>Pipilo chlorurus</i>	34.0	Foliage	GS	40
Rufous-sided Towhee	<i>Pipilo erythrophthalmus</i>	39.0	Foliage	GS	30
Canyon Towhee	<i>Pipilo fuscus</i>	45.9	Ground	GS	40
Chipping Sparrow	<i>Spizella passerina</i>	12.2	Foliage	GI	30
Dark-eyed Junco	<i>Junco hyemalis</i>	20.3	Ground	GS	30
Brewer's Blackbird	<i>Euphagus cyanocephalus</i>	65.1	Ground	GI	30
Brown-headed Cowbird	<i>Molothrus ater</i>	34.8	Parasitic	GS	30
Cassin's Finch	<i>Carpodacus cassinii</i>	27.6	Foliage	FS	40
House Finch	<i>Carpodacus mexicanus</i>	19.3	Foliage	FS	40
Red Crossbill	<i>Loxia curvirostra</i>	38.5	Foliage	FS	30
Pine Siskin	<i>Carduelis pinus</i>	12.1	Foliage	FS	30
Lesser Goldfinch	<i>Carduelis psaltria</i>	8.7	Foliage	FS	30
Evening Grosbeak	<i>Coccothraustes vespertinus</i>	64.2	Foliage	FS	30

Appendix 2: Survey data (birds/40 ha). An asterisk marks each transect where a species breeds. Statistical uncertainty in each population estimate is indicated by plus or minus 1 standard error, except on Apache in 1977, where only 1 prefire survey occurred.

Species	Breed Transect	1977	1978	1979	1981	1983	1991
Turkey Vulture	Apache	0	0.2 ±.2	0.3 ±.3	0	0	0.7 ±.3
	Escobas	0	0	0	0	0	0
	Burnt	0	0	0	0	0	2 ±.3
	Frijoles	0	0	0.3 ±.3	0.7 ±.3	—	0.7 ±.7
Sharp-shinned Hawk	* Apache	0	0	0	0	0.8 ±.3	0
	Escobas	0	0	0	0	0	0
	Burnt	0	0	0	0	0	0.3 ±.3
	Frijoles	0	0	0	0	—	0
Cooper's Hawk	* Apache	0	0	0	0	0	1 ±.7
	* Escobas	0	0	2 ±1	0.9 ±.4	2 ±.7	0
	* Burnt	1 ±.5	0.9 ±.4	0	0	0	0
	Frijoles	0	0	0	0	—	0.3 ±.3
Northern Goshawk	* Apache	0	0	1 ±.7	0	0	0
	Escobas	0	0	0	0	0	0
	* Burnt	0	0	0	3 ±1	0	0
	Frijoles	0	0	0	0	—	0
Red-tailed Hawk	Apache	0	0	0	0	0	0
	Escobas	0	0	0	0	0	0.3 ±.3
	Burnt	0.3 ±.3	0	0	0.3 ±.3	0.4 ±.2	0
	Frijoles	0	0	0	0	—	0
American Kestrel	* Apache	0	0	0	0	0	3 ±.7
	* Escobas	0	0	0	3 ±1	2 ±0	2 ±.7
	* Burnt	0	0.9 ±.4	0	3 ±1	5 ±.8	3 ±.7
	Frijoles	0.2 ±.2	0	0	0	—	1 ±0
Peregrine Falcon	Apache	0	0	0	0	0	0
	Escobas	0	0	0	0	0	0
	Burnt	0	0.2 ±.2	0	0	0	0
	Frijoles	0.2 ±.2	0	0	0	—	0
Band-tailed Pigeon	Apache	0	0	5 ±5	0	0.3 ±.3	0
	Escobas	0.7 ±.7	0	0	0	0.5 ±.5	0
	Burnt	0	0	0	0	0	0.3 ±.3
	Frijoles	0	0	0	0	—	0
Mourning Dove	* Apache	0	0	2 ±1	5 ±2	2 ±.8	2 ±.7
	* Escobas	3 ±1	0	3 ±1	0	0	11 ±4
	* Burnt	7 ±3	4 ±2	2 ±0	5 ±2	3 ±1	11 ±4
	* Frijoles	14 ±4	13 ±6	10 ±3	2 ±1	—	7 ±2
Great Horned Owl	Apache	0	0	0	0	0	0
	Escobas	0	0	0	0	0	0
	Burnt	0	0	0	0.5 ±.5	0	0
	Frijoles	0	0	0	0	—	0
Northern Pygmy-Owl	* Apache	0	0	0	0	0	0
	Escobas	0	0	0	0	0	0
	* Burnt	3 ±1	0	0	0	0	0
	* Frijoles	0	3 ±2	0	0	—	0
Common Nighthawk	Apache	0	0	0	0	0	0
	* Escobas	0	0	0	0	4 ±2	8 ±5
	* Burnt	3 ±1	0	3 ±2	4 ±2	0	2 ±1
	* Frijoles	0	0	0	3 ±2	—	0
Common Poorwill	Apache	0	0	0	0	0	0
	Escobas	0	0	0	0	0	0
	* Burnt	0	0	0	0	0	5 ±3
	* Frijoles	4 ±2	0	0	0	—	0
White-throated swift	Apache	3+	0	0.9 ±.9	0	0	0
	Escobas	0	0	0	0	0	0
	Burnt	0.7 ±.7	0.3 ±.3	2 ±.9	1 ±.6	0	0
	Frijoles	2 ±.8	1 ±.8	0	0.9 ±.9	—	0.4 ±.4
Black-chinned Hummingbird	Apache	0	0	0	0	0	0
	Escobas	0	0	0	0	0	0
	Burnt	0	0	0	0	0	0

continued

Appendix 2: Survey data (birds/40 ha). An asterisk marks each transect where a species breeds. Statistical uncertainty in each population estimate is indicated by plus or minus 1 standard error, except on Apache in 1977, where only 1 prefire survey occurred (continued).

Species	Breed Transect	1977	1978	1979	1981	1983	1991
Broad-tailed Hummingbird	Frijoles	0	0	0	0	—	0.7 ±.7
	* Apache	4+	11 ±4	9 ±3	5 ±2	12 ±4	18 ±5
	* Escobas	3 ±1	11 ±5	10 ±3	8 ±3	14 ±4	34 ±12
	* Burnt	11 ±2	26 ±8	25 ±10	28 ±10	16 ±3	32 ±6
Lewis' Woodpecker	* Frijoles	15 ±2	16 ±5	34 ±9	18 ±5	—	24 ±9
	Apache	0	0	0	0	0	0
	Escobas	0	0	0	0	0	0
	* Burnt	0	0	0	0	2 ±1	8 ±3
Red-headed Woodpecker	Frijoles	0	0	0	0	—	0
	Apache	0	0	0	0	0	0
	* Escobas	0	0	0	2 ±.8	0	0
	Burnt	0	0	0	0	0	0
Acorn Woodpecker	Frijoles	0	0	0	0	—	0
	Apache	0	0	0	0	0	0
	* Escobas	0	0	0	0	2 ±1	13 ±3
	* Burnt	0	0	0	0	4 ±2	4 ±1
Red-naped Sapsucker	Frijoles	0	0	0.3 ±.3	0	—	0
	* Apache	0	2 ±.8	0	2 ±.8	0	0
	Escobas	0	0	0	0	0	0
	Burnt	0	0	0	0	0	0
Williamson's Sapsucker	Frijoles	0	0	0	0	—	0
	* Apache	12+	9 ±3	5 ±1	4 ±.8	11 ±1	2 ±.7
	* Escobas	0	8 ±4	0	0	2 ±.8	0
	Burnt	0	0	0	0	0	0
Downy Woodpecker	Frijoles	0	0	0	0	—	0
	* Apache	3+	5 ±2	0	0	0	3 ±2
	Escobas	0	0	0	0	0	0
	Burnt	0	0	0	0	0	0
Hairy Woodpecker	Frijoles	0	0	0	0	—	0
	* Apache	4+	19 ±4	26 ±12	17 ±4	7 ±2	15 ±5
	* Escobas	5 ±2	19 ±8	23 ±6	17 ±5	8 ±1	8 ±3
	* Burnt	11 ±4	26 ±9	29 ±6	16 ±3	10 ±2	6 ±3
Three-toed Woodpecker	* Frijoles	6 ±1	5 ±0	14 ±6	11 ±5	—	3 ±1
	* Apache	0	8 ±3	11 ±5	5 ±2	3 ±1	0
	* Escobas	2 ±1	0	13 ±7	4 ±1	9 ±2	0
	* Burnt	0	2 ±1	4 ±2	0	5 ±2	0
Northern Flicker	Frijoles	0	0	0	0	—	0
	* Apache	0	6 ±2	15 ±6	6 ±2	7 ±2	7 ±2
	* Escobas	4 ±2	14 ±6	5 ±3	8 ±2	10 ±2	6 ±1
	* Burnt	6 ±2	7 ±2	2 ±1	5 ±2	12 ±3	7 ±3
Olive-sided Flycatcher	* Frijoles	6 ±2	2 ±1	7 ±3	0	—	3 ±.7
	* Apache	0	2 ±.8	0	7 ±2	6 ±2	1 ±.7
	* Escobas	0	3 ±1	2 ±1	3 ±1	2 ±.7	3 ±1
	* Burnt	0	0	0	3 ±1	2 ±0	1 ±.7
Western Wood-Pewee	Frijoles	0	0	0	0	—	0.3 ±.3
	* Apache	3+	6 ±2	5 ±3	28 ±7	29 ±4	6 ±3
	* Escobas	13 ±8	6 ±2	15 ±7	9 ±2	19 ±4	19 ±3
	* Burnt	14 ±5	15 ±5	29 ±12	33 ±7	22 ±6	9 ±3
Hammond's Flycatcher	* Frijoles	15 ±5	7 ±2	6 ±2	10 ±5	—	6 ±1
	* Apache	42+	23 ±5	61 ±23	22 ±5	42 ±7	25 ±3
	* Escobas	30 ±5	57 ±22	59 ±10	40 ±8	21 ±6	31 ±6
	* Burnt	35 ±12	16 ±3	13 ±3	8 ±2	12 ±4	13 ±4
Dusky Flycatcher	* Frijoles	0	0	0	0	—	7 ±4
	* Apache	0	0	0	0	0	15 ±6
	* Escobas	16 ±8	0	0	0	0	17 ±6
	* Burnt	4 ±2	0	0	0	0	0
Gray Flycatcher	Frijoles	0	0	0	0	—	0
	Apache	0	0	0	0	0	0
	Escobas	0	0	0	0	0	0

continued

Appendix 2: Survey data (birds/40 ha). An asterisk marks each transect where a species breeds. Statistical uncertainty in each population estimate is indicated by plus or minus 1 standard error, except on Apache in 1977, where only 1 prefire survey occurred (continued).

Species	Breed Transect	1977	1978	1979	1981	1983	1991
Cordilleran Flycatcher	Burnt	0	0	0	0	0	0
	* Frijoles	30 ±6	38 ±9	41 ±9	36 ±13	—	24 ±4
	* Apache	11+	6 ±2	12 ±6	12 ±3	4 ±.9	5 ±3
	* Escobas	12 ±4	6 ±3	0	0	2 ±.9	0
Say's Phoebe	* Burnt	0	2 ±1	3 ±2	3 ±1	0	0
	Frijoles	0	0	0	0	—	0
	Apache	0	0	0	0	0	0
Ash—throated Flycatcher	Escobas	0	0	0	0	0	0
	Burnt	0	0	0	0	0	0
	Frijoles	0	0	0	0	—	0.3 ±.3
	Apache	0	0	0	0	0	0
Cassin's Kingbird	* Escobas	0	3 ±1	0	0	0	0
	* Burnt	14 ±7	6 ±2	4 ±2	4 ±2	2 ±1	1 ±0
	* Frijoles	21 ±7	21 ±6	17 ±5	12 ±2	—	21 ±3
	Apache	0	0	0	0	0	0
Violet—green Swallow	Escobas	0	0	0	0	0	0
	* Burnt	0	0	0	0	0	2 ±0
	Frijoles	0	0	0	0	—	0
	* Apache	8+	15 ±6	16 ±8	29 ±10	38 ±7	35 ±13
Cliff Swallow	* Escobas	15 ±4	10 ±3	12 ±4	23 ±6	22 ±4	32 ±9
	* Burnt	51 ±9	24 ±8	56 ±15	45 ±7	42 ±4	27 ±5
	* Frijoles	24 ±9	16 ±4	18 ±2	18 ±5	—	19 ±3
	Apache	0	0	0	0	0	0
Steller's Jay	Escobas	0	0	0	0	0	0
	Burnt	0	0	0	0	0	0
	Frijoles	0	0.4 ±.4	0	0	—	0
	* Apache	2+	24 ±8	4 ±1	11 ±3	5 ±.8	13 ±3
Scrub Jay	* Escobas	8 ±4	18 ±7	7 ±3	12 ±3	12 ±2	14 ±5
	* Burnt	17 ±6	19 ±7	12 ±7	12 ±4	21 ±5	11 ±2
	Frijoles	0	0	0.3 ±.3	0	—	0
	Apache	0	0	0	0	0	0
Pinyon Jay	Escobas	0	0	0	0	0	0
	Burnt	0	0	3 ±3	0	0	0
	Frijoles	1 ±1	0	1 ±.9	0	—	0.3 ±.3
	* Apache	0	0.9 ±.4	0	7 ±3	2 ±.7	3 ±1
Clark's Nutcracker	* Escobas	0	1 ±.5	0	1 ±.5	2 ±.8	3 ±1
	Burnt	0.3 ±.3	2 ±1	0	1 ±.4	0.2 ±.2	5 ±2
	Frijoles	0.2 ±.2	2 ±.3	0.3 ±.3	0.3 ±.3	—	0
	Apache	1+	0.4 ±.2	1 ±.6	0.6 ±.2	0.8 ±.4	0.7 ±.3
Common Raven	Escobas	0.3 ±.3	1 ±.4	0.3 ±.3	0.6 ±.2	1 ±.4	1 ±.6
	Burnt	0.3 ±.3	1 ±0	0.3 ±.3	0.3 ±.3	0	2 ±.7
	Frijoles	1 ±.4	1 ±0	0.5 ±.5	0.3 ±.3	—	0.7 ±.7
	* Apache	46+	15 ±3	27 ±15	26 ±8	13 ±3	24 ±5
Mountain Chickadee	* Escobas	24 ±9	6 ±2	5 ±3	4 ±2	0	3 ±1
	* Burnt	22 ±8	0	0	4 ±2	5 ±2	7 ±4
	* Frijoles	13 ±4	18 ±5	10 ±2	14 ±6	—	7 ±3
	Apache	0	0	0	0	0	0
Plain Titmouse	Escobas	0	0	0	0	0	0
	Burnt	0	0	0	0	0	0
	* Frijoles	16 ±4	44 ±18	14 ±3	34 ±15	—	15 ±2
	Apache	0	0	0	0	0	0
Bushtit	Escobas	0	0	0	0	0	0
	Burnt	0	0	0	0	0	0
	* Frijoles	2 ±.8	5 ±3	4 ±2	10 ±5	—	3 ±1
	* Apache	0	3 ±1	3 ±2	5 ±2	2 ±.9	5 ±3

continued

Appendix 2: Survey data (birds/40 ha). An asterisk marks each transect where a species breeds. Statistical uncertainty in each population estimate is indicated by plus or minus 1 standard error, except on Apache in 1977, where only 1 prefire survey occurred (continued).

Species	Breed Transect	1977	1978	1979	1981	1983	1991
	Escobas	0	0	0	0	0	0
	Burnt	0	0	0	0	0	0
	Frijoles	0	0	0	0	—	0
White—breasted Nuthatch	* Apache	3+	2 ±1	3 ±2	15 ±6	5 ±1	3 ±1
	* Escobas	9 ±3	8 ±4	0	8 ±2	12 ±4	10 ±2
	* Burnt	6 ±3	5 ±2	8 ±4	17 ±5	11 ±3	8 ±3
	* Frijoles	9 ±3	12 ±3	11 ±3	3 ±0	—	0
Pygmy Nuthatch	* Apache	52+	31 ±9	10 ±5	18 ±3	29 ±8	55 ±8
	* Escobas	77 ±18	48 ±15	19 ±8	29 ±6	19 ±3	57 ±13
	* Burnt	71 ±3	54 ±17	18 ±5	28 ±6	17 ±5	17 ±3
	* Frijoles	17 ±4	21 ±6	6 ±2	10 ±5	—	16 ±0
Brown Creeper	* Apache	4+	8 ±3	5 ±3	10 ±4	5 ±2	5 ±1
	* Escobas	2 ±1	0	0	0	3 ±1	0
	Burnt	0	0	0	0	0	0
	Frijoles	0	0	0	0	—	0
Rock Wren	Apache	0	0	0	0	0	0
	Escobas	0	0	0	0	0	0
	* Burnt	0	0	3 ±2	4 ±2	4 ±1	0
	* Frijoles	0	0	4 ±2	3 ±2	—	0
Canyon Wren	Apache	0	0	0	0	0	0
	Escobas	0	0	0	0	0	0
	* Burnt	0	2 ±1	0	0	3 ±1	3 ±1
	Frijoles	0	0	0	0	—	0
Bewick's Wren	Apache	0	0	0	0	0	0
	Escobas	0	0	0	0	0	0
	Burnt	0	0	0	0	0	0
	* Frijoles	1 ±.5	0	0	3 ±2	—	0
House Wren	* Apache	0	14 ±2	26 ±9	28 ±3	33 ±4	34 ±12
	* Escobas	0	21 ±8	25 ±7	16 ±2	18 ±2	20 ±3
	* Burnt	0	6 ±2	5 ±3	19 ±1	27 ±4	16 ±4
	Frijoles	0	0	0	0	—	0
Golden—crowned Kinglet	* Apache	0	4 ±2	0	0	0	0
	* Escobas	6 ±3	0	0	0	0	0
	Burnt	0	0	0	0	0	0
	Frijoles	0	0	0	0	—	0
Ruby—crowned Kinglet	* Apache	21+	14 ±6	10 ±2	6 ±2	5 ±2	7 ±1
	* Escobas	0	0	3 ±2	0	0	0
	Burnt	0	0	0	0	0	0
	Frijoles	0	0	0.3 ±.3	0	—	0
Blue—gray Gnatcatcher	Apache	0	0	0	0	0	0
	Escobas	0	0	0	0	0	0
	* Burnt	0	4 ±2	0	0	0	0
	* Frijoles	19 ±6	14 ±6	21 ±6	18 ±5	—	5 ±3
Western Bluebird	* Apache	0	2 ±1	3 ±2	8 ±1	11 ±2	24 ±9
	* Escobas	5 ±3	18 ±8	9 ±1	20 ±5	28 ±5	53 ±10
	* Burnt	11 ±4	24 ±7	7 ±2	34 ±4	42 ±10	31 ±4
	* Frijoles	12 ±3	18 ±9	4 ±1	3 ±0	—	27 ±7
Mountain Bluebird	* Apache	0	0	0	2 ±1	0	0
	* Escobas	0	0	0	0	2 ±.9	0
	* Burnt	0	2 ±1	0	20 ±7	14 ±5	0
	Frijoles	0	0	0	0	—	0
Townsend's Solitaire	* Apache	3+	10 ±4	3 ±2	6 ±2	11 ±3	0
	* Escobas	5 ±3	6 ±2	7 ±2	4 ±1	4 ±1	3 ±2
	* Burnt	3 ±0	9 ±3	3 ±0	3 ±1	2 ±1	0
	Frijoles	0	0	0	0	—	0
Hermit Thrush	* Apache	44+	10 ±3	11 ±2	12 ±2	12 ±3	8 ±3
	* Escobas	39 ±12	8 ±3	7 ±2	4 ±1	3 ±1	0
	* Burnt	28 ±10	6 ±2	0	6 ±3	0	0
	Frijoles	0.3 ±.3	0	1 ±1	0	—	0.4 ±.4

continued

Appendix 2: Survey data (birds/40 ha). An asterisk marks each transect where a species breeds. Statistical uncertainty in each population estimate is indicated by plus or minus 1 standard error, except on Apache in 1977, where only 1 prefire survey occurred (continued).

Species	Breed Transect	1977	1978	1979	1981	1983	1991
American Robin	* Apache	10+	10 ±3	2 ±0	6 ±2	7 ±2	7 ±1
	* Escobas	6 ±2	3 ±1	8 ±3	2 ±.8	4 ±1	7 ±1
	* Burnt	0	7 ±3	0	6 ±3	7 ±2	4 ±1
	* Frijoles	7 ±2	0	0	4 ±2	—	6 ±2
Solitary Vireo	* Apache	5+	2 ±1	7 ±3	10 ±3	11 ±2	5 ±1
	* Escobas	20 ±7	17 ±4	25 ±6	16 ±6	9 ±2	12 ±3
	* Burnt	13 ±2	8 ±3	18 ±4	19 ±4	11 ±2	8 ±1
	* Frijoles	12 ±3	12 ±3	19 ±5	7 ±4	—	2 ±1
Warbling Vireo	* Apache	27+	28 ±9	26 ±8	42 ±8	30 ±7	13 ±2
	* Escobas	2 ±1	6 ±3	10 ±5	6 ±2	0	1 ±0
	* Burnt	0	0	3 ±2	7 ±3	0	5 ±3
	Frijoles	0	0	0.7 ±.7	0	—	0
Orange—crowned Warbler	* Apache	11+	2 ±1	3 ±0	4 ±1	0	6 ±2
	* Escobas	0	0	3 ±2	0	0	0
	Burnt	0	0	0	0	0	0.4 ±.4
	Frijoles	0	0	0	0	—	0
Virginia's Warbler	* Apache	8+	0	0	8 ±3	0	3 ±1
	* Escobas	21 ±10	0	0	6 ±2	12 ±3	15 ±5
	* Burnt	26 ±9	8 ±3	14 ±3	14 ±5	8 ±3	32 ±7
	* Frijoles	13 ±4	5 ±3	25 ±12	10 ±6	—	5 ±3
Yellow Warbler	Apache	0	0	0	0	0	0
	Escobas	0	0	0	0	0	0
	Burnt	0	0	0	0.3 ±.3	0	0
	Frijoles	0	0	0	0	—	0
Yellow—rumped Warbler	* Apache	27+	40 ±10	37 ±11	24 ±4	29 ±4	24 ±9
	* Escobas	29 ±10	13 ±3	18 ±5	4 ±1	7 ±2	3 ±1
	* Burnt	6 ±2	5 ±2	7 ±4	6 ±2	18 ±6	2 ±1
	Frijoles	4 ±3	3 ±3	0	0	—	0
Black—throated Gray Warbler	Apache	0	0	0	0	0	0
	Escobas	0	0	0	0	0	0
	Burnt	0	0	0	0	0	0
	* Frijoles	5 ±2	23 ±10	21 ±7	23 ±10	—	6 ±1
Grace's Warbler	* Apache	0	16 ±4	26 ±10	16 ±3	16 ±4	0
	* Escobas	39 ±15	28 ±9	33 ±15	12 ±3	11 ±3	29 ±3
	* Burnt	40 ±7	11 ±3	14 ±5	8 ±2	5 ±2	13 ±4
	* Frijoles	12 ±4	10 ±5	13 ±3	11 ±5	—	11 ±3
MacGillivray's Warbler	Apache	0	0	0	0	0	0
	Escobas	0	0	0	0	0	0
	Burnt	0	0	0	0	0	0.4 ±.4
	Frijoles	0	0	0	0	—	0
Hepatic Tanager	Apache	0	0	0	0	0	0
	Escobas	0	0	0	0	0	0
	Burnt	0	0	0	0	0	0
	* Frijoles	3 ±.8	0	0	3 ±1	—	2 ±.7
Western Tanager	* Apache	5+	12 ±4	16 ±4	19 ±2	18 ±4	11 ±5
	* Escobas	10 ±4	7 ±3	13 ±6	11 ±3	18 ±4	6 ±2
	* Burnt	17 ±6	12 ±4	24 ±9	17 ±6	16 ±4	7 ±2
	* Frijoles	2 ±1	0	4 ±2	7 ±3	—	11 ±2
Black—headed Grosbeak	* Apache	4+	5 ±2	4 ±1	6 ±2	5 ±1	0
	* Escobas	14 ±5	21 ±10	5 ±1	4 ±2	3 ±.8	5 ±1
	* Burnt	2 ±1	0	5 ±3	14 ±6	6 ±2	3 ±1
	* Frijoles	5 ±2	7 ±4	4 ±2	7 ±4	—	8 ±4
Green—tailed Towhee	* Apache	0	0	0	0	2 ±.7	8 ±4
	* Escobas	0	0	0	0	5 ±1	9 ±5
	* Burnt	0	0	0	5 ±2	4 ±1	7 ±2
	Frijoles	0	0	0	0	—	0
Rufous—sided Towhee	* Apache	0	0	0	0	0	3 ±2
	* Escobas	0	0	0	0	6 ±2	22 ±7
	* Burnt	12 ±5	7 ±2	4 ±2	23 ±3	19 ±3	35 ±6

continued

Appendix 2: Survey data (birds/40 ha). An asterisk marks each transect where a species breeds. Statistical uncertainty in each population estimate is indicated by plus or minus 1 standard error, except on Apache in 1977, where only 1 prefire survey occurred (continued).

Species	Breed Transect	1977	1978	1979	1981	1983	1991
Canyon Towhee	* Frijoles	22 ±7	48 ±7	41 ±10	22 ±9	—	24 ±8
	Apache	0	0	0	0	0	0
	Escobas	0	0	0	0	0	0
	Burnt	0	0	0	0	0	0
Chipping Sparrow	* Frijoles	0	3 ±1	0	0	—	0
	* Apache	8+	6 ±1	3 ±2	6 ±2	3 ±1	0
	* Escobas	3 ±2	8 ±4	8 ±4	6 ±2	5 ±1	8 ±3
	* Burnt	17 ±4	21 ±3	18 ±3	21 ±5	8 ±1	3 ±2
Dark-eyed Junco	* Frijoles	27 ±7	23 ±2	23 ±3	21 ±3	—	16 ±3
	* Apache	13+	43 ±12	26 ±11	21 ±3	18 ±5	6 ±1
	* Escobas	15 ±6	35 ±12	14 ±6	18 ±4	20 ±4	8 ±4
	* Burnt	11 ±3	6 ±2	6 ±2	20 ±6	7 ±2	0
Brewer's Blackbird	* Frijoles	0	0	4 ±2	0	—	0
	Apache	0	0	0	0	0	0
	Escobas	0	0	0	0	0	0
	Burnt	0	0	0	0	0	0
Brown-headed Cowbird	Frijoles	0.5 ±.5	0	0	0	—	0
	* Apache	0	3 ±1	3 ±2	8 ±3	10 ±3	6 ±3
	* Escobas	0	0	7 ±2	6 ±2	5 ±1	9 ±2
	* Burnt	2 ±.8	3 ±1	3 ±2	7 ±2	4 ±.5	7 ±3
Cassin's Finch	* Frijoles	1 ±.5	13 ±6	9 ±4	20 ±8	—	6 ±2
	* Apache	0	0	0	0	2 ±.7	2 ±1
	* Escobas	0	0	0	0	0	6 ±4
	* Burnt	0	2 ±.8	0	0	0	0
House Finch	Frijoles	0	0.3 ±.3	0	0	—	0
	Apache	0	0	0	0	0	0
	Escobas	0	0	0	0	0	0
	Burnt	0	0.2 ±.2	0	0	0	0
Red Crossbill	* Frijoles	2 ±.8	2 ±1	2 ±1	0	—	3 ±.7
	* Apache	5+	4 ±2	0	26 ±11	2 ±.9	40 ±10
	* Escobas	7 ±3	3 ±1	0	7 ±2	4 ±2	40 ±14
	* Burnt	14 ±6	11 ±4	0	0	2 ±1	20 ±11
Pine Siskin	* Frijoles	2 ±1	6 ±3	0	7 ±4	—	13 ±6
	* Apache	12+	3 ±1	0	16 ±5	36 ±8	24 ±4
	* Escobas	11 ±6	6 ±3	0	3 ±1	5 ±1	7 ±3
	* Burnt	4 ±1	2 ±.7	0	5 ±2	15 ±6	0
Lesser Goldfinch	Frijoles	2 ±2	1 ±1	0	0	—	0.4 ±.4
	* Apache	0	0	0	0	0	2 ±1
	* Escobas	2 ±1	0	0	0	0	0
	* Burnt	4 ±2	5 ±2	3 ±2	13 ±5	8 ±3	3 ±2
Evening Grosbeak	* Frijoles	0	12 ±6	7 ±3	25 ±8	—	3 ±2
	* Apache	7+	22 ±5	19 ±8	22 ±7	19 ±5	2 ±1
	* Escobas	0	5 ±2	3 ±2	3 ±1	3 ±1	0
	Burnt	0	0.5 ±.5	0	0	0	0
	Frijoles	0.5 ±.5	0	1 ±1	0	—	0

Appendix 3. Nesting guild data (birds/40 ha). Statistical uncertainty in each population estimate is indicated by plus or minus 1 standard error, except on Apache in 1977, where only 1 prefire survey occurred.

Nesting Guild	Transect	1977	1978	1979	1981	1983	1991
Ground	Apache	21+	43 ±12	26 ±11	30 ±4	18 ±5	9 ±2
	Escobas	37 ±12	35 ±12	14 ±6	24 ±4	36 ±6	32 ±8
	Burnt	40 ±10	17 ±4	27 ±4	42 ±8	22 ±4	42 ±8
	Frijoles	16 ±5	8 ±3	33 ±12	17 ±6	—	5 ±3
Cavity	Apache	99+	142 ±14	139 ±21	168 ±14	165 ±12	196 ±22
	Escobas	137 ±19	162 ±22	113 ±15	132 ±12	144 ±9	203 ±19
	Burnt	175 ±14	169 ±23	140 ±18	197 ±14	197 ±14	129 ±10
	Frijoles	96 ±13	99 ±14	76 ±9	60 ±9	—	89 ±8
Foliage	Apache	283+	262 ±20	276 ±34	325 ±22	308 ±18	269 ±19
	Escobas	288 ±29	225 ±28	242 ±24	156 ±12	155 ±11	289 ±25
	Burnt	268 ±24	180 ±16	179 ±22	247 ±19	202 ±15	201 ±17
	Frijoles	233 ±18	316 ±29	292 ±22	293 ±29	—	219 ±17
Parasitic	Apache	0	3 ±1	3 ±2	8 ±3	10 ±3	6 ±3
	Escobas	0	0	7 ±2	6 ±2	5 ±1	9 ±2
	Burnt	2 ±.8	3 ±1	3 ±2	7 ±2	4 ±.5	7 ±3
	Frijoles	1 ±.5	13 ±6	9 ±4	20 ±8	—	6 ±2
Nesting totals	Apache	403+	449 ±27	445 ±41	530 ±26	500 ±22	481 ±29
	Escobas	461 ±37	422 ±38	377 ±29	318 ±18	341 ±16	533 ±32
	Burnt	484 ±29	368 ±28	350 ±28	493 ±25	425 ±21	378 ±22
	Frijoles	348 ±22	436 ±33	410 ±27	389 ±32	—	319 ±19

Appendix 4. Foraging guild data (birds/40 ha). Statistical uncertainty in each population estimate is indicated by plus or minus 1 standard error, except on Apache in 1977, where only 1 prefire survey occurred.

Foraging Guild	Transect	1977	1978	1979	1981	1983	1991
Ground seed	Apache	13+	45 ±12	37 ±12	33 ±4	32 ±6	25 ±5
	Escobas	19 ±6	35 ±12	24 ±7	24 ±4	37 ±5	59 ±10
	Burnt	32 ±6	20 ±4	16 ±3	61 ±7	37 ±4	60 ±8
	Frijoles	37 ±8	77 ±11	64 ±11	44 ±12	—	37 ±9
Foliage seed	Apache	26+	54 ±10	23 ±8	82 ±15	65 ±10	85 ±11
	Escobas	29 ±8	32 ±8	10 ±3	27 ±4	27 ±4	70 ±16
	Burnt	39 ±9	40 ±9	18 ±8	31 ±6	49 ±9	41 ±11
	Frijoles	21 ±4	41 ±8	29 ±7	45 ±9	—	34 ±7
Foliage nectar	Apache	4+	11 ±4	9 ±3	5 ±2	12 ±4	18 ±5
	Escobas	3 ±1	11 ±5	10 ±3	8 ±3	14 ±4	34 ±12
	Burnt	11 ±2	26 ±8	25 ±10	28 ±10	16 ±3	32 ±6
	Frijoles	15 ±2	16 ±5	34 ±9	18 ±5	—	24 ±9
Ground insect	Apache	65+	59 ±7	64 ±12	73 ±5	83 ±7	80 ±15
	Escobas	63 ±13	78 ±13	70 ±9	59 ±6	74 ±6	96 ±11
	Burnt	64 ±11	84 ±10	39 ±5	118 ±10	120 ±12	69 ±8
	Frijoles	56 ±8	43 ±10	39 ±5	31 ±4	—	52 ±8
Timber drilling insect	Apache	19+	43 ±6	42 ±13	28 ±5	21 ±3	20 ±5
	Escobas	6 ±2	28 ±9	36 ±9	23 ±5	22 ±3	21 ±4
	Burnt	11 ±4	29 ±9	33 ±7	16 ±3	21 ±4	18 ±4
	Frijoles	6 ±1	5 ±0	14 ±6	11 ±5	—	3 ±1
Timber searching insect	Apache	105+	61 ±10	49 ±16	74 ±11	53 ±9	93 ±10
	Escobas	113 ±20	62 ±16	24 ±8	40 ±7	34 ±5	70 ±13
	Burnt	99 ±9	59 ±18	27 ±6	49 ±8	34 ±6	33 ±6
	Frijoles	39 ±7	51 ±8	27 ±4	27 ±8	—	23 ±3
Foliage insect	Apache	108+	124 ±16	129 ±18	136 ±11	115 ±10	69 ±11
	Escobas	141 ±23	92 ±14	110 ±19	59 ±8	60 ±6	71 ±7
	Burnt	104 ±13	48 ±8	86 ±13	86 ±12	64 ±8	73 ±9
	Frijoles	93 ±11	123 ±24	126 ±17	135 ±22	—	70 ±7
Air perching insect	Apache	55+	37 ±5	78 ±24	70 ±9	81 ±8	53 ±7
	Escobas	72 ±13	75 ±22	77 ±12	52 ±8	43 ±7	69 ±10
	Burnt	67 ±15	39 ±7	50 ±13	51 ±8	38 ±8	25 ±5
	Frijoles	66 ±10	65 ±11	64 ±11	58 ±14	—	60 ±6
Air soaring insect	Apache	11+	15 ±6	17 ±8	29 ±10	38 ±7	3 5 ±13
	Escobas	15 ±4	10 ±3	12 ±4	23 ±6	26 ±5	40 ±10
	Burnt	54 ±9	25 ±8	61 ±15	50 ±7	42 ±4	31 ±5
	Frijoles	26 ±9	18 ±4	18 ±2	22 ±6	—	19 ±3
Ground predator	Apache	1+	0.6 ±.3	3 ±1	0.6 ±.2	2 ±.5	5 ±1
	Escobas	0.3 ±.3	1 ±.4	3 ±1	4 ±1	5 ±.8	4 ±1
	Burnt	4 ±2	3 ±.6	0.3 ±.3	7 ±2	5 ±.8	6 ±1
	Frijoles	2 ±.5	4 ±2	0.8 ±.6	1 ±.5	—	3 ±1
Total foraging	Apache	406+	449 ±27	452 ±42	531 ±26	501 ±22	482 ±29
	Escobas	462 ±37	423 ±38	377 ±29	319 ±18	342 ±16	534 ±32
	Burnt	486 ±29	373 ±28	354 ±29	497 ±25	426 ±21	388 ±22
	Frijoles	359 ±22	445 ±33	416 ±27	391 ±32	—	325 ±19

Geomorphic Response of Six Headwater Basins Fifteen Years After the La Mesa Fire, Bandelier National Monument

William D. White

Abstract.—Factors important to hillslope erosion immediately following the La Mesa forest fire included: 1) degree of ash development; 2) amount of upslope catchment area; 3) degree of slope; and 4) type or complexity of slope. Efficiency of transport of fire-derived sediment proved to be related to the density and continuity of drainage lines. Early controls to fire related erosion proved to be needle cast from unburned crowns, and climatic variability (e.g., the precipitation differences between elevations).

Fifteen years following the La Mesa fire, hillslope erosion has been interrupted by: 1) downed, burned trees; and 2) increased ground surface microtopography afforded by the aggradational building of grass pedestals and cryptogamic crusts. The increased ground surface roughness encourages infiltration from the intensely burned areas. Infiltration becomes shallow ground-water interflow which surfaces at the top margins of tributary canyons. The gathering of sediment-free runoff in the tributary and trunk canyons entrains the temporarily stored sediment derived from the mesa tops immediately following the fire. Present day sediment delivery from burned areas of the mesa tops appears to be derived primarily from moderately burned basins. While the characteristic needle cast protects the moderately burned basin's ground surface from rain drop impact and channelized overland flow (rilling), the needle cast discourages the growth of cryptogamic crusts. Without the combined infiltration-encouraging factors of cryptogamic crusts and downed trees (which are fewer in moderately burned basins), precipitation in moderately burned areas generally concentrates in the drainages and channel incision results. Storage of this sediment occurs where drainages widen, such as the mouth of the moderate burn basin on Burnt Mesa, and on the lower gradient, mesa top trunk channels.

INTRODUCTION

Beginning three months following the June 1977 La Mesa Fire, six small (thousands of square meters) headwater basins in the Rito de los Frijoles watershed were instrumented to gauge their geomorphic response to the disequilibrium conditions created by the fire (White and Wells 1984). I conducted this work as a master's thesis project (White 1981). The basins were selected to represent different burn intensities (intense, moderate, light), at two different elevations (Burnt Mesa = 2225 meters elevation (7300 feet), BMINT, BMMOD,

BMLIT, respectively; Apache Springs = 2500 meters elevation (8200 feet), ASINT, ASMOD, ASLIT, respectively). All basins were intended to have similar aspects without fire lines or roads within basin perimeters (White 1981). It proved difficult to locate accessible basins, so variance in aspects and basin areas had to be accepted. Primary instrumentation consisted of erosion pins spaced along three transects per basin (headwater = Transect A;

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midbasin = Transect B; basin mouth (when present) = Transect C or D). Five headwater basins were instrumented in September, 1977 (BMINT, BMMOD, BMLIT, ASINT, ASMOD); ASLIT was instrumented in March, 1978, as was a mesa-top archeological site as a control (BM ARCH).

This paper presents results from the 1992 remeasurement of more than 400 of the original erosion pins and qualitative observations on factors of geomorphic significance fifteen years following the La Mesa fire. Among the factors thought to influence the utility of recent erosion pin measurements is the possibility of trampling by the protected elk and deer populations within the Park boundaries. Factors of geomorphic significance include the check dams formed by the downed, burned trees, and cryptogamic crusts. Detailed descriptions of the study basins, their relative locations, and drainage basin characteristics, are provided in the proceedings of the first La Mesa Fire Symposium (White and Wells 1984). It is important to note that the original study did not include a long term plan to make use of the original instrumentation, and that there are limitations to the utility of the recent erosion data.

METHODS

Erosion Pin Measurements

Methods used in the initial post-fire study are detailed in White (1981). Erosion pin measurement dates are shown in Table 1. Nearly all rebar stakes marking erosion pin transects were located and the individual pins were located with a metal detector. If a pin or washer was not visible, navigational dividers were used to probe the accumulated soil and organic debris and to excavate a channel for access to the top of the pin and washer for measurements. The dividers were then used to measure the separation between the pin head and the washer (recording soil loss), and the accumulation on top of the washer (soil gain). The measurements were recorded on reproductions of the old data forms, along with comments relative to the ground surface conditions influencing the orientation of the pins and/or washers (e.g., grasses, logs, pine needles, crusts).

Elevation Survey of Pin Transects

Relative pin elevations were determined using a total survey station (Sokkia Set 2B with data collector, SDR33) or an automatic level with a

Table 1.— Dates of erosion pin measurements. I = intense-burn basin; M = moderate; L = light; A = archeological site.

Date	Burnt Mesa				Apache Springs		
	I	M	L	A	I	M	L
10-77	I	M	L		I	M	
11-77	I						
12-77	I	M	L				
4-78	I	M	L		I	M	L
5-78	I	M	L	A			
6-78	I	M	L	A	I	M	L
7-78	I	M	L	A	I	M	L
9-78				A			
11-78				A			
5-79	I	M	L	A	I	M	L
6-79	I	M	L	A	I	M	L
7-79	I	M	L				
9-79	I	M	L	A	I	M	L
10-79	I	M	L				
11-79					I		L
4-80	I	M	L	A			
5-80					I	M	L
5-92	I	M	L	A			
6-92					I	M	L

philadelphia rod along each transect length. These data were used to construct transect profiles upon which to depict each measurement period's gain and loss data (Figure 1). The original study only surveyed breaks in slope of the pin transect, and did not survey each pin's relative elevation; accordingly, it was not possible to simply compare early and late pin head elevations to determine the possibility of elk-trampling.

Photo-Documentation

There were 4 photo stations established during the original study in and near the lower elevation, intense-burn basin (BMINT). These were photographed during 1992-1993 without the aid of the framing provided by the previously erect, burned trees. Additionally, each pin transect was photographed (viewed along the transect from the beginning of each), and multiple photographs depicting ground surface characteristics were taken. All photography from the original study and 1992-1993 is archived at Bandelier National Monument.

Basin Mouth Stratigraphy

The basin mouth (or the main channel reach below the lowest pin transect) of each basin was trenched (< 30 cm) to determine the character of any accumulation above the level of post-burn channel incision. Maximum depth of channel incision at any site during the original study was less

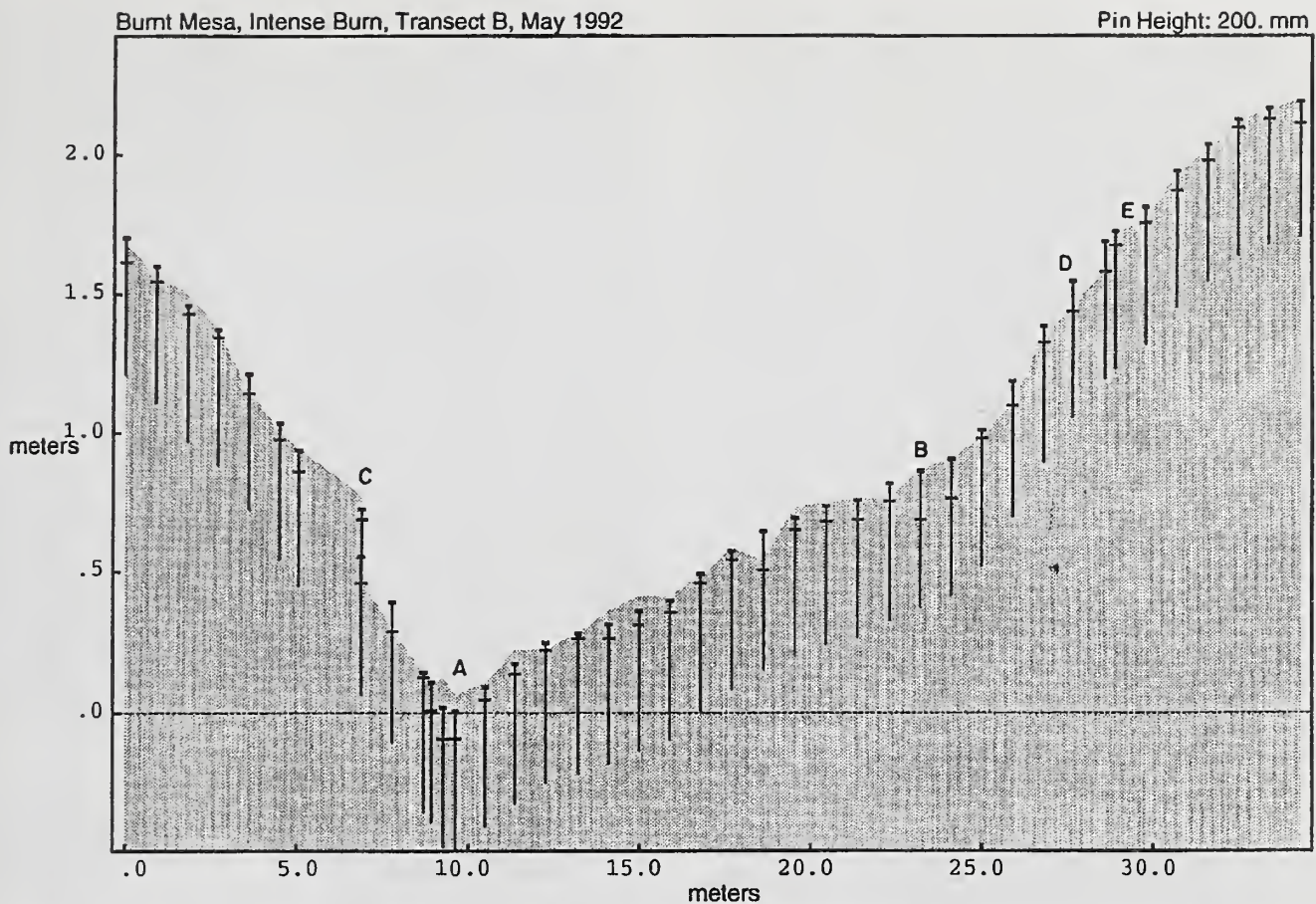


Figure 1. Example profile of erosion pin transect; BMINT, Transect B, May 1992 data set. Horizontal and vertical axes are distances in meters; a third scale, depicted by the vertical lines in the profile, represents erosion pins at a rounded value of 200mm per pin length. Erosion (loss) is depicted by the separation between the horizontal tick marks on the vertical lines; aggradation (gain) is depicted by shading of the profile relative to the location of the washer (lower tick mark on individual vertical lines).

In this example, the basin's channel (at A, between 9 and 10 meters) has cut and filled approximately 50mm and 60mm, respectively, as did the tributary drainage below the photographed rill plot (at B, between 24 and 25 meters; see Fig. 9). A pre-burn scarp has been preserved (C, at 7 meters) by sheep fescue ground cover, while another scarp has experienced net reduction (D, at 28 meters), with a grass clump of mountain muhly persisting above it (E, at 29 meters).

than 5 cm (at BMINT). Additionally, the trunk channel (largest drainage of a given area) was trenched at each elevation at a point below the confluence(s) of the study basins. A total of eight cross sections were described in the field and samples collected to determine grain size distributions.

RESULTS

Erosion Pins

Fifteen years of deployment was suspected to be too long for the effective use of erosion pins. Concerns included: removal by downcutting; rotation by soil creep; rust; or trampling by the abundant

elk population within the Park boundaries. I relocated 411 of 415 total pins in the six study basins. Of the four missing pins, only one is suspected of having been eroded from its steep hillslope placement. The original vertical installation of the pins was not disturbed by downslope soil creep (the 26 cm pin length penetrates the less weathered tuff, through the soil mantle). Rusting was not observed to have frozen washers to the pin shafts. Finally, although an abundance of fresh elk sign was noted in and around the study basins at both elevations, fewer than 2% of the pins were observed to be directly affected by recent trampling.

An indirect measure of the degree of trampling may be obtained from comparisons of loss measurements; pins showing less loss in 1992 relative

to the last previous measurement in 1980 may be a result of having been stepped on (thereby decreasing the separation between the pin head and the washer). Table 2 shows the number of pins per transect with less loss after twelve years between measurements. Testing the probability that elk prefer higher elevation habitat, the difference in percentage of pins with less loss between upper and lower elevation basins is insignificant (probability value of 0.27). Elk sign in May 1992 was at least as frequent on Burnt Mesa as in the Apache Springs area. Additionally, of the pins showing less loss in 1992 (34 pins at Burnt Mesa; 33 pins at Apache Springs), roughly a third of those pins may be considered to be within measurement error (± 2 mm). Alternatively, of those 67 pins showing less loss, only 3% had observed associations with trampling, 46% had no comment recorded, while 31% had associations with grass and/or cryptogamic crusts, and 19% were associated with other factors (e.g., decomposed logs; shrubs, gopher mounds). These data suggest that elk-trampling is not the most significant factor affecting pin measurements.

Table 2.—Number of erosion pins showing less loss in May 1992 than in April 1980. Percentage shown by transect, basin, and between elevations.

Basin	Transect	#/Tran.	By Tran.	Percent #/Basin	Percent By Basin
BMINT	A	7/88	8	12/146	8
	B	3/42	7		
	C	2/16	12		
BMMOD	A	2/13	15	3/47	6
	B	0/15	0		
	C	1/14	7		
	D	0/5	0		
BMLIT	A	3/16	19	19/55	34
	B	9/20	45		
	C	7/19	37		
				34/248 = 14 Burnt Mesa	
ASINT	A	4/43	9	19/36	22
	B	13/34	38		
	C	2/7	28		
ASMOD	A	2/21	9	6/42	14
	B	4/21	19		
ASLIT	A	4/21	19	8/35	22
	B	4/14	28		
				33/163 = 20 Apache Springs	

For the sake of completeness, the number of pins showing less gain in 1992 relative to the 1980 measurements are shown in Table 3. There is no significant difference between elevations (probability value 0.22). Although between 13% and 26% of all pins have less gain in 1992 than in 1980, approximately 90% of all the pins had some measure of gain in 1992, relative to the time of their installation. The fact that the vast majority of pins exhibit gain indicates that those materials eroded after the time of pin installation, while locally redistributed, are still in storage within these headwater basins.

Table 4 presents cumulative values of gain and loss per transect as measured in May 1992. The average values suggest the lower portions of the study basins have net gain over the 15-year period of pin installation while the upper portions of the study basins generally experienced net loss. Field observations confirm that the steeper headwater areas, where the hillslope profiles are convex upward, are the hillslope areas visually expressing greater mineral soil losses (e.g., less vegetative den-

Table 3.—Number of pins showing less gain in May 1992 as compared to April 1980. Percentage shown by transect, basin, and between elevations.

Basin	Transect	#/Trans.	Percent By Tran.	#/Basin	Percent By Basin
BMINT	A	11/88	12	21/146	14
	B	10/44	23		
	C	0/16	0		
BMMOD	A	1/13	8	9/47	19
	B	6/15	40		
	C	2/14	14		
	D	0/5	0		
BMLIT	A	2/16	12	7/55	13
	B	2/20	10		
	C	3/19	16		
				37/248 = 15 Burnt Mesa	
ASINT	A	10/43	23	17/86	20
	B	5/34	15		
	C	2/7	28		
ASMOD	A	5/21	24	5/42	12
	B	0/21	0		
	"C"	0/4	0		
ASLIT	A	5/21	24	9/35	26
	B	4/14	28		
				31/163 = 19 Apache Springs	

sity; stripped burn horizons). The large average value for BMARCH is the result of a large burrowing animal having buried two pins, and the NET value is divided by 14, not 16, since two pins were missing from this transect (the number of pins in this transect do not figure into the total pins of the study basins).

The 1992 average change data per transect (e.g., "AVERAGE" column, Table 4) were subtracted from the 1980 average change data (White and Wells, 1984), and used to calculate "average change per year" values for the time period between measurements. These values (e.g., 4/80-5/92) were tabulated with the prior study's average change data and are presented in Tables 5 and 6. The exceptionally large sediment yield per unit area values for BMARCH result from comparatively large surface elevation changes divided by the small area of the archeological site (the effects of the large burrow have been removed to calculate the change per year value for the 5/80-5/92 time period).

Basin Mouth Stratigraphy

Except at BMMOD and the trunk channel below BMMOD and BMINT, the study basin mouths

Table 4.—Summary of gain, loss and average values of ground surface elevation change along all transects, May 1992 (in mm).

Study Basin	Transect	Sum +	Sum -	Net	Average
BMINT	A	2063	2504	-441	-5
	B	865	952	-87	-2
	C	376	353	23	1
BMMOD	A	193	155	38	3
	B	175	264	-89	-6
	C	291	345	-54	-4
	D	307	77	230	5
BMLIT	A	331	205	126	8
	B	595	334	261	13
	C	331	222	109	6
ASINT	A	736	896	-160	-3
	B	647	413	234	7
	C	131	58	73	9
ASMOD	A	215	398	-183	-9
	B	352	169	183	9
	"C"	126	25	101	25
ASLIT	A	181	449	-268	-13
	B	162	210	-48	-3

were all well vegetated in June 1993 and the trenched cross sections were dominated by dense mats of organic debris and rootlets. BMINT's basin mouth was so overgrown with grasses that the well defined, post-burn channel (Figure 2) was completely obliterated (Figure 3). However, the shallow profile of BMINT's channel did not exhibit the cohesiveness that characterizes the other, densely vegetated, non-stratified channel profiles of the upper elevation study basins, the upper elevation trunk channel, and BMLIT.

The grain size distributions for the upper elevation cross sections generally depict heterogenous, poorly sorted profiles, dominated by a fine fraction (Figure 4). Their cohesiveness primarily results from the fine-grained materials, and binding by roots from grasses. The greater percentage of fines in the upper elevation study basins, compared to the lower elevation study basins (Figure 5), primarily results from the increased influence of biological

Table 5.—Average annual change in ground-surface elevation per transect for all study basins.

Study Basin	Time Period	Transects Avg. Change/Year (mm)			
		A	B	C	D
BMINT	9/77-6/78	-4.7	-2.7	-5.5	—
	6/78-6/79	-5.9	-4.1	-9.5	—
	6/79-4-80	+1.6	+2.6	+6.5	—
	4/80-5/92	+0.2	+0.1	+0.8	—
BMMOD	9/77-6/78	-2.4	-2.5	-0.7	-1.7
	6/78-6/79	-3.3	-2.2	-6.9	+7.9
	6/79-4-80	-0.5	+4.2	-2.2	-3.1
	4/80-5/92	+0.6	-0.4	+0.1	+3.5
BMLIT	9/77-6/78	-4.3	-5.1	-4.3	—
	6/78-6/79	-5.7	-8.4	-8.9	—
	6/79-4-80	+5.3	+5.5	+7.7	—
	4/80-5/92	+1.0	+1.7	+0.9	—
ASINT	9/77-6/78	-3.5	-2.8	-4.3	—
	6/78-6/79	-3.4	-3.0	+2.7	—
	6/79-5/80	+4.6	+5.1	+0.5	—
	5/80-6/92	-0.1	+0.9	+0.7	—
ASMOD	9/77-6/78	-6.3	-2.5	—	—
	6/78-6/79	-4.6	-4.1	—	—
	6/79-5/80	+3.6	+1.4	—	—
	5/80-5/92	-0.2	+1.1	—	—
ASLIT	10/77-6/78	-1.7	-4.8	—	—
	6/78-6/79	-6.7	-9.0	—	—
	6/79-5/80	+1.3	+5.1	—	—
	5/80-5/92	-0.5	+0.3	—	—



Figure 2. The channel of study basin BMINT in May 1979 where it crosses Transect C (erosion pin #10 in mid-channel, to right of 15cm ruler). Light toned areas are fire-derived deposits of medium to coarse sand-sized quartz crystals and pumice fragments. Medium toned area in upper right of photo results from frost heave disrupting the finer textured ground surface outside of the channel.

cal activity on soil formation where precipitation is greater (Earth Environmental Consultants, Inc. 1978). The high percentage of fines of the AS TRUNK sample results from its shallow topographic gradient relative to the steeper, mesa side slopes of the study basins.

The mouth of BMMOD widens before the drainage line joins the trunk drainage and a deltaic accumulation of sediment results. BMMOD's cross section is described as two poorly-sorted, coarse sand sized horizons (6–8 cm thick) of quartz crystals and tuff fragments separated by a 1 cm thick, loosely cohesive, finer textured horizon. This stratigraphy is similar to that observed 20 meters downgradient in the trenched section of the trunk channel (BM CONF) where it widens upstream of a bedrock constriction. However, the grain size distributions for these two cross sections fail to define a fine textured middle horizon (Figure 5).

Upon closer examination of the apparently finer textured horizon, an abundance of fine charcoal frag-

ments are noted along with blackened quartz crystals in a fine matrix. Under binocular inspection, the fine matrix appears as glassy flakes or needlelike forms. The loosely cohesive character of the horizon was derived from the charcoal content which was washed away during the sieve analysis, and to a lesser degree, the interlocking character of the glassy, volcanic ash.

The charcoal content of the middle horizon identifies the horizon as the first deposition of sediment derived from the 1977 La Mesa fire, before the break up of the hydrophobic layer. This horizon may be considered analogous to the charcoal-rich debris flow deposits of Mayer et. al. (1992), albeit on a much smaller scale and deposited much higher in the landform system than the debris flows of Yellowstone. Similar to the findings of Mayer et. al. (1992), the overlying horizon is poor in charcoal fragments but its directly overlying relationship implies its fire association (which was confirmed by trenching done in 1980 and time lapsed photography showing the colonization of



Figure 3. View toward the south, up-basin, BMINT, August 1993. Log crosses view approximately along the line of Transect C where the well-defined channel of Fig. 2 is now obliterated by grasses, shrubs and log check dams.

stabilizing vegetation). This uppermost horizon resulted from the increased sediment availability following the break up of the hydrophobic layer by frost action during the first year after the fire but prior to effective sediment trapping by the returning vegetation.

The distinctly different grain size distribution of BMLIT defines it as a meadow (i.e., > 50% fines, Figure 5). The coarse tail is a result of the burrowing by the well-established gopher population which brings pumice fragments to the ground surface.

It should be noted that charcoal fragments were found embedded centimeters below the ground surface in nearly all cross section profiles, well below the level of incision that resulted from the La Mesa Fire. These fragments were isolated and did not define a horizon. I conclude that the fragments were from earlier fires and mixed into the profile by pedoturbation. Additionally, while all cross sections contained some material derived from the La Mesa Fire (e.g., burned bark and/or burned pumice fragments), the only cross sections with preserved, fire-associated sediments were BMMOD, BM CONF, and BMINT.

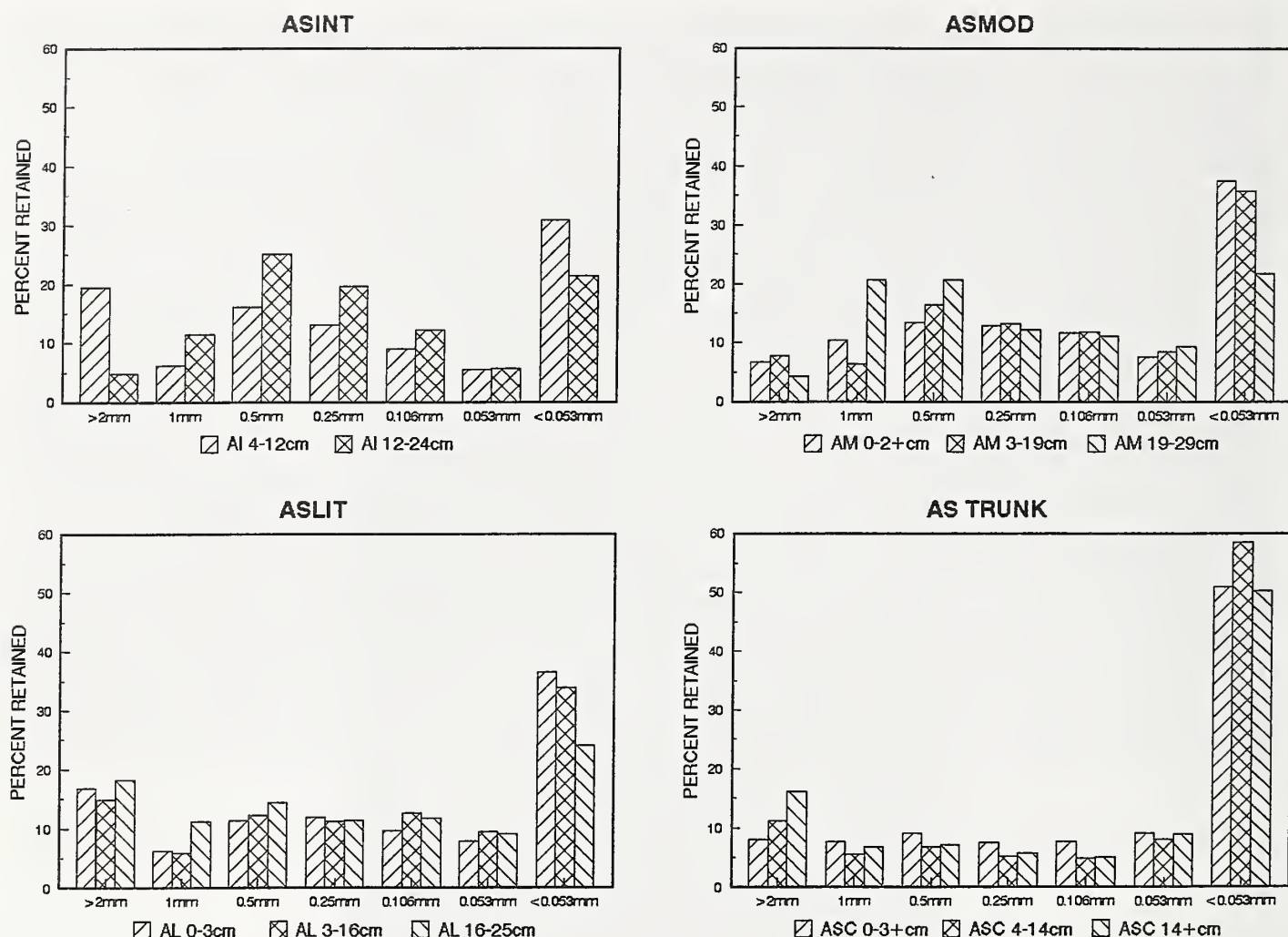


Figure 4. Grain size distributions, upper elevation (Apache Mesa) sections. "Percent Retained" refers to the percent of the material retained in a sieve of the size specified on the x-axis. The separate, textured bars indicate the depth at which the graphed samples were collected in the field.

DISCUSSION

White and Wells (1984) describe the early post-burn response of the six study basins; this paragraph summarizes their findings. They concluded that a principle physiographic difference between the upper and lower elevation study basins was the long valley side slopes that exist at the upper elevation. The long valley side slopes result in discontinuous drainage lines from the study basins to the trunk drainage. Although similar magnitudes of sediment yield per unit area were computed for the study basins, fire-associated sediment was temporarily stored along the valley side slopes and not delivered to the trunk drainage line on Apache Springs as was clearly the case on Burnt Mesa (see Figure 6 in White and Wells, 1984). Besides drainage density, (and continuity), early post-burn fac-

tors that increased sediment yield were found to be the hydrophobic ash layer and frost action, whereas early factors limiting sediment yield were identified as needle cast and climatic variability. Finally, fire-induced erosion rates were found to be of similar magnitude as a pre-burn rate calculated from pedestaled vegetation (5.3 mm/yr, Earth Environmental Consultants, Inc. 1978).

My 1992 pin measurements and recent field observations indicate that a well-defined, pedestaled ground surface has developed since the La mesa Fire through *non*-erosional processes in portions of my study basins. These observations may call into question the methodology and thus the validity of the EEC calculated pre-burn erosion rate. My observations suggest that a pedestaled ground surface can develop through aggradational processes

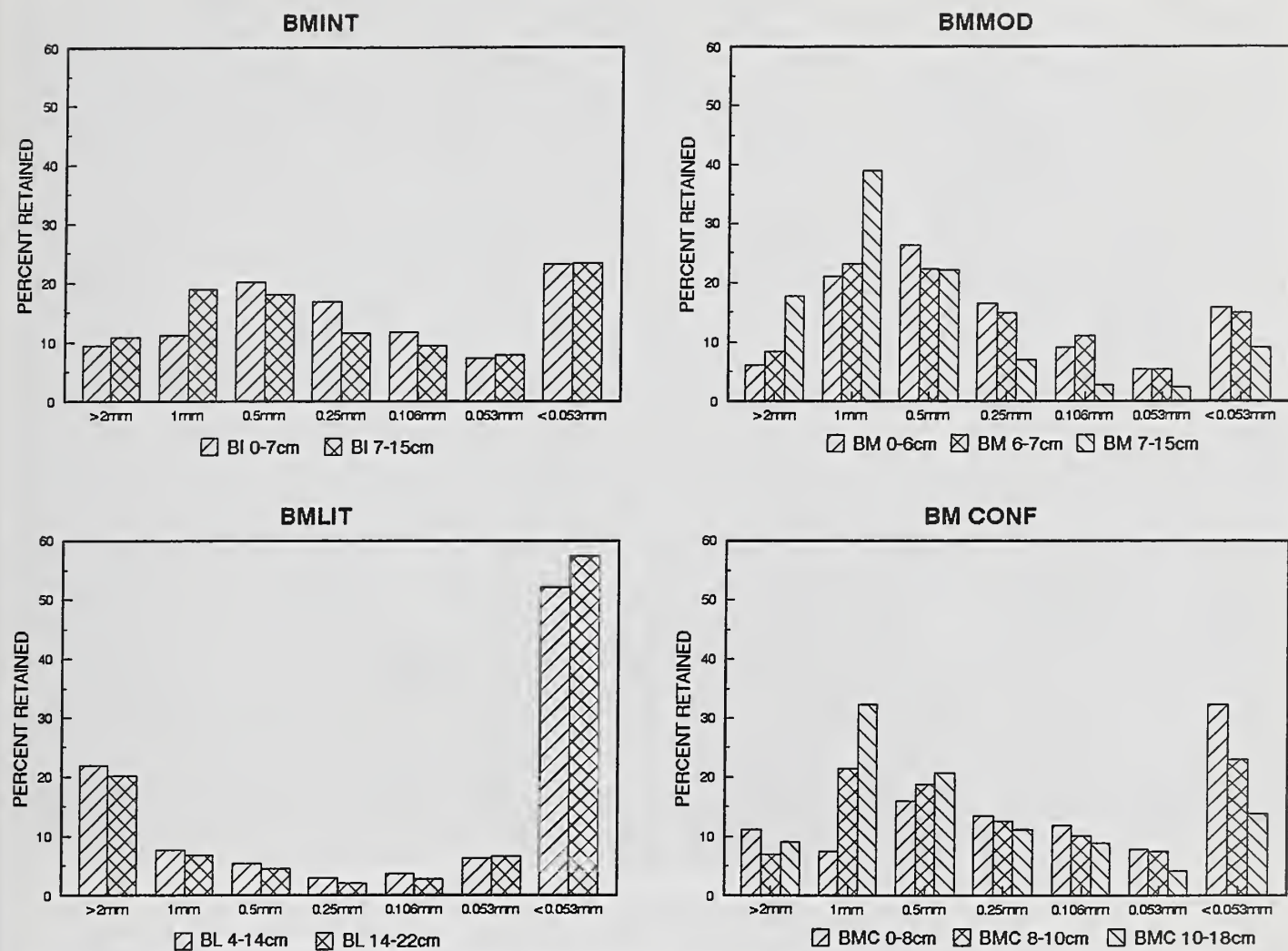


Figure 5. Grain size distributions, lower elevation (Burnt Mesa) sections. "Percent Retained" refers to the percent of the material retained in a sieve of the size specified on the x-axis. The separate, textured bars indicate the depth at which the graphed samples were collected in the field.

associated with the growth of grass clumps and cryptogamic crusts.

Pedestaled vegetation was observed in the study basins during the period of instrumentation in September 1977 (Figure 6), and survives in places seemingly little changed (Figures 7-a and 7-b). The hillslope gradient and pedestals shown in Figure 6 appear to define a classic condition of pedestaling as a result of sheetwash (probably correctly). Alternatively, Watt (1947) describes pedestaling associated with a building phase of a grassland community that spatially redistributes its microtopography without an overall reduction of ground surface elevation. He suggests that the mineral soil rises within grass tussocks by trapping "wind-borne particles and particles water-borne in

the splash of heavy rain" (Watt 1947: 672). My field observations of erosion pins during 1992-93 clearly document grasses growing up and over pin heads. Such growth raises the question of whether or not the grasses may actually lift the washer, thereby affecting pin measurements. More importantly, grass pedestals should be recognized as potentially expressive of constructive processes (i.e., trapping locally redistributed material with net dust deposition), and not necessarily erosional when viewed in other locations in the field.

At the time the erosion pins were deployed, cryptogamic crusts were not noted anywhere, nor were such crusts observed to develop during the three years of post-burn pin measurements. However, grass pedestals armored with cryptogamic



Figure 6. Remains of pre-burn, pedestaled ground surface, Burnt Mesa, September 1977. Pedestals and orientation of pine needles define a classic example of sheetwash eroding a low gradient hillside. Pedestals were assessed to be pre-burn due to their charred edges. View includes the deployment of scattered erosion pins on a hillside near BMINT's Transect C. Such deployments were quickly lost in the returning vegetation and abandoned within a year of their deployment.

crusts, and free-standing crusts (microtopography dominantly comprised of cryptogamic crusts), are clearly expressed over most present day ground surfaces, particularly in the areas that were intensely burned.

Campbell et al. (1989) describe a microbially formed soil cover known as desert crust, an accretionary phenomenon in a generally erosional setting. They describe binding of mineral grains by extracellular metabolic products (polysaccharide sheaths) of filamentous organisms. Some cryptogamic crusts are phototactic and tend to migrate upward toward the light, trapping and binding soil particles as they grow. Gillette and Dobrowolski (1993) determined that agents of cryptogams and rainwater caused a range of dust deposition of 206–617 g/m²/yr in Tadzhik, S.S.R. Assuming a bulk density of 1 g/cc, Gillette and Dobrowolski's dust deposition values can be converted to ground surface elevation changes per year of 0.2 - 0.6 mm/yr. These values compare well to values computed

from erosion pin measurements at Bandelier spanning a twelve year period (1980–1992), particularly for the intense burn basins which were observed to have well developed cryptogamic crusts (BMINT & ASINT, Table 5). The upward motility of the cryptogamic crusts was clearly observed in association with erosion pins (Figure 8).

Erosion pin data cannot separate eolian deposition (i.e., dust) from water borne aggradation (e.g., rain splash, sheetwash). However, it would be interesting to research the visibility studies that have been conducted in the area to see if estimates of dust deposition could be derived from that data. Such an effort would seem to be particularly worthy when the calculated sediment yield data for the instrumented archeological site on Burnt Mesa is compared to those values computed for the rest of the study basins (Table 6).

Since the early estimate for surface elevation change (–5.7 mm/yr, White and Wells 1984) did not result in exposure of the ruin, and the long

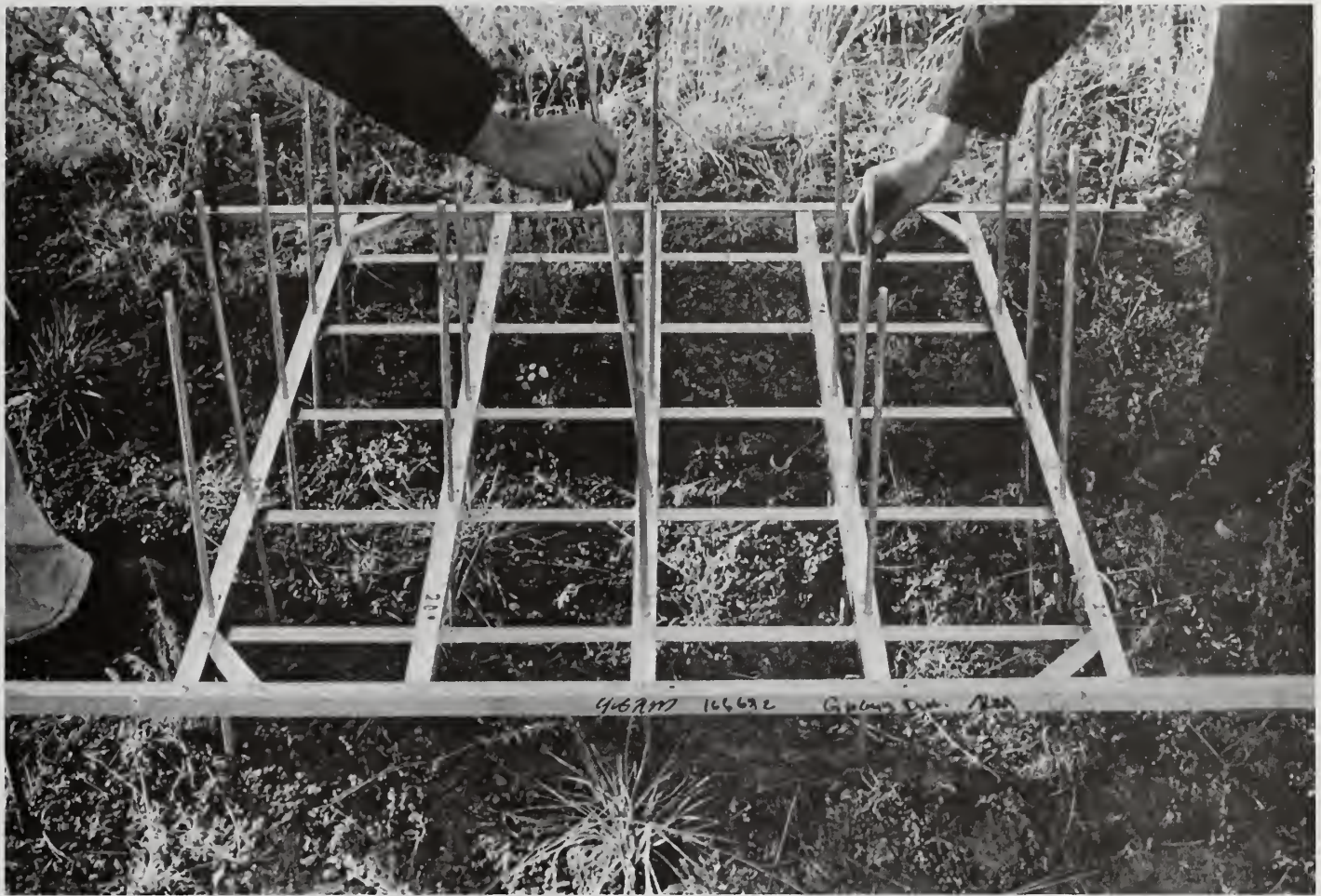


Figure 7-a. Photograph of Mobile Erosion Plot (MEP) equipment being used in BMLIT, November 1977. View is from the right side of view in 7-b. Although specific pedestals cannot be identified between views, the generally pedestaled ground condition can be identified in both views.

term value for surface elevation change is positive, dust deposition must be a factor (even though no cryptogamic crusts were noted on the mound). Also, despite being on a ridgecrest and having been abandoned for about 600 years, this two or three room archeological site appears as a mound, infilled with fine sediment between stone block walls, further attesting to the importance of eolian inputs through time.

Further review of Table 6 indicates a distinct turn around in sediment yield during the third year of the original study. The turn-around is attributed to an evolving sequence of geomorphic processes, beginning with devegetation and induced hydrophobicity leading to increased runoff in the form of sheetwash and increased rilling (year one). Year two is marked by pronounced frost heave which increases the availability of easily entrained sedi-

ment but also initiates the break-up of post-burn rilling (which had increased the effectiveness of sediment delivery in year one and into year two). By the third year after the fire, re-establishing vegetation interrupts sheetwash, traps rain-splashed sediment, and reduces the volume of overland flow delivered to channels via fading post-burn rills. The twelve-year period between the original study and the 1992 remeasurement of the erosion pins shows positive sediment yields for all study basins except ASLIT. Although cryptogamic crusts were evident in ASLIT, this basin did not have the added factor of geomorphic importance, log check dams, to protect against its comparatively steep gradient (see White and Wells, 1984, for comparative table of study basin characteristics).

The study basin most visibly affected by the above sequence of geomorphic processes following



Figure 7-b. View of MEP site, BMLIT, June 1993, looking upslope toward the northeast. The visibly deflected condition of the rebar stake in lower left of view eliminated the possibility of reemploying this instrumentation. Note pedestaled character of the blue grama grass, the apparent lack of cryptogamic crusts, and elk droppings in the foreground.

the fire was BMINT. Figure 9 is a series of photographs showing the evolution of rilling and revegetation of one BMINT hillslope through time. The first-year, post-fire condition of a hydrophobic ash layer producing increased sheetwash and rilling was followed by mechanical break up of the ash layer through frost action. The frost action performed two opposing actions: 1) produced a greater surface area for particle entrainment and transport by overland flow; and 2) initiated the break-up of the well-defined, post-burn rilling. By the third year of recovery, less overland flow was occurring due to the interference of returning vegetation and log check dams, and the post-burn rill systems were distinctly fading (Figure 9-b).

The pre-burn stand of pine trees in BMINT was dense (as also was the case for ASINT); the majority of these burned poles did not fall during the first three years of post-burn study (Figure 9-a and 9-b). Through time, more and more burned poles fell, each creating check dams against sheetwash and rilling (Figure 9-c). Finally, by 1992–93 the resultant

jack-straw pattern of downed trees both encourages infiltration of rainwater and seemingly discourages elk-trampling. (An abundance of elk sign was noted in the more open areas around the perimeter of BMINT, particularly the area immediately west of the lower basin divide, leaving the observer with the impression of preferred (or disliked) habitat. Additionally, the comparatively steeper and varied relief of the headwater transects generally show the lowest percentage of pins with less loss; Table 2).

The increased runoff and sediment delivery from the hillslopes during the first two years after the fire produced a well-defined channel (Figure 2). However, 12 years later, the well-defined drainage line is obliterated and no sediment is being transported due to downed trees and the dense and vibrant regrowth of grasses and shrubs (Figure 3). The interrelated factors inhibiting sediment transport include the increased density of vegetation and associated build-up of ground-cloaking litter, the log dams formed by downed trees, and the development of cryptogamic crusts.

Table 6. Summary of mean annual surface change and sediment yield for each study basin. The data in the Change per Year column are averages of the data in Table 5. A plus (+) sign under the yield columns denotes a net gain value (modified from White and Wells, 1981).

Study Basin (m ²)	Time Period	Change per Year (mm/yr)	Total Sediment Yield (m ³ /yr × 10 ⁻³)	Sediment Yield per Unit Area (m ³ /m ² /yr × 10 ⁻⁶)
BMINT Area = 4116.5	9/77-6/78	-4.3	17.2	4.2
	6/78-6/79	-6.5	26.0	6.3
	6/79-4/80	+3.6	+14.4	+3.4
	4/80-5/92	+0.4	+ 1.6	+0.3
BMMOD Area = 813.0	9/77-6/78	-1.8	3.6	4.4
	6/78-6/79	-1.1	2.2	2.7
	6/79-4/80	-0.4	0.8	0.9
	4/80-5/92	+0.9	+1.8	+2.2
BMLIT Area = 1426.0	9/77-6/78	-4.6	12.1	8.5
	6/78-6/79	-7.7	20.2	14.2
	6/79-4/80	+6.2	+16.3	+11.4
	4/80-5/92	+1.2	+ 3.1	+ 2.2
ASINT Area = 1421.4	9/77-6/78	-3.5	9.1	6.4
	6/78-6/79	-1.2	3.1	2.2
	6.79-5/80	+3.4	+8.8	+6.2
	5/80-6/92	+0.5	+1.3	+0.9
ASMOD Area = 677.7	9/77-6/78	-4.4	5.5	8.2
	6/78-6/79	-4.4	5.5	8.2
	6/79-5/80	+2.5	+3.1	+4.6
	5/80-5/92	+0.4	+0.5	+0.7
ASLIT Area = 380.4	10/77-6/78	-3.2	2.2	5.8
	6/78-6/79	-7.8	5.4	14.3
	6-79-5/80	+3.2	+2.2	+ 5.7
	5/80-5/92	-0.1	0.1	0.1
BM ARCH Area = 53.0	3/78-5/92	+0.4	+0.2	+ 3.7

Other researchers have shown cryptogamic crusts to increase soil moisture retention in sandy soils and enhance soil fertility by incorporating nutrient-binding clay particles into the sheath material of the crust (Harper and Pendelton 1993, Belnap and Gardner 1993). The cyanobacteria in local crusts fixes atmospheric nitrogen (Belnap 1990, West 1990), and Loftin and White (This Volume) provide evidence that crust-mediated nitrogen-fixation is ecologically significant in the La Mesa Fire area. I suggest that the vibrancy and density of vegetation in BMINT (and ASINT) is in part due to the enhancement of site productivity conditions by these characteristics of cryptogamic crusts.

The role of cryptogamic crusts in water infiltration is poorly understood (cf. West 1990, Eldridge 1993). Some researchers have proposed that cryptogamic crusts simply increase the ground surface roughness, thereby inhibiting sheetwash and presumably pro-

moting infiltration. My observations at Bandelier suggest that a microtopography of grass and soil pedestals armored by cryptogamic crusts and log check dams with bare hollows in between, creates a broken ground surface with characteristics favorable for infiltration (Figure 10). The emergent pedestals impede surface runoff, forcing the water around them in circuitous routes across the intervening bare hollows. These hollows appear to be depleted of fine-textured particles which are apparently splashed onto the adjacent grass and cryptogam pedestals, leaving an erosion pavement of quartz crystals where infiltration can readily occur. This scenario for pedestal formation is remarkably similar to the phases of grassland dynamics described by Watt (1947: 672).

On August 27, 1993, a long, heavy rainfall occurred on Burnt Mesa. I was fortunate enough to be at the Monument headquarters during the rain and stopped at the Burnt Mesa sites shortly after



Figure 8. Cryptogamic crust growing through washer, ASLIT, June 1993. The crust incorporates pumice fragments below the washer, and can be seen above the washer, growing through the space between the pin and the washer.

the rain stopped. While I was observing the obvious, freshly scoured channel of BMMOD (Figure 11), I could hear water flowing in the canyon tributary below the study basin's confluence. Traversing the short distance to the canyon tributary, I noted the confluence channel began to show puddles remaining in the channel with very little flow occurring between, yet the canyon tributary was flowing. Upon closer examination, I could discern many rivulets flowing over the canyon walls, their origins being seeps from the colluvial mantle (Figure 12) over the less weathered bedrock as it thins adjacent to the canyon margins. There was no sediment produced from the BMINT study basin during this event, in contrast to the BMMOD basin (Figure 13), as the incident rainfall was obviously being conducted from BMINT to the canyon tributary as shallow ground-water interflow instead of as surface runoff.

CONCLUSIONS

Although the protected and growing elk population in Bandelier National Monument must have significant ecological effects on the Monument (see

contributions in This Volume by Allen; Wolters; and C. White), their effect on hillslope erosion in my study basins appears to be minimal. My 1992 pin measurements and my field observations during 1992 and 1993 have identified two primary factors in the long-term control of post-burn erosion and at least one factor contributing to present day erosion that was a principle control to early, post-burn erosion.

I have evaluated the utility of 15-year old erosion pins in an area known to support a large protected population of elk. While the apparent likelihood of trampling by elk must be great, only 16 percent of 411 erosion pins were measured to have less loss than measurements twelve years earlier, and only one pin was observed to have the pin head flush to the washer (the expected result of trampling). Thirty-one percent of those 16 percent with less loss had observed associations with cryptogamic crusts or grasses. Unfortunately, the pins were not individually surveyed for relative elevation during the original study; thus no conclusive statement can be made as to whether the separation between individual pin heads and their associated washers



Figure 9-a. Evolution of a hillslope, BMINT, September 1977. The total consumption of forest litter and herbaceous undergrowth (in addition to the total consumption of pine needles of the trees) produced a hydrophobic layer on the ground surface (darker tone, center of photograph). The ash layer promoted runoff after the La Mesa fire. The runoff occurred as sheetwash on the shallower gradient slopes and progressed to rilling on steeper slopes (small channels, center of photograph).

is due to pin head depression (trampling), or due to lifting of the washer by grasses or cryptogamic growths. However, since the pins did not show signs of downslope creep, and since so few pins could be proven to be trampled, I believe the pins are still useful tools.

The most important factors controlling erosion 15 years after the La Mesa fire include: 1) the development of numerous log check dams as burnt trees have gradually fallen; and 2) the formation of cryptogamic crusts. I propose that the cryptogamic crusts may play a largely unquantified role in soil fertility that may be more important than their role in increasing surface roughness and retarding overland flow (see Loftin and White, This Volume). Aggradational growth of cryptogamic crusts is observed (Figure 8), but how much of this aggradation is due to motility or deposition (dust and/or rain splash) is not determined in this study. The possibility that cryptogamic crusts retain nutrients by sequestering clay-sized particles may help ex-

plain their prominence in the intense burn areas and the apparent vigor of the associated grasses. Bunch grasses themselves are also effective builders of the ground surface profile, as evident by their growth over pin heads.

The combination of log check dams and cryptogam/grass pedestals results in a ground surface with a well developed microtopography which breaks up overland flow and promotes infiltration. The infiltrating rain water becomes shallow ground-water interflow which perches on the lower permeability bedrock and discharges laterally at canyon margins. The gathering flow in the tributary canyons is not sediment-laden which allows present day flow events to transport the fire-derived sediment previously deposited in plunge pools, point bars and overbank deposits in the tributary and trunk canyon drainages.

The most stable basin during the original study was BMMOD, as this basin had the least negative ground surface change (White and Wells 1984;



Figure 9-b. Evolution of a hillslope, BMINT, April 1980. Frost heave has broken up the hydrophobic layer. Overland flow is interrupted by fallen trees and grass bunches which results in a reduction of rilling. Note how few trees have fallen.

Table 5). This relative stability was attributed to post-burn needle cast from the unburned canopy which protected the ground surface from rain drop impact and retarded overland flow. However, BMMOD may now be the least stable basin, based upon 1993 field observations which show the drainage line to be scoured of loose sediment and colluvial debris which is being deposited in the trunk drainage (Figures 11 and 13). This less stable condition results from the lack of downed trees and the notably limited distribution of cryptogamic crusts within the study basin. While protecting the ground surface from rain drop impact and overland flow, the needle cast discourages the growth of cryptogamic crusts. Without the encouragement of cryptogamic crusts and downed-tree check dams for infiltration, precipitation in moderately burned basins collects in the basin's drainage line. The sediment-free flow scours the generally steeper gradient channels of headwater basins, and delivers sediment to the shallower gradient, mesa-top trunk drainages where it is deposited (Figure 13).

Overall, 15 years after the La Mesa Fire, sediment delivery has ceased across most of my study basins as the development of vascular and cryptogamic ground covers and log check dams has increased infiltration and decreased surface runoff. However, modest amounts of sediment continue to be delivered by intense rainfall from the moderately burned BMMOD basin where cryptogamic crusts and log dams are relatively scarce. Nonetheless, erosion pin measurements show that even BMMOD has experienced net aggradation since 1980, as have most of the monitored basins. From a geomorphic perspective, recovery has largely been achieved in the La Mesa Fire area.

ACKNOWLEDGEMENTS

The author wishes to thank Dr. Craig Allen for providing the incentive to remeasure the 400+ erosion pins left in the field for 15 years, as well as his review of this manuscript. Special thanks are reserved for Steve Bracker for his programming as-



Figure 9-c. Evolution of a hillslope, BMINT, May 1992. The large tree trunk (right center) is the same as the upright trunk in right center of 9-a and 9-b. The fading log lying across lower left center of view is the same as the log in lower left of 9-b. Nearly all the trees killed by the La Mesa fire have fallen after fifteen years. The microtopography of the ground surface that results from the combination of fallen trees, grass pedestals, and cryptogamic crusts (not seen at the scale of the photograph) largely eliminates overland flow and promotes infiltration.



Figure 10. Grass pedestals with the bare hollows between covered with an erosion pavement of quartz crystals (white speckles, right center of photograph). The dark tone area in lower right is cryptogamic crust.



Figure 11. Scoured channel around a plug of organic debris accumulated behind two erosion pins (between rebar stake, left edge of photograph, and the lens cap, lower center), BMMOD, August 1993. The light toned area in the lower half of the photograph is tuff fragments weathering out of the bedrock. The medium toned area is sediment (upper half of the photograph) and scoured soil (lower right half of photograph).



Figure 12. White toned area in center of photograph is reflection off the surface of a gathering sweep (water emerging from the soil profile), Burnt Mesa, August 1993. Flow was observed to move from the seep toward the viewer and the tributary drainage (behind the viewer).



Figure 13. Sediment bars derived from BMMOD (and adjacent moderately burned basins) and deposited in the trunk drainage below the confluence with BMINT, August 1993. No sediment was delivered from the intense burn basin, the direction indicated by the handle of the hammer.

sistance to generate transect profiles upon which to display new and old erosion pin data. The author also wishes to thank the Bureau of Indian Affairs for contributing time and staff assistance for transect profile surveys; Dr. Carl White for accessing his cryptogamic crust library; and Chris Banet

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Flood History Reconstruction in Frijoles Canyon Using Flood-Scarred Trees

V. Alexander S. McCord¹

Abstract.—Unexceptional summer storms triggered large floods on the Rito de los Frijoles in 1977 and 1978, shortly after the intense La Mesa Fire of 1977 burned this watershed. Large numbers of trees growing on or near the stream bank in Frijoles Canyon were scarred during these flood events. These scars provide a record of the occurrence of past flood events which I used to reconstruct the flood history of the canyon. I compared the reconstructed flood history with existing fire history data to test the hypothesis that large floods have occurred following large-scale fires in the past.

I sampled 36 scarred trees at several localities along the Rito de los Frijoles. The flood scars were crossdated using reference chronologies I developed from scarred and unscarred trees in the canyon. I surveyed channel cross-sections and the top heights of the flood scars above the stream level, and then reconstructed paleoflood discharges using the slope-area method.

The riparian tree-ring chronology extends to the early 1600s, represented by at least five trees back to the mid-1700s. The scar dates range from 1773 to 1985, with most of the scar dates falling in 1977 and 1978. Floods were also identified for 1866, 1904, 1951, and 1972. Other than 1977, only the 1773 flood(?) scar matches a major fire year in the local fire scar record—this suggests that fire intensity, rather fire extensiveness, is the major factor leading to post-fire flooding in this watershed. Flood discharge estimates reconstructed from flood scars correspond well with the USGS estimates for the historic floods of 1977 and 1978. The flood scar evidence in Frijoles Canyon indicates that there have been at least four floods comparable to the 1978 flood in the last two centuries, and at least seven floods as large as the flood of 1977 during that time.

INTRODUCTION

Deforestation caused by severe forest fires exerts an important influence on flooding and debris flows by causing increased runoff and erosion (Wells 1987). The catastrophic La Mesa Fire at Bandelier National Monument in June of 1977 was followed a few weeks later by a large flood on the Rito de los Frijoles in Frijoles Canyon. This flood was larger than any that had been previously recorded in the watershed, and was itself exceeded the following year by an even larger flood, in July of 1978 (U.S. Geological survey 1978, 1979, Purtymun and Adams 1980). The storm events as-

sociated with these floods were not particularly exceptional, but a large portion of the watershed had been intensely burned, contributing to decreased infiltration capacity of the soils, and reduced retardation of surface runoff. These factors combined to produce very rapid runoff and high sediment yield from relatively moderate rainfall events (White and Wells 1984).

Large numbers of trees growing on or near the stream bank in Frijoles Canyon were scarred dur-

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ing these flood events. These scars provide a record of the occurrence of past flood events and can be used to reconstruct the flood history of the canyon.

Establishment of a flood chronology provides additional insight for the interpretation of fire history at Bandelier National Monument. The flood history can be compared with the fire history produced by the analysis of fire scars (Allen 1989, Touchan *et al.* this volume) to test the hypothesis that large floods have tended to occur following large-scale fires in the past.

Flooding is a very important process in fluvial geomorphology and riparian ecology. In mountainous and semiarid terrain, infrequent large-magnitude floods may be the most important process involved in channel change, sediment transport, and landscape change in general (Wolman and Gerson 1978, Kochel 1988). Flooding exerts profound influence on species composition and population dynamics of riparian communities (White 1979, Hupp 1988), and also drastically affects human activities. Detailed knowledge of past flood regimes is essential to the complete understanding of fluvial systems, and for the realistic assessment of future probabilities of flood risks.

Large floods are linked to important climatic events, and appear to be somewhat independent of total annual precipitation. It appears that catastrophic flooding is episodic over scales of hundreds to thousands of years. This observation is based in part on slackwater deposit evidence from the Southwest over the scale of thousands of years (Webb *et al.* 1988). Evidence from flood-scarred trees in the Colorado River basin suggests that large floods have occurred in distinct episodes over the last several hundred years as well (McCord 1990). Thus the analysis of flood-scarred trees provides evidence of one aspect of climate change (large floods) over the last several centuries. Flood scars occur on the upstream-facing sides of trees growing along rivers, streams, and minor drainages, and are caused by the impact of flood-borne debris (Sigafoos 1964, Harrison and Reid 1967, Yanosky 1982, Gottesfeld and Gottesfeld 1990, McCord 1990 and 1996). The damage caused by these impacts may be easily recognized and can be accurately dated to the exact calendar year by dendrochronological methods. Unlike fire scars, the damage often does not extend to the base of the trees. Such scars are probably caused by the impact of floating logs and branches; scars extending to the ground level are more likely to have been caused by the impact of boulders, cobbles, and

gravel moving by bouncing and rolling along the streambed. Flood scars may usually be distinguished from fire scars based on their morphology and orientation relative to the stream channel, but there may be ambiguity in some cases if the damage extends all the way to ground level. In many cases the season of the occurrence of the damage can be determined, and the event can sometimes be dated to within a month or two if it occurs during the growing season. Therefore different storm types (winter frontal type, summer convective cell type, and fall tropical storm or hurricane type) can be distinguished.

The heights of flood-scars above the stream channel provide accurate information on stage, or flow depth of past floods, and are thus good paleostage indicators. This paleostage information has been used in conjunction with stream channel geometry to successfully reconstruct discharge for floods of known magnitude. The technique shows excellent agreement with the known flood record, for both magnitude and frequency (Harrison and Reid 1967, McCord 1990).

METHODS

I sampled 36 scarred trees at several localities along the Rito de los Frijoles (in Frijoles Canyon), from the Upper Crossing to about two kilometers upstream of the Visitor Center (Figure 1). A total of 152 increment core samples were taken from living scarred trees. Cross-sections were also taken with handsaws from three dead snags. In addition, 71 increment core samples were taken from 32 unscarred trees. The scars were crossdated using reference chronologies produced from the collection of scarred trees and from the additional collections from unscarred trees. Most of the scarred trees had visible scars on the outside of the tree, but in a few cases cores from trees that were apparently unscarred were found to have scars that had been closed over by subsequent growth of the trees. The scar dates and time ranges of the trees used in the chronology were made into a flood event chronology (Figure 2) to graphically illustrate the flood history of the watershed. The flood event chronology produced in this manner is similar in appearance to a fire history chronology.

A reach of the stream just upstream from the Ceremonial Cave site was extensively studied in order to estimate the discharge of the post-fire floods. This reach of the canyon bottom has some important features which make it a good choice for the reconstruction of the discharge of prior floods.

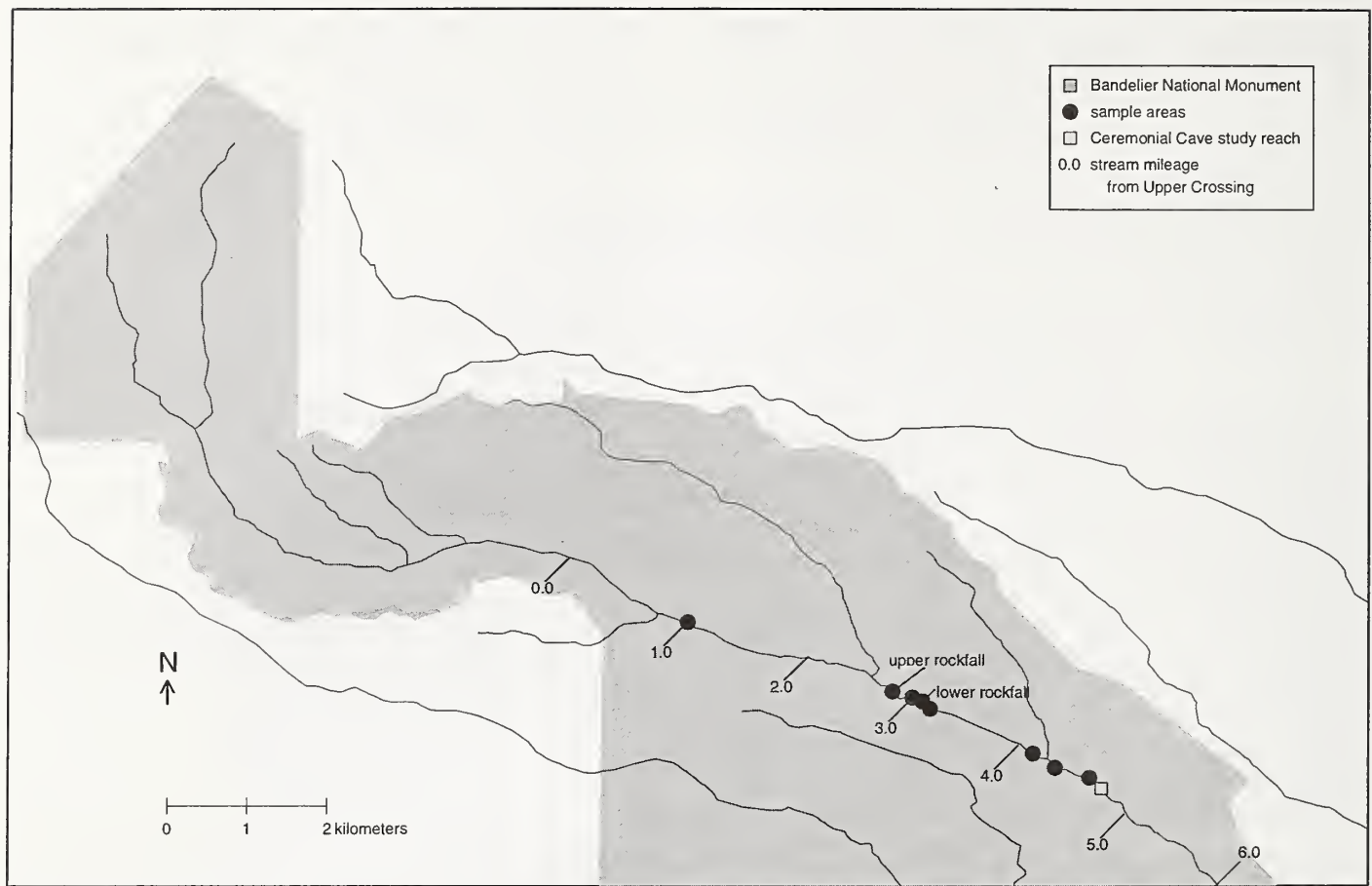


Figure 1. Locations of sample areas for flood-scarred trees in Frijoles Canyon.

There is a straight segment of stream about 100 meters in length which is fairly constant in its gradient and cross-sectional shape. There are numerous scarred trees in this reach, most of which have scars at about the same height above the stream, two to three meters, indicating a fairly constant depth for the scarring event in this reach. This study reach presents a reasonably simple hydraulic situation, so that the discharge may be modelled with some confidence.

The heights of the tops of the highest scars from the 1978 flood were taken to represent the water surface during the flood crest stage, and the discharge was estimated using the slope-area method (Dalrymple and Benson 1967). The slope-area method, commonly used for the indirect estimation of stream discharges, uses the Manning equation (Williams 1988) to determine mean flow velocity, which is given by

$$v = \frac{1}{n} R^{2/3} S^{1/2}$$

where V is the velocity, R is the hydraulic radius (the channel cross-sectional area divided by the length of the wetted perimeter of the cross-section), S is the water surface slope or channel gradient, and n is a resistance factor related to the roughness of the channel bed, called the Manning roughness coefficient. The product of the mean velocity times the cross-sectional area is equal to the discharge.

The channel slope and cross-section was surveyed at several stations in this reach, along with the positions of the tops of the flood scars. From the survey data I plotted the longitudinal profile of the stream channel bottom, added the positions of the tops of the scars to the same plot, and then fit an envelope curve over the tops of the highest scars. Finding that this curve was almost exactly parallel to the channel bottom profile, I concluded that it was a good representation of the water surface profile at the flood crest stage. I ignored the lower scars, reasoning that some of the trees would be injured and scarred during the rising and receding stages of the flood. Using the survey measure-

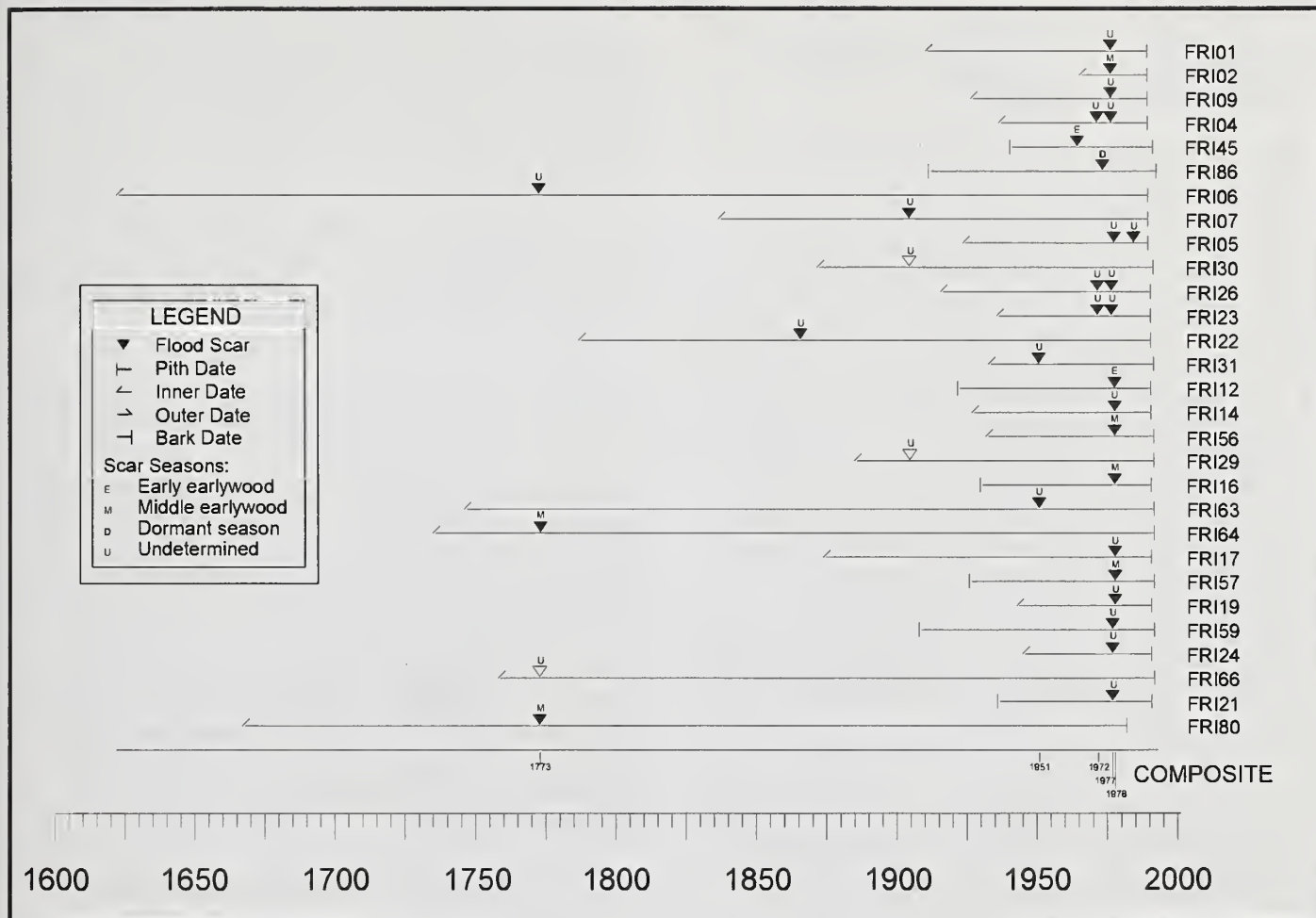


Figure 2. Flood-scarred trees in Frijoles Canyon. Horizontal lines represent individual trees. Black triangles represent flood scars, open triangles other injuries or growth disturbances. Trees are arranged from top to bottom in order proceeding downstream.

ments and the inferred water surface for the 1978 flood, I computed the channel cross-sectional area and the length of the wetted perimeter of the channel at three stations. I chose a value of 0.05 for the Manning roughness coefficient after consulting the tables in Albertson and Simons (1964) and making a comparison of the channel characteristics of this reach to those of the smaller streams described in Barnes (1967). The slope and channel cross-section measurements were then used with the Manning equation to estimate the mean flow velocity and discharge, which I calculated in cubic meters per second (m^3/sec), and then converted to cubic feet per second (CFS).

Discharges were also estimated for the 1977 flood and for five probable floods prior to that, although the information obtained from the scars caused by the 1977 and earlier floods was not adequate to define the water surface with much confi-

dence. A flood in August of 1991 left a well-defined line of debris at about a meter or so above the stream bank, well below the scars from the 1978 flood. This debris line was surveyed, and the inferred water surface was used to estimate the discharge, so that it could be compared to the discharge reported by the US Geological Survey at the gage downstream near the Monument headquarters.

RESULTS

Flood Scar Dates

The flood scar dates on trees from Frijoles Canyon are summarized and shown as a flood event chronology in Figure 2. The scar dates range from 1773 to 1985, with most of the scar dates falling in 1977 and 1978. Floods were also identified for 1866,

1905, 1951, and 1972. No scars were found dating from the August 1991 flood. The chronology extends to the early 1600s, represented by at least five trees back to the mid-1700s.

Data for the flood-scarred trees are summarized in Table 1, including species, locations, tree dates, and scar dates. Heights above the channel bottom are shown for the scars in the surveyed stream reach where I estimated the water surface profiles for the various floods. For the trees upstream of the surveyed reach, the heights of the scars above the base flow water surface are shown. The scars from the 1977 flood (marked by single asterisks) are more common in the upstream reaches, and are generally a meter or two higher than they are in the lower reaches. In contrast, virtually all of the 1978 scars (double asterisks) appear in the downstream portion of the stream where the discharge was estimated, and are generally a meter or so higher than the 1977 scars in this reach of the stream. This suggests that the 1977 flood was more widespread than the 1978 flood, and was of greater magnitude in the upper part of the watershed.

Field inspection of the scars in the Ceremonial Cave study reach seemed to indicate that they had been caused by the same flood event. When the wood was crossdated, however, it became apparent that they are a mixed population, about half of them from 1978, but also including scars from 1977 and other years. Where seasonality could be determined, most of the trees scarred in 1978 show clearly that the damage occurred in the middle portion of the earlywood, consistent with a mid-summer flood event. Replicated scars, injuries, and growth suppressions in this reach dating from 1773, 1905, 1951, and 1972 indicate that there were floods in those years also.

In the upstream part of this reach there is an overflow channel about 60 meters long, off to the right (looking downstream) of the main channel. This channel is a shortcut path across a meander bend just upstream from the straight reach, and is about one meter in elevation above the current active channel. Scarred trees in the overflow channel indicate that it becomes active during high flows. A scar on a ponderosa pine growing on the edge of the channel dates to 1866; other trees have more recent scars from 1951, 1972, and 1977 (Table 1). No scars from 1773, 1905, or 1978 were found here. The debris line from the August 1991 flood, which comes to just below the mouth of the overflow channel, is not present in the channel itself, indicating that the 1991 flood was not large enough to cause the overflow channel to be used.

About a kilometer upstream from the Ceremonial Cave reach one of the scars dated to 1773. This scar is on a large ponderosa pine dating back to the early 1600s. Downstream from this tree two other old ponderosas had internal (closed over) scars that also dated to 1773, and two others showed a severe growth suppression starting in 1773. On two of these trees, the 1773 scar can be clearly seen to be in the early part of the earlywood growth layer, showing that the damage was initiated during the early part of the growing season.

Reconstructed Flood Discharge Estimates

The channel characteristics and the velocity and discharge calculations for the 1978 flood at three cross-sections in the surveyed study site near Ceremonial Cave are shown in Table 2. The mean values, standard deviations, and coefficients of variation (CV) are also given. The mean discharge for the three stations is 2704 CFS. The discharge estimate for all eight floods that were reconstructed are shown in Table 3. Standard deviation and CV are given only for those floods where the water surface was defined by scars in at least two different spots along the study reach.

DISCUSSION AND CONCLUSIONS

The distribution of the flood dates suggests that the occurrence of floods in Frijoles Canyon is largely independent of the occurrence of fire. Of the pre-1977 flood dates, only one (1773) occurs in a fire year or in the following year. The interpretation of the 1773 scars is complicated by the widespread occurrence of a fire in that year (Allen 1989, Touchan *et al.* 1996). It seems reasonable to suspect that only very intense fires would sufficiently alter the watershed characteristics to increase its susceptibility to massive runoff from moderate rainfall events. The 1773 fire was widespread, and it is possible that it was such an intense fire, but that is not known with any certainty.

It is also possible that the 1773 scars and growth suppressions that I observed on riparian ponderosas in Frijoles Canyon were actually fire scars, and not related to floods at all. Two of the five trees showing 1773 scars or subsequent suppressions may be too far away from the present stream channel to have been reached by flood waters. Of the remaining three (on or near the stream bank), one has an internal scar and one has a growth suppression after 1773. Only one shows an

Table 1.—Flood scarred tree samples from Frijoles Canyon.

ID	Species	Dates	Scar Date	Pos	Ht above Water SFC	Ht Above Streambed	Mile Below Upper Crossing
FRI01	POAN	1911–1990	1977 U	*	3.75 m	—	1.0
FRI02	ABCO	1966–1990	1977 M	*	3.75 m	—	1.0
Upper Rockfall							
FRI09	ACNE	1927–1990	1977 U	*	3.5 m	—	2.8
Below Upper Rockfall							
FRI04	ABCO	1937–1990	1972 U		2.5 m	—	3.0
			1977 U	*	2.5 m	—	
Lower Rockfall							
FRI45	PSME	1941–1992	<u>1965</u> E		—	—	3.1
FRI86	PSME	1912–1993	1974 D		—	—	3.2
Below Lower Rockfall							
FRI06	PIPO	1622–1990	1773 U		4.2 m	—	4.1
FRI07	PSME	1837–1990	1905 U		2.5 m	—	4.1
Above Study Reach							
FRI05	PSME	1924–1990	1978 M	**	2.5 m	—	4.3
			1985 E		2.5 m	—	
Study Reach							
FRI30	PIPO	1872–1992	1905 U		—	1.6 m	4.7
FRI26	POAN	1916–1991	1972 U			1.7 m	4.7 (Overflow channel)
			1977 U	*	—	1.7 m	
FRI23	POAN	1936–1991	1972 U		—	1.8 m	4.7
			1977 U	*	—	1.8 m	
FRI22	PIPO	1787–1991	1866 U		—	3.3 m	4.7 (Overflow)
FRI31	ACNE	1933–1992	1951 U		—	2.9 m	4.7 (Overflow)
FRI15	ACNE	ND	ND		—	2.98 m	4.8
FRI11	POAN	1921–1990	ND		—	2.69 m	4.8
FRI13	POAN	ND	ND		—	2.67 m	4.8
FRI12	PIPO	1922–1991	1978 E	**	—	2.36 m	4.8
			1985 E		—		
FRI14	POAN	1927–1991	1978 U	**	—	2.37 m	4.8
FRI56	PIPO	1932–1992	1978 M	**	—	2.80 m	4.8
FRI29	PIPO	1885–1992	<u>1905</u> U		—	2.3 m	4.8
FRI16	JUSC	1930–1991	1978 M	**	—	2.94 m	4.8
FRI74	ACNE	ND	ND		—	>2.7 m?	4.8
FRI18	JUSC	ND	ND		—	2.08 m	4.8
FRI63	PIPO	1747–1992	<u>1951</u> U		—	2.9 m?	4.8
FRI64	PIPO	1735–1992	<u>1773</u> M		—	2.9 m?	4.8
FRI17	POAN	1874–1991	1978 U	**	—	2.56 m	4.8
FRI57	PIPO	1926–1992	1978 M	**	—	3.01 m	4.8
FRI58	JUSC	1941?1992	1951? U		—	2.9 m?	4.8
			1978? U		—	2.92 m	
FRI19	PSME	1943–1992	1978 U	**	—	2.17 m	4.8
FRI59	POAN	1908–1992	1977 U	*	—	2.18 m	4.8
FRI24	ACNE	1945–1991	1977 U	*	—	1.2 m?	4.8
FRI25	ACNE	ND	ND	—	—	1.3 m?	4.8
FRI66	PIPO	1758–1992	(1773) U		—	3 m??	4.8
FRI21	POAN	1936–1991	1977 U	*	—	1.3 m?	4.8
Below Study Reach							
FRI55	PIPO	ND	ND		—	—	4.9
FRI80	PIPO	1667–1982	<u>1773</u> M		—	—	—

Trees are listed in order proceeding downstream from Upper Frijoles Crossing. The scar dates are underlined for those scars that were closed over by subsequent tree growth. Dates in parentheses represent growth suppressions beginning in that year. The abbreviation ND indicates that the sample could not be dated. Column labelled POS gives the ring position of the injury; E = early earlywood, M = middle earlywood, D = dormant season, U = undetermined. Single asterisks (*) mark 1977 scars, double asterisks(**) 1978 scars.

external scar; the scar is facing upstream and has the general appearance of a typical flood scar, but unlike "classic" flood scars, it extends all the way to the base of the tree. Many flood scars do extend to the tree base, but this makes it difficult to rule out the possibility that it may be a fire scar. There is no charcoal on the scar, but this also does not rule out fire as the cause, because a tree scarred only a single time by fire may not show any charring if the bark was not burned through, as is typically the case when trees are fire-scarred for the first time.

Nevertheless, the scar does not really look very much like a fire scar. It does not have the typical triangular-shaped "catface" pattern, and the outline is irregular rather than smooth. There is a narrow strip of thin bark down the center of the scar connecting the upper and lower borders of the scar, with bare wood showing on either side of it. Growth continued under this narrow strip after 1773 (though highly suppressed), indicating that this portion of the cambium was not killed by the scarring event. I know of no fire scars showing

such a feature. The general appearance of this scar is very much that of a flood scar; if it is a fire scar, it is one of a very unusual character. More rigorous criteria to distinguish flood scars from fire scars would be very useful.

Virtually all of the scars on the conifer trees could be reliably dated using the riparian conifer chronologies for both ponderosa pine and Douglas-fir that have been prepared from the Frijoles Canyon ponderosa pine and Douglas fir specimens. Of the 19 scarred conifer trees sampled, 22 scars out of 24 have been dated from 17 of the trees. However, only 12 out of 17 scars on the deciduous trees have been dated from 10 trees out of 15 sampled, due to the lack of a sufficiently robust chronology to crossdate them against. The deciduous trees (primarily cottonwood and boxelder) display much greater between-tree variation in ring width, making it very difficult to crossdate single specimens against what are fairly weak chronologies based on insufficient numbers of trees. More robust chronologies using many more specimens of these species will likely be necessary in order to reliably crossdate all of the flood scars on the hardwoods.

The value of 2704 CFS for the discharge estimate of the 1978 flood is fairly close to the figure of 3030 CFS reported by the U.S. Geological Survey (1979) for the same flood on the basis of slope-area measurements made at a site about 500 meters downstream. The standard deviation of the discharge estimates at the three cross-sections is 117 CFS; the coefficient of variation is 4.3%, showing good agreement between the three stations.

It is encouraging to see such close agreement between the three stations, especially since there were proportionally larger differences in most of the channel characteristics. In any reach of a channel, if there are no tributaries or diversions between stations the discharge at any cross section should be the same as the discharge through any other cross section. This is due to a fundamental principle of fluid motion known as the *continuity equation* (Albertson *et al.* 1960). Only the water depth at channel center is as similar at the three stations as the discharge estimates, and the channel

Table 2. Channel characteristics and discharge calculations for the 1978 flood at three different cross-sectional locations in the Ceremonial Cave reach.

Cross-section Identification	2	A-A'	3
Water Depth at Channel Center	2.99 m	2.78 m	3.00 m
Channel Cross-sectional Area	23.81 m ²	23.38 m ²	29.33 m ²
Length of Wetted Perimeter	20.79 m	18.39 m	26.76 m
Hydraulic Radius	1.15 m	1.27 m	1.10 m
Channel Slope	0.0217	0.0178	0.0163
Flow Velocity	3.23 m/sec	3.13 m/sec	2.72 m/sec
Discharge	76.91 m ³ /sec (2716 CFS)	73.18 m ³ /sec (2584 CFS)	79.78 m ³ /sec (2817 CFS)
Mean Discharge for 3 Stations	76.62 m ³ /sec (2704 CFS)		
Standard Deviation	3.31 m ³ /sec (117 CFS)		
Coefficient of Variation	4.3%		

Table 3. Flood discharge estimates for 8 floods in Frijoles Canyon.

Flood Date	1991	1978	1977	1972	1951	1905	1866	1773
Discharge (CFS)	374	2706	724	724	2526	1495	3552	2526
Std Dev	43	117	53	—	64	—	—	—
CV (%)	11.5	4.3	7.3	—	2.5	—	—	—

depth is not used in the Manning equation. There was a dispersion of 13% between the three cross-sectional areas, and nearly 20% between the wetted perimeter lengths, but when the cross-sectional areas were divided by the frictional effects of the wetted perimeters, the resulting hydraulic radii were considerably more similar ($CV = 7.5\%$). The channel slope dispersions ($CV = 15\%$) were partially offset by the different hydraulic radii, leading to fairly similar velocities ($CV = 8.9\%$). The velocity at station 3 was lower than that at the other two stations, but the cross-sectional area was larger, so that the product of the velocity times cross-sectional area (discharge) was quite similar for all three stations ($CV = 4.3\%$)

The discharge estimates for the floods in 1977 and earlier years are less certain, because there were fewer trees with flood scars from those years that could be used to define the water surface. The water surface for 1977 is fairly well defined by scars on five trees in the study reach, two of them from above the three surveyed cross sections, and three of them from below.

The discharge estimate of 724 CFS is slightly larger than the slope-area estimate of 653 CFS made by the U.S. Geological Survey (1978), but is in reasonably close agreement. The 1972 event is defined in the study reach on only two trees from upstream of the measured cross-sections. These scars were partly concealed under 1977 scars, at about the same height as the 1977 scars, leading me to the conclusion that the 1972 flood may have been about as large as the 1977 flood. The 1951 flood is defined by a scarred tree in the study reach above the measured cross sections, and by two other trees with internal scars, one near cross section 3, and the other about 30 meters downstream. The water level seems to have been nearly as high as it was in 1978.

The magnitudes of the 1905, 1866, and 1773 floods are considerably more uncertain, because the water levels were inferred on the basis of only one or two scarred trees for each of the floods. I inferred the water level for the 1905 flood on the basis of an internal scar from a tree in the meander bend above the cross sections, and on an internal injury in a tree near cross section A-A'. The 1866 flood is represented by a single scar on a large ponderosa pine growing on the right bank of the over-flow channel. This flood may have been even larger than the 1978 flood. The 1773 water level was inferred from an internal scar on one tree near cross section 3. No survey data was obtained for

this scar, but based on the location of the tree it appears that the water level may have been at least as high as it was in 1951, and possibly as high or higher than 1978.

The water surface for the August 19, 1991 flood was well defined by the survey data from the debris line, but my estimate of 374 CFS for the discharge is not in good agreement with the figure of 105 CFS reported by the U.S. Geological Survey (1992) for the crest-stage partial-record station located downstream from Monument headquarters. I can only speculate as to why the figures do not agree. One possibility is that the stream was temporarily dammed during the flood in the Ceremonial Cave reach by coarse debris such as logs and branches, allowing the line of fine debris that I observed to be left stranded at a level higher than the running water, but I consider this possibility to be fairly unlikely. It is also possible that the Manning roughness coefficient for this stream should be larger for relatively low flows due to the large boulders that are in the channel. It has been noted that some streams have larger channel roughness factors at lower flood levels (Barnes 1967), but the difference is usually less than a factor of two, which would not be enough to explain the discrepancy here.

The flood scar evidence in Frijoles Canyon indicates that there have been at least four floods comparable to the 1978 flood in the last two centuries, and at least seven floods as large as the flood of 1977 during that time. There are many more flood-scarred trees in Frijoles Canyon that have not been sampled. It would be useful to sample more of these scarred trees in order to increase the robustness of the estimates on the occurrence of the earlier floods. In addition it would be very desirable to prospect and sample flood-scarred trees in other canyons in adjoining portions of New Mexico, in order to build up a more regional picture of the flood history in this area.

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The Effects of Fire on Nitrogen Cycling Processes Within Bandelier National Monument, NM

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Abstract.—Nitrogen is often the nutrient limiting production in conifer forests. Fire acts as a mineralizing agent, releasing nutrients in available forms. However, nitrogen is lost during fires, which can further deplete this limiting nutrient. Without fire, nitrogen becomes tied up in partially decomposed litter (needles and woody debris). The problems faced by managers of these forest systems are how and when to use fire from a nutrient perspective. A chronosequence of fire intervals in ponderosa pine forests (*Pinus ponderosa*) was studied to determine (1) if nitrogen cycling processes (mineralization and nitrification) decrease and (2) if concentrations of organics that inhibit these processes increase along the fire chronosequence. Patterns were not statistically significant, but fairly clear trends occurred. Nitrogen mineralization and nitrification patterns were higher in sites recently burned (within two years) and were lowest in sites without fire since the 1890's. The patterns at intermediate age sites varied, perhaps because of differential usage by elk and variable amounts of needle scorch which resulted in differential needle litterfall after fire. Within a site, concentrations of certain monoterpenes were consistently negatively correlated with rates of nitrification and mineralization. In these systems, fire promotes more rapid cycling of nitrogen, in part through combustion of monoterpene inhibitors.

INTRODUCTION

Within the nutrient cycling literature, there is considerable controversy about the role of fire in ecosystems. At the center of the controversy is the fact that fire causes a net loss of nitrogen while most other nutrients are released in available mineral forms (Raison 1979). Nitrogen loss occurs through volatilization and with particulates in smoke during combustion. Those on one side of the controversy argue that frequent fires would create severe nitrogen limitation within the ecosystem (Vitousek and Howarth 1991), leading to replacement of existing vegetation. However, in many ecosystems with high historical fire frequencies, net nitrogen mineralization and production actually declines in the absence of fire. This has led those on the other side of the controversy to believe that fire is necessary to keep nitrogen cycling

within the ecosystem and maintain productivity (White 1991a). Thus, the role of fire in ecosystems is not well understood from a nitrogen cycling perspective.

In general, soils of ponderosa pine ecosystems are fairly low in nutrients and have low rates of nitrogen mineralization (Vitousek et al. 1982). In a ponderosa pine (*Pinus ponderosa*) stand near Bear Springs in the southern part of the Jemez Mountains, two separate prescribed burns increased rates of nitrogen mineralization and nitrification in the residual forest floor and mineral soil horizons (White 1986a, White 1991a). The low pre-burn rates of nitrogen mineralization and nitrification were attributed in part to high concentrations of monot-

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erpenes (found in "turpentine") within needle litter and the forest floor (White 1991a, 1991b). Monoterpenes are highly flammable and are mostly consumed during fires (White 1991a). These results suggest that frequent, low-intensity fires consume flammable monoterpenes, which in the absence of fire act to inhibit nitrogen mineralization and nitrification. Higher rates of nitrogen cycling are promoted by fire, but nitrogen losses during frequent, low-intensity fires must be replenished to be long-term sustainable. One way to replenish losses is to increase nitrogen fixation rates (see Loftin and White, This Volume). However, studies of changes in nitrogen fixation after fires have not identified increases substantial enough to offset losses from frequent fire, so the controversy continues (Vitousek and Howarth 1991).

The purpose of this article is to investigate the relationship between time since last fire, rates of nitrogen cycling, and the amount of monoterpenes in the forest floor and mineral soils of ponderosa pine. Nitrogen cycling characteristics and monoterpene content of soils were determined for sites within Bandelier National Monument with known durations since the last fire. The theoretical approach and earlier experimental results that form the foundation for this research and terminology used in ecosystem nutrient cycling will be presented first.

The Nitrogen Cycle

The supply of nitrogen often limits production in terrestrial ecosystems (Vitousek and Howarth 1991). Inputs of nitrogen to terrestrial ecosystems are from precipitation, air-borne particles trapped by the vegetation and soil (dry deposition and impaction), and through gaseous fixation (N-fixation; Figure 1). N-fixation occurs through free-living organisms (i.e., cyanobacteria and lichens) and symbiotically with plants and their root-associated microorganisms. On an annual basis, inputs of nitrogen are thought to be small relative to the amount obtained from the soil.

To a large extent, the supply of nitrogen for plant growth in terrestrial ecosystems is determined by the rate at which organic-bound soil nitrogen is released in inorganic form—a process termed nitrogen mineralization (Fig. 1). The first inorganic form of nitrogen is ammonia (NH_3), which readily converts to ammonium (NH_4^+) in the soil solution. Ammonium (or ammonia) can be converted to nitrate (NO_3^-) through the two-step process of nitrifi-

cation. Through the nitrification process, a portion of the ammonium-nitrogen can be lost to the atmosphere as nitrous oxide. Both ammonium and nitrate are assimilated by the soil microbial community and by higher plants. If demand for inorganic nitrogen by the microbial community is high, then concentrations of inorganic nitrogen within the soil may decline, which is termed 'immobilization.' Only when the demand by the microbial population is satisfied can concentrations of inorganic nitrogen increase within the soil, representing net mineralization.

Unlike ammonium, nitrate is negatively charged (an anion) and is mobile within the soil, which can lead to loss of nitrate from the terrestrial system to streams or ground water. Nitrate can be utilized by other microorganisms as a terminal electron acceptor, which results in the production of nitrous oxide or di-nitrogen (N_2) gas, through the process of denitrification. Di-nitrogen gas can return to the atmosphere, completing the cycle. Nitrous oxide also can escape to the atmosphere, where it can undergo reactions with other chemicals.

Both nitrate and ammonium are assimilated into plant and microbial biomass through growth.

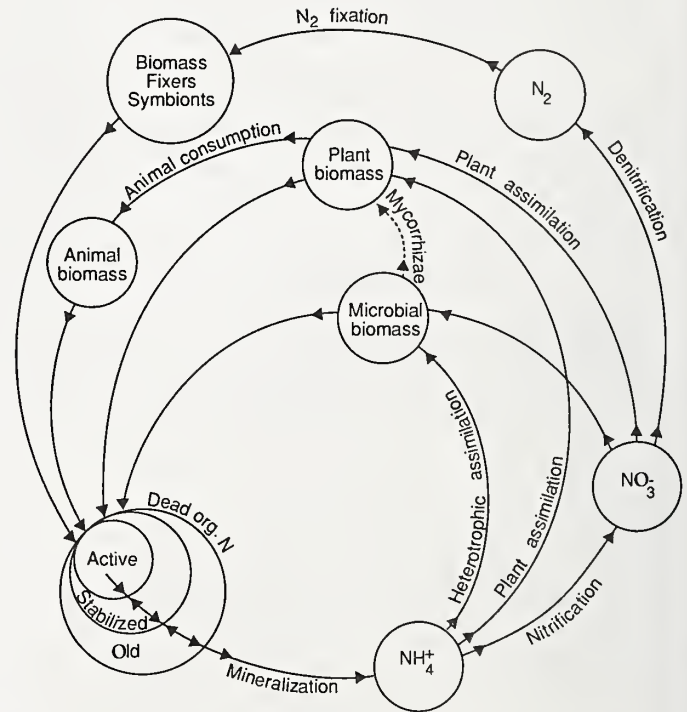


Figure 1.—The universal nitrogen cycle indicating pools (circles) and processes (arrows). Inputs (wet and dry deposition) and losses (leaching, erosion) are not indicated. The soil nitrogen pool (Dead org. N) is divided into three conceptual compartments (from Jansson 1981).

Plants and microorganisms can move nitrate towards themselves through diffusion, but they must grow or move to sources of ammonium which is more tightly bound to soil particles. Nitrogen assimilated by a portion of the microbial community contributes to plant growth through mycorrhizal associations (Figure 1). A portion of the microbial and plant biomass is consumed by animals. Eventually, microorganisms, higher plants, animals and their associated wastes become part of the soil organic matter pool, a portion of which rapidly decomposes and undergoes the process of mineralization to continue the cycle. In general, monoterpenes alter rates of nitrogen cycling by slowing both the mineralization and nitrification processes (see White 1994 for a detailed review of the role of monoterpenes throughout the nitrogen cycle).

Patterns Of Nitrogen Cycling Processes Within Forest Ecosystems

Factors that regulate rates of nitrogen mineralization and nitrification for 17 forests located throughout the United States were studied by Vitousek et al. (1979, 1982). Although their main interest was to determine the potential for loss of nitrate from forest ecosystems following disturbance from clearcutting, their studies made two valuable contributions. First, they described nitrogen mineralization and nitrification patterns for sites that show a wide range in net productivity. Second, they demonstrated that patterns measured in laboratory studies mimicked those patterns displayed in field studies.

Vitousek et al. (1982) predicted that certain changes in soil inorganic nitrogen concentrations would occur in the absence of plant uptake (Figure 2; redrawn from Vitousek et al. 1982). In laboratory incubations which eliminate plant uptake (termed mineralization "potentials" because temperature and moisture are kept near optimum), these patterns are reflected in the changes in concentrations of inorganic nitrogen. After short incubation times, inorganic nitrogen levels may decline, which represents net immobilization. This period prior to net production of ammonium is termed the 'lag phase.' Once net production of ammonium occurs (termed 'net mineralization'), the mineralized ammonium may be converted to nitrate (termed 'nitrification'), which may cause a concurrent decrease in ammonium. There may be a lag in nitrification, which allows ammonium to accumulate (as shown in Figure 2), or nitrification may occur so rapidly that no increase in ammonium is apparent with only an

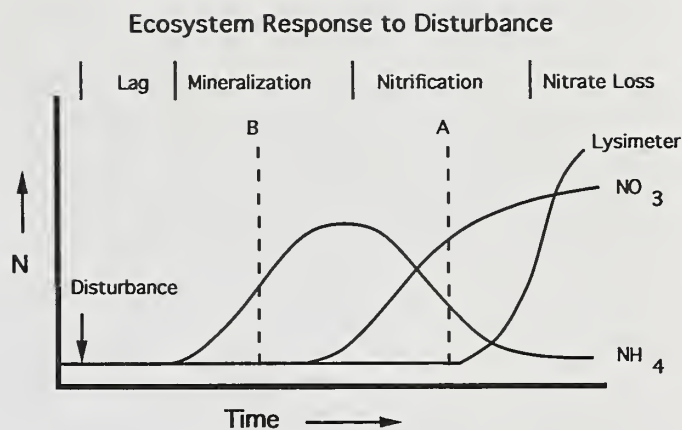


Figure 2.—Responses of soil ammonium, soil nitrate, and lysimeter nitrate concentrations to disturbance in a hypothetical ecosystem. The lines represent changes in a disturbed system relative to a control or to the levels prior to treatment. The phases of the response are given above that portion of the graph. Refer to the text for the meaning of lines A and B. (Redrawn from Vitousek et al. 1979, with permission)

increase in nitrate. In the field, nitrate may be transported to lower soil horizons, which can be detected in lysimeters (mechanisms for sampling soil water), or to surface streams if sufficient moisture is available.

Time for the entire response sequence (lag, mineralization, nitrification) to occur varies between sites within forest ecosystems and between different ecosystems. The range in patterns of responses for both nitrate and ammonium concentrations during incubation is shown in Figure 3. Very slow responses (C in Figure 3) included only the lag phase with a slight rise in ammonium at the end of the measurement period. A slow response includes only the portion of the predicted pattern from the disturbance to line "B" in Figure 2. Intermediate responses (B in Figure 3) had a short lag, followed by an increase in mineralization, and finally an increase in nitrification. An intermediate response corresponds to the portion of the predicted pattern from the disturbance up to line "A" in Figure 2. Very rapid responses (A in Figure 3) demonstrated an immediate increase in nitrate, corresponding to the portion of the predicted pattern beginning at line "A" in Figure 2, with the entire preceding pattern of lag and net mineralization condensed into such a short time period that it does not get measured (within the first sampling period).

The three Indiana forests studied by Vitousek et al. (1982) show responses that are typical of sites with rapid, intermediate, and slow responses (Fig-

ure 4). The Indiana Maple site is a rapid response, corresponding to A of Figure 3, with an immediate increase in nitrate and a gradual decline in ammonium. The Indiana Oak site is an intermediate response, corresponding to B in Figure 3, with an increase in ammonium followed by an increase in nitrate after a short lag. The Indiana Pine site is a slow response, corresponding to C in Figure 3,

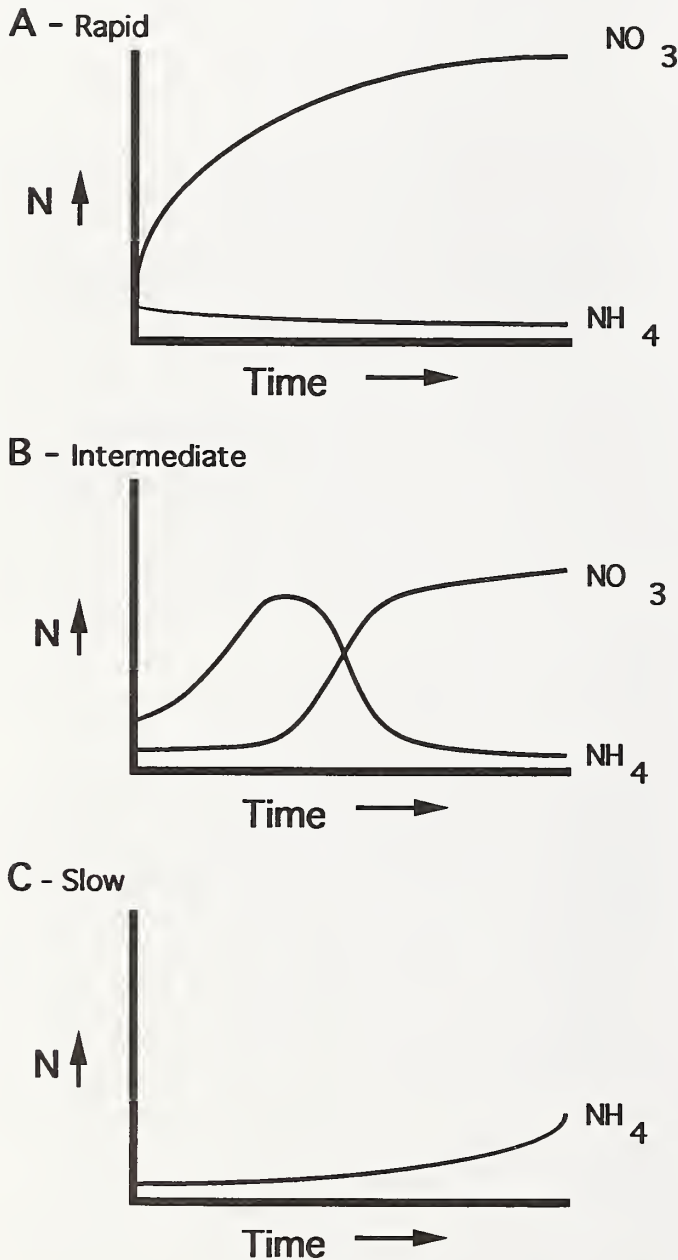


Figure 3.—Potential patterns for ammonium and nitrate concentrations in a soil following disturbance or during laboratory incubations for determination of mineralization and nitrification potentials. Patterns range from rapid (A), through intermediate (B), to slow (C).

with a protracted lag phase and a slight rise in ammonium at the end of the experiment.

Vitousek et al. (1979, 1982) also studied ponderosa pine, mixed conifer, aspen, and spruce-fir sites located in the Tesuque Watersheds, New Mexico. That ponderosa pine stand showed a slow response in laboratory mineralization potential experiments (Figure 5), similar to the Indiana Pine site (Figure 4). Nitrogen mineralization potentials

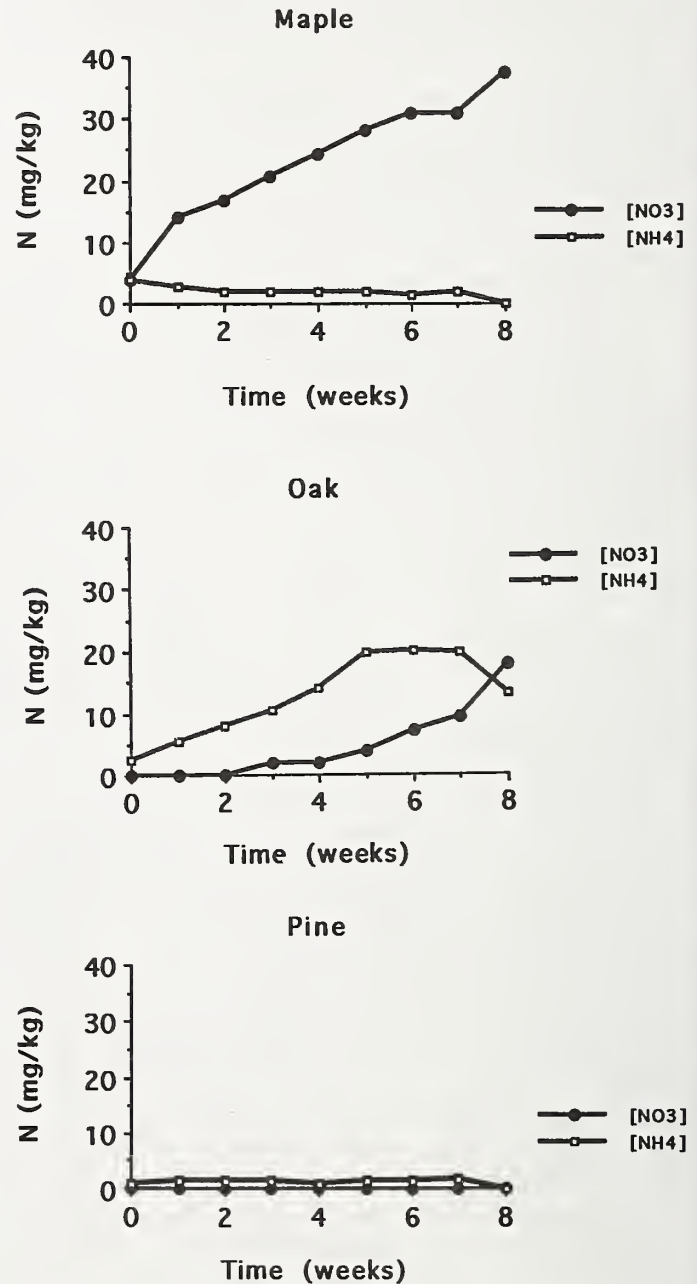


Figure 4.—Changes in inorganic nitrogen during laboratory incubation of mineral soil samples from the Indiana Maple, Oak, and Pine forests reported in Vitousek et al. (1982, redrawn with permission).

of soils from a ponderosa pine stand in the Jemez Mountains also showed either net immobilization

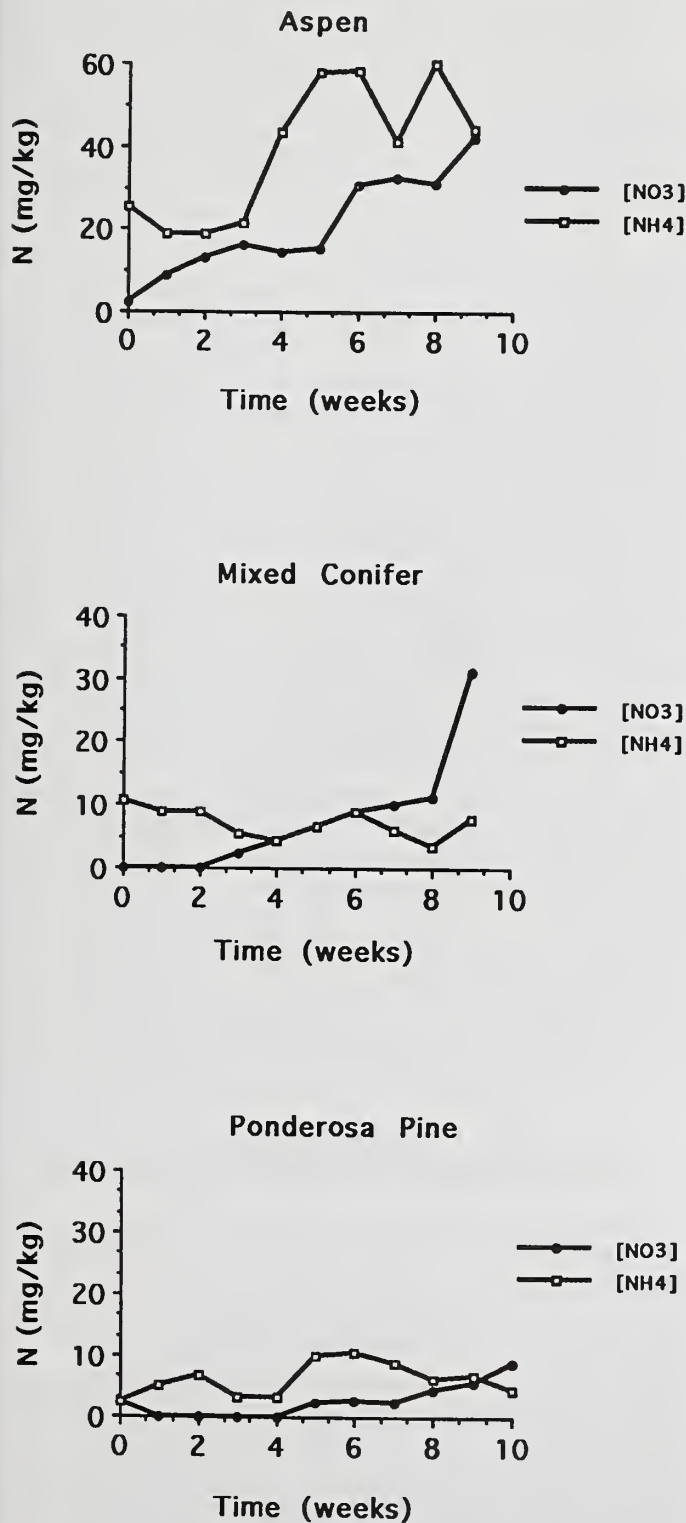


Figure 5.—Changes in inorganic nitrogen during laboratory incubation of mineral soil samples from the New Mexico Aspen, Mixed Conifer, and Ponderosa Pine forests reported in Vitousek et al. (1982, redrawn with permission).

or low mineralization (pre-burn in Figure 6), typical of sites with slow responses (White 1986a).

For most sites studied by Vitousek et al. (1979, 1982), the rate of response was correlated to "site quality" (estimated potential productivity of the site), with lower quality sites having the slowest responses and highest quality sites with rapid responses; the Indiana Maple site was the highest quality site, oak intermediate, and pine the lowest quality site. Based upon these patterns, the ponderosa pine site is a low quality site. Conversely, if ponderosa pine displayed mineralization patterns like that of Indiana Maple, one could conclude that ponderosa pine occurs on high quality sites. The studies of Vitousek et al. (1979, 1982) tend to leave the impression that these patterns are inherent characteristics of each system that are unlikely to change. However, these patterns are known to change seasonally, annually (Gosz and White 1986), and following prescribed fire (White 1986a). To truly manage forests for long-term health and sustainability, managers need to understand the dynamics in patterns of these processes and the effects that various management practices have on nutrient cycling patterns.

Factors Controlling Nitrogen Mineralization and Nitrification

White and Gosz (1987) investigated the factors controlling nitrogen mineralization and nitrification in the New Mexico forest sites reported in Vitousek et al. (1979, 1982). They added potentially limiting nutrients (nitrogen, phosphorus, and/or micronutrients) to forest floor and mineral soil from the ponderosa pine site of Vitousek et al. (1982) in attempts to alter the mineralization patterns in laboratory incubations. A positive response to nutrient additions would shorten the lag in min-

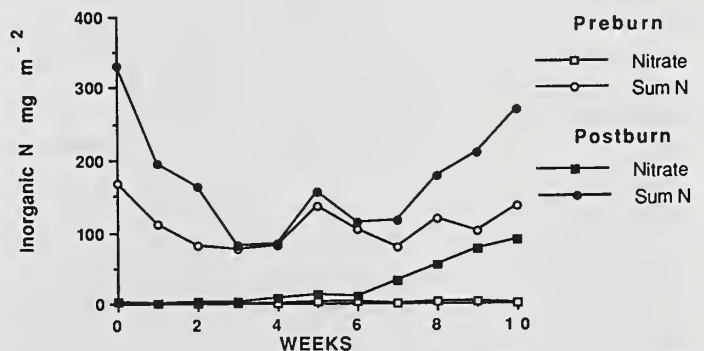


Figure 6.—Changes in inorganic nitrogen during laboratory incubation of mineral soil samples from control (pre-burn) and burned plots within a ponderosa pine site located near Bear Springs (from White 1986a).

eralization or nitrification and increase production of inorganic N. They found the mineralization pattern to be very resistant to change. White and Gosz (1987) concluded that nitrogen mineralization in the New Mexico Ponderosa Pine site was limited by (1) organic quality factors (which includes inhibition by an organic inhibitor) or by (2) the availability of a combination of limiting nutrients (including combinations of N, P, and/or micronutrients).

Given the low rates of net mineralization and nitrification and the resistance to amendments designed to increase these rates in laboratory studies (White and Gosz 1987), high concentrations of ammonium and nitrate in the field were not expected in a ponderosa pine site. However, high concentrations of ammonium and nitrate were reported in a single field collection from both trenched and control plots in the New Mexico Ponderosa Pine site of Vitousek et al. (reported in Gosz and White 1986). In September of 1977, concentrations of ammonium and nitrate in the forest floor (organic soil horizons) of both trenched and control plots were approximately 20 and 0 mg N/kg, respectively. Both ammonium and nitrate concentrations increased to approximately 80 mg N/kg soil (a total of about 160 mg N/kg soil) in the October 1977 collection, but returned to the September 1977 levels by the next collection (February 1978).

The obvious question is how did such dramatic and rapid changes in soil inorganic nitrogen occur? Between the collection with low inorganic nitrogen concentrations (Sept. 1977) and the next collection with high concentrations of ammonium and nitrate (Oct. 1977), exceptionally hot, dry conditions forced complete closure of the forest to the public because of extreme fire danger. The high ammonium and nitrate concentrations (indicating rapid mineralization and nitrification) were measured in forest floor collections taken after rains had moistened the forest floor and reduced the fire danger. This suggested that the hot, dry conditions altered some critical controlling factor, which allowed rapid mineralization and nitrification to occur in the forest floor. Higher than normal precipitation and an early freeze after the Oct. 1977 collection prevented further collection at the New Mexico Ponderosa Pine site until later that winter. Low concentrations of ammonium and nitrate in Feb. 1978 indicate limited mineralization and nitrification. Since needle-cast (senescence of older needles) occurred during the interim period, it is likely that the controlling factor was contributed in litterfall and/or throughfall. If the controlling factor was an organic inhibitor, the inhibitor had to (a)

be denatured and/or removed (perhaps volatilized) during heating and drying of the forest litter, (b) contributed through litterfall and/or throughfall, and (c) persist within frozen soils.

I collected all samples of forest floor and soils from that ponderosa pine site. Before closure during the September 1977 collection, the "turpentine" aroma of a pine forest was very strong. I remember this clearly because I have an allergy to turpentine in "oil-based" paints, and I suffered from allergic symptoms during that collection. While collecting precipitation samples the following month when rain lessened the fire danger, I noted the lack of "turpentine" aroma and had no allergic symptoms. It was as if the turpentines were "volatilized" from the needles on the forest floor during the hot, dry conditions. Turpentine is a mixture of various monoterpenes, which are highly volatile, with smaller amounts of sesquiterpenes, which are less volatile. Since monoterpenes have physical characteristics that are consistent with those of a potential organic inhibitor (highly volatile, in relatively high concentration in litterfall and throughfall, and freezing is a means of preserving monoterpenes in living tissues), this observation suggested the potential role of monoterpenes in the processes of nitrogen mineralization and nitrification. Since those first observations, considerable progress has been made investigating the role of monoterpenes in nitrogen cycling processes (White 1986a, 1986b, 1988, 1991a, 1991b), which is reviewed in White (1994). In ponderosa pine forest systems, monoterpenes act to limit the rate of nitrogen mineralization (production of ammonium) and nearly halt the rate of nitrification, which results in very low rates of inorganic nitrogen cycling in these systems.

Fire and Monoterpenes: Their Role as Flammable Compounds

Mutch (1970) hypothesized that fire-adapted tree species produced compounds that enhanced the probability of fire at more frequent intervals. His hypothesis was based upon comparisons of the amount of extractable plant material in species with differing fire frequencies. Ponderosa pine had the highest amount of extractable compounds and had a high fire frequency (or short fire interval). Since 1970, improvements in analytical techniques and the availability of instruments (principally in gas chromatographs and associated techniques) have led to the understanding that monoterpenes are a major portion of the extractable plant material referred to by Mutch.

Monoterpenes are highly flammable compounds and can reach parts-per-thousands concentration in ponderosa pine litter, and conifer litter in general. Monoterpenes are de-gassed early in the combustion process, and heat from their combustion provides the energy for direct pyrolysis of the solids to occur (Chandler et al. 1983). Thus, higher monoterpene concentrations would increase the probability of ignition and increase the ability to carry a fire, which could lead to shorter fire intervals in these systems.

The apparent sequence of events that link monoterpenes, soil nitrogen cycling processes and fire are as follows: low monoterpene concentrations and high rates of mineralization and nitrification in soil and the litter that remains after a fire, followed by a buildup of monoterpenes and a decline in mineralization and nitrification rates, which inevitably leads to a high fire potential because of the buildup of these flammable monoterpenes. A question left unanswered is: how much time is needed between fires before mineralization and nitrification processes are inhibited and the higher probability of fire? By sampling soils and litters from sites with increasing time since fire, aspects of this question may be addressed. Sites within Bandelier National Monument were of particular interest because documentation existed on fire history and the dominant soils in the Monument are derived from the same parent material as the soils near Bear Springs sampled in earlier studies by White (1986a, 1991a).

Hypotheses.—The specific hypotheses to be tested by this research were:

1. Monoterpenes in the soil organic horizons will increase along a fire chronosequence.
2. Soil mineralization and/or nitrification will decrease along the same fire chronosequence.

METHODS

Site Selection

A total of 6 sites were sampled (Figure 7), including: (1) a site south of Lummis Canyon (Lummis), which was sampled before and four times following a prescribed burn; (2) a site east of Corral Hill (Corral Hill); (3) a site near the back gate (Back Gate); (4) a site on Escobas Mesa (Foxy) near sites established by Teralene Foxy (Foxy 1984); and two sites outside of the area burned by the La Mesa Fire, (5) a cluster of three plots below highway NM

4 in salamander habitat (Salamander) and (6) a site on Sawyer Mesa (Sawyer Mesa). The elevations and interval since the last fire at all sites are listed in Table 1. All sites occur on Bandelier tuff parent material, which is the same parent material at the Bear Springs site reported by White (1986a, 1986b, 1991a), except for the Salamander site which is on Tschicoma Formation (Smith et al. 1970). Sites varied in other respects, ranging from lower elevation stands of ponderosa pine interdigitating with piñon and juniper woodlands (Lummis and Corral Hill sites), to a mid-elevation ponderosa pine stand with nearly closed canopy conditions (Back Gate), with the Foxy site approximately intermediate in elevation and ponderosa pine overstory density. The Salamander and Sawyer Mesa sites are in upper ponderosa pine/lower mixed conifer habitat with ponderosa pine, limber pine (*Pinus flexilis*), Douglas-fir (*Pseudotsuga menziesii*), and white fir (*Abies concolor*), with Rocky Mountain maple (*Acer glabrum*) and aspen (*Populus tremuloides*) the major deciduous species. The Salamander site, which is scheduled for treatment with prescribed fire in fall 1995 (C. Allen, personal communication), is more mesic than the Sawyer Mesa site, which is on an exposed ridge. A variable that may have particular influence on nitrogen cycling processes at some or all of these sites is use by elk and deer. Nearly the entire area is used by elk and deer, but use of the more remote sites by elk (Lummis and Foxy sites in particular, and to a lesser degree Corral Hill) appeared greater than at the Back Gate site. Areas with obvious elk disturbance (i.e., droppings) were not sampled, but the potential for unrecognized impacts from elk at time of sampling to altered patterns of nitrogen mineralization/nitrification was high (e.g. through urination).

Table 1.—Names for sites sampled in this study, elevations, and time since last fire.

Site #	Site Name	Elevation (m)	Time since last fire
1	Lummis	2000	
	Pre-burn		15 years
	Post-Burn		1 day
	5 month		5 months
	12 month		12 months
	17 month	17 months	
2	Corral Hill	2000	1.5 years
3	Foxy	2245	15 years
4	Back Gate	2325	7 years
5	Salamander	2720	94 years*
6	Sawyer Mesa	2670	99 years*

* Based on fire scars collected at nearby sites. (Allen 1989)

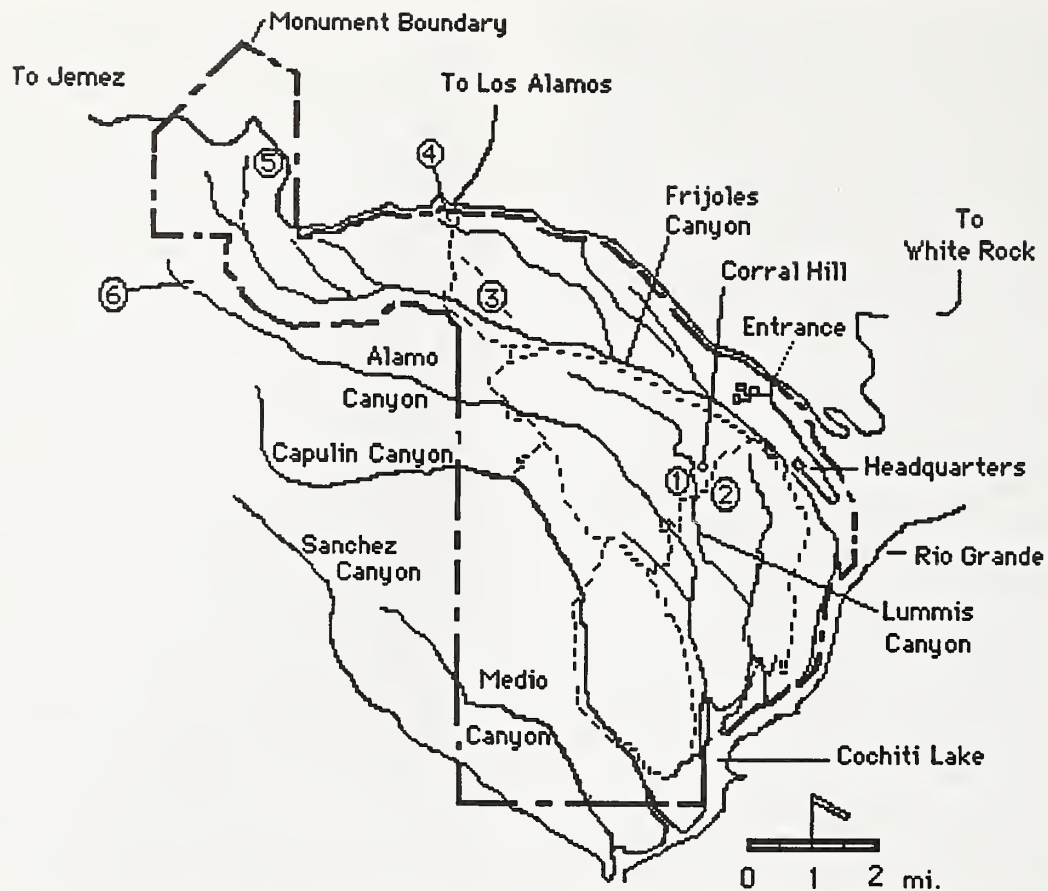


Figure 7.—Map of Bandelier National Monument indicating approximate location of sites collected in this study: 1 = Lummis; 2 = Corral Hill; 3 = Foxx Site; 4 = Back Gate; 5 = Salamander habitat; and 6 = Sawyer Mesa. Major trails within the Monument are indicated by dashed lines.

Sample Collection

The Back Gate was sampled on 15 May 1992, as was the Lummis site (1 day post-burn) following the prescribed fire on 14 May 1992. Corral Hill, Lummis pre-burn, Foxx, and Sawyer Mesa sites were sampled on 6 May 1992. These samples (collected in May 1992) were analyzed for monoterpene content of the organic horizon and nitrogen mineralization potentials for the mineral soils. Mineral soil was resampled on 2 October 1992, 28 May 1993, and 12 October 1993) at the Lummis site and analyzed for nitrogen mineralization and nitrification potentials only. Samples were taken from 4 points within each site. Effort was made to take samples from microsites representative of the range observed rather than the average at each site. Separate samples of the organic horizon and 0- to 10-cm depth mineral soil horizon were collected at each point. The organic horizons were sampled by harvesting all organic horizons beneath a 200 cm² template (White 1991a). The organic horizon was

separated into an L (fresh litter) and a F-H (fermentation and humus) horizon for the Foxx site and the pre-burn collection at Lummis (data later summed to get organic horizon totals). The entire organic horizon was collected at all other sites. Mineral soil was collected with a 7.8-cm diameter tube driven to a depth of 10 cm.

At the Sawyer site, samples were taken from areas where the overstory was dominated by (1) limber pine, (2) Douglas-fir, (3) aspen, and (4) ponderosa pine, although litter of other species were also present in the samples. Also, samples of freshly fallen needles of ponderosa pine, limber pine, and Douglas fir were collected for monoterpene analyses (2 samples for each species). A sample of scorched ponderosa pine needles from a prescribed burn were collected on top of the mesa along the trail to Corral Hill for monoterpene analyses. Samples of freshly fallen needles were collected within 1 m of the soil samples at Corral Hill and analyzed for monoterpenes.

The sampling design at the Salamander site differed from that at other sites. Samples were taken adjacent to three previously established arthropod pitfall transects, each 50 m long, on 9 September 1993. Two of the transects are adjacent to each other below NM 4, the other transect is also below NM 4 about one kilometer away. A total of six samples were taken from each of the transects (18 total samples). The entire forest floor was harvested from beneath a 200 cm² template (White 1991a). The dry mass of each forest floor sample was measured to determine pre-burn organic matter content; monoterpenes were not analyzed on these samples. The underlying soil was collected in a 7.8-cm diameter tube driven to a depth of 10 cm and analyzed for nitrogen mineralization potentials.

Analytical Methods

Methods detailed in White (1991a) were used to analyze all samples. The May 1992 samples of organic horizons and needles were analyzed for monoterpene content by gas-liquid chromatography following extraction in ether. All mineral soil samples were analyzed for nitrogen mineralization/nitrification potentials by aerobic incubation and subsequent extraction with KCl. The KCl extracts were analyzed for ammonium and nitrate with a Technicon AutoAnalyzer.

Statistical Analyses

All statistical analyses were performed with StatView SE© (BrainPower, Inc.). Correlation coefficients were generated by correlating nitrification rates with forest floor monoterpene concentrations. These coefficients were then analyzed by chi-square method to determine if randomly distributed.

RESULTS

Mineralization Patterns

The mineralization pattern for the Lummis pre-burn samples showed a fairly rapid rise in nitrification (Figure 8), even though the site had not burned since the La Mesa Fire (15 years). The relatively rapid rise in nitrate is characteristic of higher quality sites and is not characteristic of sites with heavy fuel loads. One day after the prescribed burn, the shape of the nitrification pattern was not significantly changed (Figure 8), but the amount of ammonium was substantially increased. Five

months after the fire, both the rate of nitrate production (indicated by a steeper rise in nitrate) and initial ammonium levels were greater than pre-burn samples (Figure 8). The most rapid rate of nitrate production occurred in the 1 year post-burn collection (Figure 8), although total concentrations were lower than 1-day and 5 month post-burn collections. The 17-month collection started to show slight immobilization and a lag period before rapid mineralization and nitrification occurred (Figure 8).

Mineralization pattern at the Corral Hill site (1.5 years after a prescribed burn) also showed high rates of nitrification (Figure 9), very similar to the pattern at the Lummis site 12 month post-burn. This pattern is characteristic of high quality sites, similar to the pattern shown by the Indiana Maple site (Figure 4).

The Back Gate site (7 years since last burn) had relatively low rates of ammonium production and very low rates of nitrification (Figure 9), similar to the ponderosa pine reported in Vitousek et al. (1979, 1982). These patterns are typical of slow mineralization responses of low quality sites (Figures 3 and 4).

The Foxx site (15 years since last burn, La Mesa Fire) had a mineralization pattern more like an intermediate response with an initial lag before significant nitrate production occurred (Figure 9), much like the Indiana Oak site (Figure 4).

The mineralization pattern at the Sawyer site (Figure 9) reflected the influence of the single sample beneath the aspens, which showed a pattern very similar to the aspen site in the Tesuque Watersheds. The three samples taken beneath the conifers showed lags in mineralization with little or no nitrification, similar to Back Gate or the Salamander sites (Figure 9). Thus, the rise in nitrate (and ammonium) for the site as a whole is due to the higher production in the single aspen sample.

Mineralization patterns at the Salamander site (94 years since last fire) are the lowest of all sites (mean of all sites shown in Figure 9). Fourteen of the 18 sites showed net immobilization throughout the incubation period and only slight nitrification, with net mineralization and net nitrate production only in four samples. These patterns are characteristic of very poor quality sites, even though this is the most mesic site sampled in this study.

Monoterpene Concentrations

The amount of variation encountered in the monoterpene concentrations of the forest floor

samples was high, both within and between sites (as shown by large standard error bars). There was

a general trend with increasing forest floor mass and fire interval (Figure 10); however, that trend is

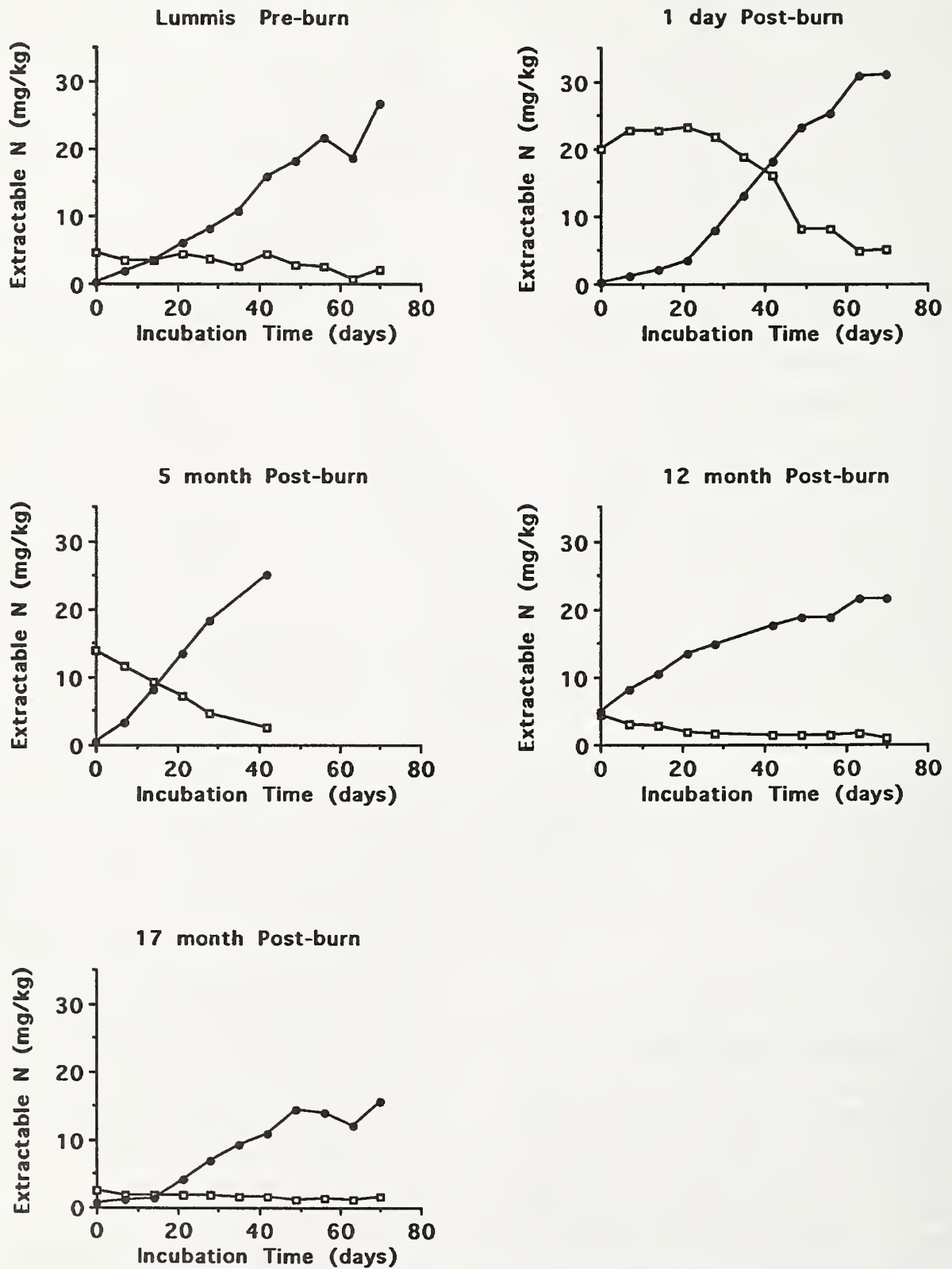


Figure 8.—Changes in inorganic nitrogen (ammonium open squares, nitrate closed circles) during laboratory incubation of mineral soil samples from the Lummis site before and with time after a prescribed burn (burned 14 May 1992).

largely a function of the first and last sites in the chronology. Similarly, the general trend in increasing monoterpene concentrations was due to the first and last sites in the chronology. If the first and last sites of the chronology are excluded, no real

pattern appeared for the intermediate sites for all monoterpenes and their sum (Figure 10). Also, there was not statistically significant relationship between mineralization or nitrification potentials and total monoterpenes when all samples from all

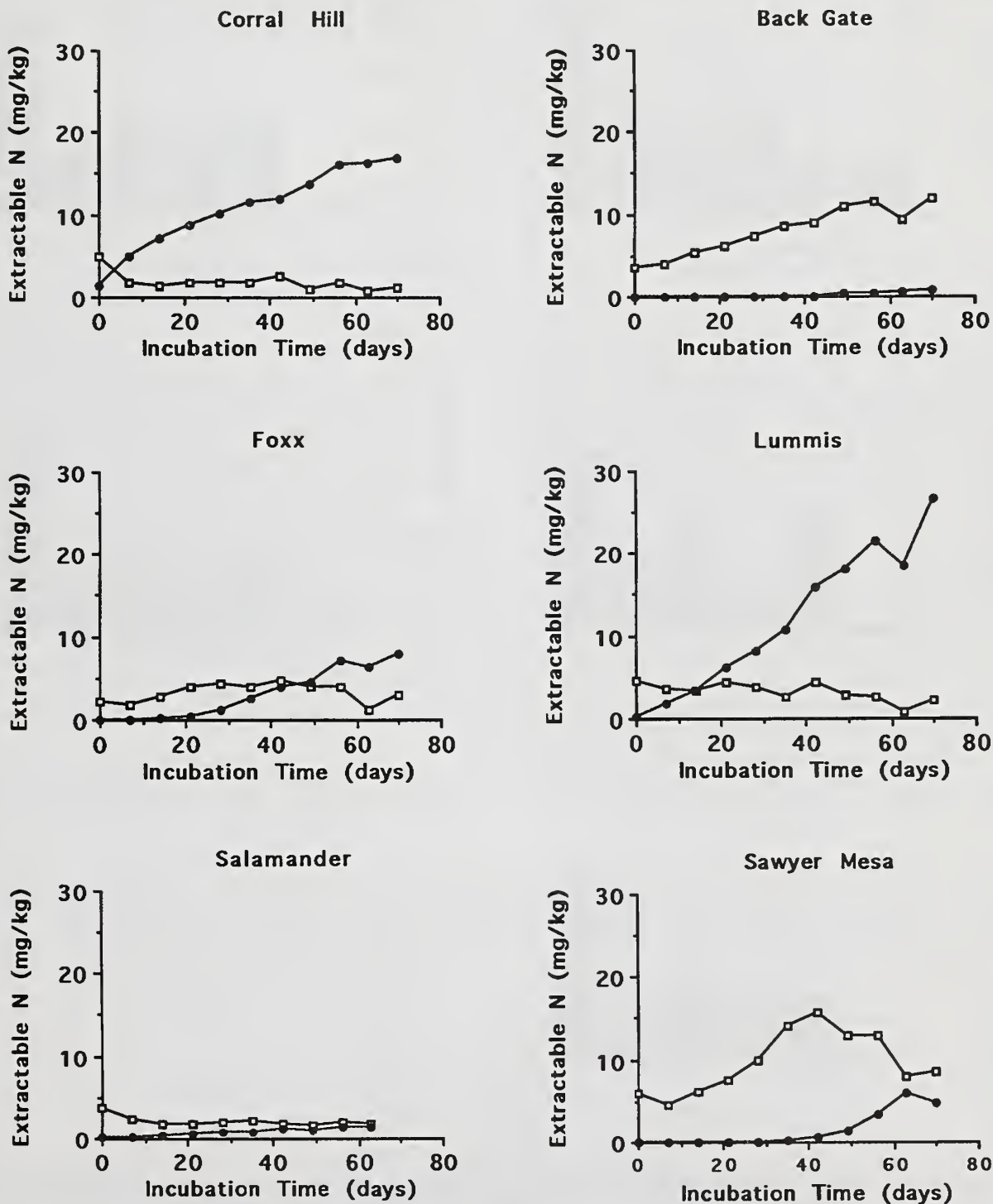


Figure 9.—Changes in inorganic nitrogen (ammonium open squares, nitrate closed circles) during laboratory incubation of mineral soil samples from the sites in and near Bandelier National Monument, NM. Sites are arranged from top left to right bottom with respect to increasing length of fire interval (see Table 1).

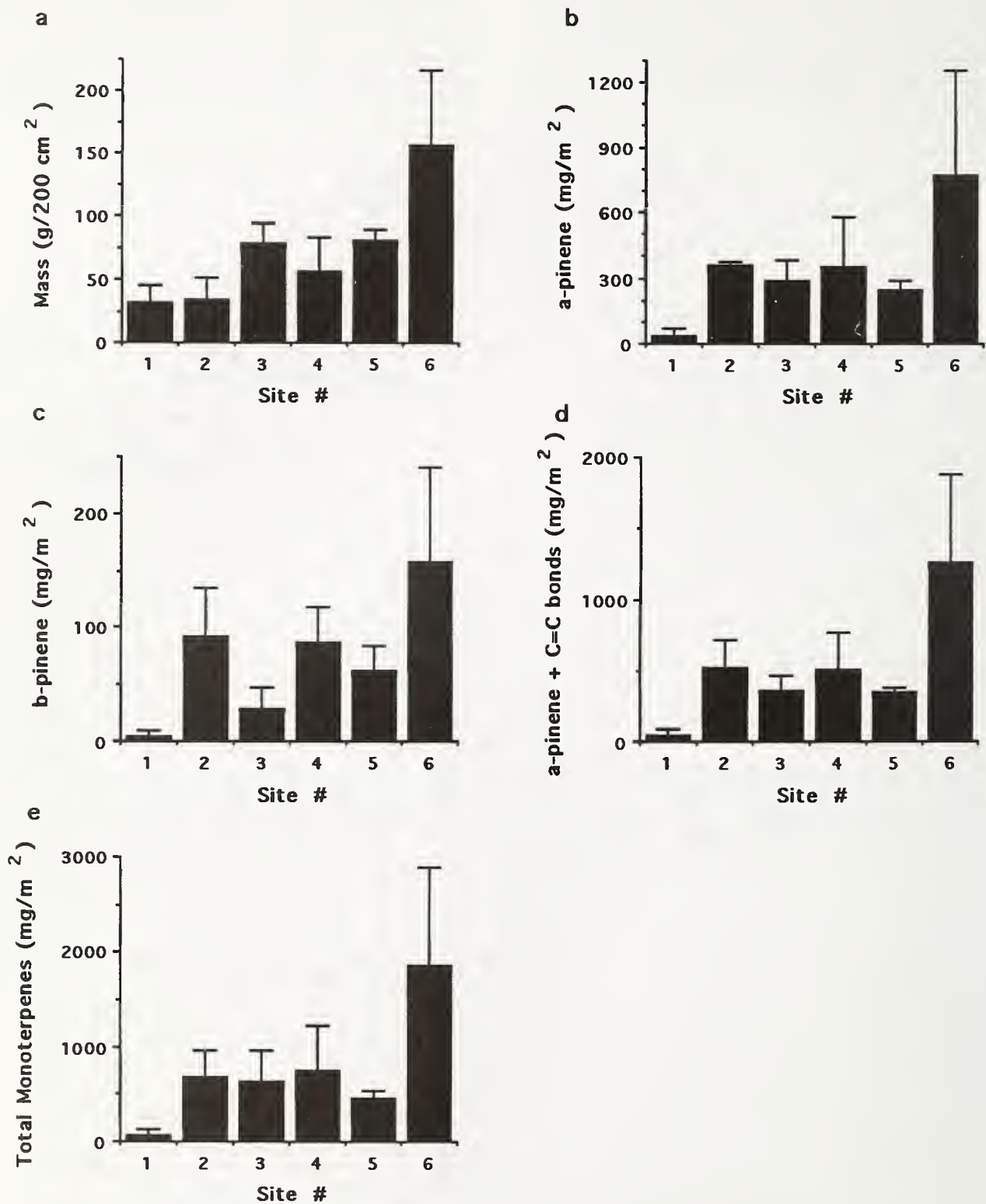


Figure 10.—The amount of forest floor mass (a), a-pinene (b), b-pinene (c), the sum of a-pinene and monoterpenes with carbon-carbon double bonds (d), and sum of all monoterpenes (e) present at each site (mean of four samples with standard errors). Sites are arranged with increasing time since fire from left to right. Sites with years since fire in parentheses are: 1= Lummis 1 day Post-Burn (0); 2= Corral Hill (1.5); 3= Back Gate (7); 4 = Lummis Pre-Burn (15); 5= Foxx (15); and 6= Sawyer Mesa (99).

sites are included in this analysis. However, there was a consistent and strong negative relationship between monoterpenes and nitrification potentials *within* individual sites, as shown by the negative correlation coefficients (Table 2). Using a Chi-square test, the probability of obtaining consistently negative correlations between two random and unrelated variables is less than 1 in 10,000 ($P < 0.0001$).

DISCUSSION

White (1991b) proposed a conceptual model for the effects of increasing monoterpene concentrations on the inorganic nitrogen content of a soil. The model also may mimic the effects of fire on soil inorganic nitrogen because natural dynamics of monoterpenes in soils should follow the fire cycle. After fire, monoterpenes are in low concentration and net mineralization and nitrification are high (White 1991a). With time since fire, monoterpenes increase, lowering net mineralization (by increasing immobilization) and inhibiting nitrification by inhibiting the enzyme initially involved in the conversion of ammonium to nitrate (ammonium mono-oxygenase). Eventually, monoterpenes accumulate to the point that nitrogen cycling processes are greatly reduced, while their elevated concentrations concurrently increase the probability of another fire. The occurrence of low net nitrogen mineralization and net nitrification rates might indicate when a fire could be beneficial from a nutrient cycling perspective, regardless of the apparent fuel loads.

The results presented here only partially support this conceptual model. Mineralization and nitrifica-

tion rates were among the highest at sites with recent burns (post-burn Lummis and Corral Hill, Figure 9), whereas sites with the longest fire intervals (Sawyer and Salamander site, Figure 9) have the lowest rates of mineralization and nitrification (when aspen is excluded from the Sawyer site), which supports the model. However, the two sites with 15 year fire intervals (Foxy and Lummis pre-burn, Figure 9) had intermediate, but relatively high rates of nitrification, particularly the Lummis site. Explanations for deviation from the predicted model may include differences in microclimate that result in greater loss of monoterpenes from these sites and/or the use of these areas by elk. The Foxy and Lummis sites are fairly remote and are used rather heavily by elk during the winter months. Usage by elk would increase the nitrogen inputs to these forest stands through urine and feces. In laboratory experiments, forest floor samples from a spruce-fir forest in the Tesuque Watersheds only produced nitrate following the addition of urea (White and Gosz 1987). Fairly long-term inputs of nitrogen from elk may partially eliminate the normal condition of nitrogen limitation within ponderosa pine ecosystems and allow higher rates of mineralization and nitrification.

The Back Gate site, which was last burned 7 years before sampling, showed steadily increasing net mineralization but almost no nitrification (Figure 9). This site only gets migratory usage by elk and deer because of its proximity to the highway and a campground, so the influence of elk and deer on the mineralization and nitrification pattern is expected to be relatively slight. Based on fire scars on trees in that area, the historic mean fire interval for that ponderosa pine stand was approximately 7 years (estimated at 7.3 average; Allen 1989). Thus,

Table 2. Correlation coefficients for comparison of relative nitrification rate and listed factors (Factors) at the indicated sites (n=4). Correlation coefficients can range between 1 and -1. The probability of the frequency of inverse correlation obtained by completely unrelated factors is $P < 0.0001$ for all sites. Sum All Sites is the summation of all correlation coefficients for all sites; highly negative numbers would indicate the strongest negative relationship across all sites.

Factor	Lummis Pre-Burn	Corral Hill	Foxy	Back Gate	Sawyer Mesa	Sum All Sites
Total Mass	-.256	-.252	.279	-.748	.933	-0.044
Camphene	-.501	-.583	-.052	-.347	-.102	-1.585
a-Pinene	-.917	-.589	-.827	-.497	-.752	-3.582
b-Pinene	.352	-.634	-.115	-.491	.654	-0.234
Myrcene	-.291	-.011	.056	-.643	-.449	-1.338
d-3-Carene	-.913	-.306	-.887	-.329	-.457	-2.892
Limonene	-.724	.012	.181	-.297	-.627	-1.455
Unknown #31	-.428	-.907	-.987	-.470	-.735	-3.527
Total	-.890	-.562	-.994	-.441	-.721	-3.426
a-Pinene + C=C bonds	-.841	-.643	-1.00	-.604	-.608	-3.696

the pattern of little or no nitrification may occur at or near the time of historic fires. Perhaps the lack of nitrification can be used as a cue for when fires could be used for management of areas without known fire histories.

Response to Prescribed Fire

In previous studies, both the forest floor and mineral soil showed an increase in response pattern following prescribed fire (White 1986a, 1991b), although the response was faster and greater in the forest floor. In the present study, it was uncertain if the fire would consume the entire forest floor, leaving nothing for post-burn samples. Thus, only the mineral soil was analyzed in this study.

Regrettably, the area scheduled for prescribed burning at the time of this study, the Lummis site, was affected by elk use. The expected low rates of mineralization and nitrification did not occur (Figure 8), so there was not much room for fire to improve rates. One day after the prescribed burn, ammonium concentrations were increased (shown by higher initial concentrations) and the nitrification pattern was nearly the same as pre-burn. About five months after the fire, ammonium concentrations remained higher and rate of nitrate production was increased. This pattern of increased ammonium and a delay before nitrification rates can increase was also shown on two occasions at a site on the southern part of the Jemez Mountains (White 1986a, 1991b). The response to fire appeared to peak at about 12 months after the fire and slightly declined after 17 months (short lag in mineralization present, Figure 8). Similarly, a year and half after fire at the Corral Hill site (Figure 9), mineralization and nitrification patterns are typical of high quality sites. Assuming that these results are not purely an artifact of elk usage, these results suggest that (1) the results of previous burns at the Bear Springs site (White 1986a, 1991) were not site-specific, at least with respect to the direction of change with fire (positive) and (2) the effect of fire lasts through at least a full growing season following a fall burn (based upon Corral Hill results).

The duration of effect of fire on soil processes is important, because needle cast from needles scorched by fire is very high after prescribed fires in these systems in which fires have been suppressed for about a century (see Touchan et al., This Volume). This major pulse of needles and monoterpenes after the first use of fire may shorten the duration of fire effects on N cycling processes.

Thus, areas with long periods since the last fire may need to have a follow up fire shortly after the first prescribed burn to consume the typically heavy litterfall of scorched needles. With more frequent fires, fewer needles remain on low branches and fire intensities should be less, thus the degree of scorch should be less and subsequent needle cast would be reduced.

Chronosequence and Monoterpenes

The pattern of increasing monoterpene content in the forest floor along the chronosequence was weak at best. However, the strong negative relationship between monoterpenes and nitrification *within each site* (Table 2) is strong support of the proposed mechanism of inhibition (White 1988, 1994). The predicted response to monoterpenes and fire was based upon work at a single site (or *within-site* patterns; White 1986a, 1986b, 1991a, 1991b). The results from this study show that the pattern extends to five additional sites. The pattern of high monoterpene/low mineralization and nitrification is obscured by *between-site* differences, because samples from other sites had lower absolute amounts of monoterpenes yet nitrification appeared to be completely inhibited. Thus, the results of the present study show that the pattern is very consistent *within* a site, but indicate that differences *between* sites mask this pattern along the chronosequence.

I feel these results are especially strong in light of the number of uncontrolled (or unmeasured) site factors that could influence the pattern. Other major factors include stand density or basal area, annual litterfall, site overstory production, and microclimate. An additional site factor that could alter the relationship between monoterpenes and nitrification along the chronosequence is the variable amount of needle cast following fires at each site. The scorched but unburned needles have high monoterpene concentrations (Figure 11). The amount of scorching-induced needlecast could vary with canopy cover and height, time since last fire, fuel loads, and many other factors. These scorched needles add to normal litterfall, but the amount of needle scorch should diminish as the height of the canopy increases after the first few uses of fire within the stand.

CONCLUSIONS

HYPOTHESIS 1. Monoterpenes in the soil organic horizons will increase along a fire chronosequence.

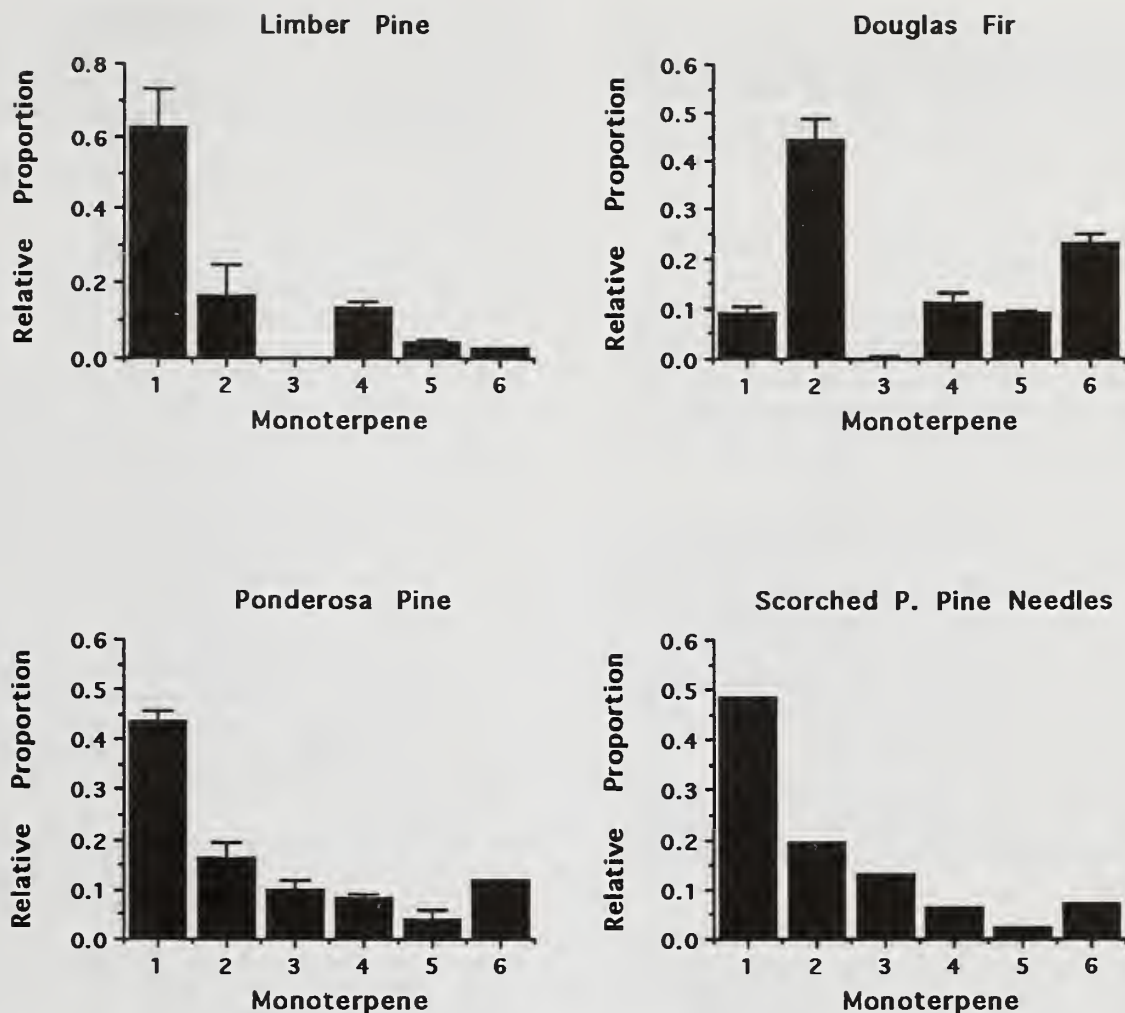


Figure 11.—Relative proportions (amount of individual monoterpene divided by total) of the major monoterpenes in freshly fallen needles of Limber Pine, Douglas Fir, and Ponderosa Pine at the Sawyer Mesa site, and scorched ponderosa pine needles on a tree located along the trail to the Lummis site. Monoterpenes are α -pinene (1), β -pinene (2), camphene (3), d-3-carene (4), limonene (5), and bornyl acetate (6). Bars are mean of two samples with standard errors, except scorched needles which is a single sample.

Monoterpene concentrations were low in sites with recent fire and very high in sites with long periods since a fire, but the trend is not clear in the intermediate sites (Figure 10). Factors that could 'cloud' the overall predicted pattern include:

(1) Differential use of the sites by elk, which add nitrogen in the form of feces and urea, stimulating both the decomposition of the carbon-rich monoterpenes and increasing mineralization/nitrification rates;

(2) Following prescribed fires, needles scorched during the fire still contain high concentrations of monoterpenes and are dropped soon afterward. The amount of needle cast could vary with canopy cover and height, time since last fire, fuel loads,

and many other factors. This needle cast adds to normal litterfall, but should diminish as the height of the canopy increases after the first few fires.

(3) Other site factors (basal area, site productivity, aspect, elevation, actual evapotranspiration, etc.).

HYPOTHESIS 2. Soil mineralization and/or nitrification will decrease along the same fire chronosequence.

Again, the sites at the tails of the chronosequence fit the predicted pattern well, but the intermediate sites do not have a clear pattern (Figure 9). The two sites that differ the most from predicted are the

Foxx site and the Lummis pre-burn site, both of which have higher mineralization and nitrification rates than predicted by fire interval. Both sites had evidence of heavy elk use, which may contribute to the higher rates of mineralization and nitrification (White and Gosz 1987).

There are four major conclusions that can be drawn from this study:

(1) It is clear at these sites that monoterpenes are effective regulators of nitrification *within* each site (Table 2). Differences between sites alter the relationship, making it difficult to extrapolate results from one site to another with respect to the effect of a specific monoterpene concentration;

(2) Elk may be having major effects on nutrient cycling patterns within Bandelier National Monument. Elk alter the distribution of nutrients within a site, removing nutrients from areas relatively rich in nitrogen (areas with grass, herbs, and species with symbiotic nitrogen fixation) and depositing nutrients in areas relative low in available nitrogen (within stands of ponderosa pine);

(3) Inhibition of nitrification may be a sensitive indicator of when management with prescribed fire may be beneficial from a nutrient cycling perspective; and

(4) The two sites outside of the area burned by the La Mesa Fire show very slow rates of nitrogen mineralization and nitrification, characteristics of poor quality sites although these probably have the potential to be the highest quality sites in this study. These results strongly indicate that low-intensity fire would improve rates of nutrient cycling at these sites. Scheduled prescribed burns at the Salamander habitat site will provide the opportunity to test this prediction.

ACKNOWLEDGMENTS

I thank Craig Allen for his willingness to support this research, help in site selection, organizing this symposium, and for editorial comments that improved this paper. Colleen Wyss provided valuable technical assistance through analysis of monoterpenes. Samuel Loftin provide valuable field sampling assistance. I thank the National Park Service and USDA Forest Service for financial support of this project. Partial financial support for my research was provided by the National Science Foundation and the Sevilleta Long-Term Ecological Research program (Pub. #56).

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Potential Nitrogen Contribution of Soil Cryptogams to Post-Disturbance Forest Ecosystems in Bandelier National Monument, NM.

Samuel R. Loftin¹ and Carleton S. White²

Abstract.—The nitrogen-fixation (N_2 -fixation) potential and annual N contribution of soil cryptogamic crusts were estimated in three previously burned ponderosa pine (*Pinus ponderosa*) and one previously grazed pinyon/juniper (*Pinus edulis/Juniperus monosperma*) forest ecosystems in Bandelier National Monument, NM. The ponderosa pine forest sites were burned in the 1977 La Mesa Fire and burro grazing on the pinyon/juniper site ended in approximately (1983). The objective of this research was to determine whether estimated post-disturbance cryptogamic N inputs could offset N losses from the disturbance. Surface cover in each habitat was divided into litter cover, herbaceous cover, bare soil, and obvious cryptogams, in an attempt to quantify the spatial heterogeneity of soil properties. Line intercept transects were used to estimate percent surface cover of each cover type. Soil samples from each cover type were analyzed for total N, C, P, $\delta^{15}N$, and N_2 -fixation potential. At this stage in the recovery process, the potential for cryptogamic N_2 -fixation was determined to occur in all sampled habitats and cover types. Correlations between N_2 -fixation potential and other soil variables indicated that none are suitable as indirect estimators of N_2 -fixation potential. Estimates of ecosystem N input as a result of cryptogamic N_2 -fixation range from 3.6–27.0 kg ha⁻¹ yr⁻¹. Evidence from soil analyses indicated that soil loss was greatest at the pinyon/juniper site.

INTRODUCTION

In a stable forest ecosystem, inputs and losses of mass and energy are considered to be in equilibrium over broad spatial and temporal scales. Decomposition, the process by which nutrients stored in organic detritus are returned to their mineral forms, is slow in ponderosa pine (PP), which leads to an accumulation of organic matter in the absence of fire (C. White, This Volume). Fire causes near immediate mineralization of nutrients. Carbon (C) is released as CO₂, nitrogen (N) as NH₄, and other mineral nutrients as their oxides in the ash. However, mineralization by fire is a radical process and results in a net loss of N by volatilization and loss of fine particulates in smoke and ash

carried to the atmosphere (Vitousek and Howarth 1991).

The significance of this problem is better understood when viewed in a broad temporal context. Ponderosa pine forests, some pinyon/juniper (P/J) associations, chaparral, and some grasslands are dependent upon frequent fires to maintain a stable species composition (Figure 1). If fire-dependent ecosystems are stable, total ecosystem N will be

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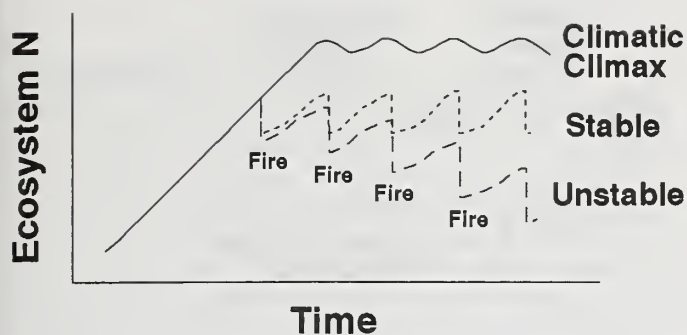


Figure 1.—A conceptual outline of changes in ecosystem N as a function of time. The solid line represents succession to a climatic climax in the absence of any disturbances. The dotted and dashed lines represent the N dynamics of stable and unstable ecosystems, respectively, when subject to recurrent fire events.

relatively stable over long time periods. However, if the loss of N following fire is not returned through inputs, the plant community will ultimately be unstable and unable to maintain itself.

Nitrogen losses from disturbed ecosystems can also occur as a result of soil erosion. The potential for soil erosion is influenced by the type and magnitude of the disturbance. Because grazing animals can disturb the structural integrity of surface soils, overgrazing can result in an increased susceptibility to soil erosion.

Cryptogamic crusts, also called microbiotic or microphytic crusts, can contain cyanobacteria, fungi, algae, lichens and mosses. Some species of cyanobacteria (free-living or as lichen symbionts) have the ability to “fix” or convert biologically unavailable atmospheric N_2 to biologically available forms. Observations of several post-disturbance habitats within Bandelier National Monument have indicated that colonization of bare mineral soils by cryptogamic crusts may be both rapid and extensive. The importance of soil lichens and cyanobacteria to the overall N budget is relatively unknown, but cryptogamic crusts may act to retain N by reducing erosion through soil stabilization (Eldridge 1993; W. White, this volume) and contribute N through atmospheric N_2 -fixation (Rychert and Skujins 1974; Jeffries et al 1992). Harper and Marble (1988) and West (1990) are excellent reviews of the ecological role of soil cryptogamic crusts in arid and semiarid regions.

This research addresses the following questions related to the role of soil cryptogamic crusts in post-fire ponderosa pine forests, and previously grazed P/J woodlands.

1. Does the potential for cryptogamic N_2 -fixation exist?

2. Can the spatial heterogeneity of potential N_2 -fixation be assessed by field observation?

3. Do other soil properties correlate with N_2 -fixation potential?

4. What is the potential N contribution of cryptogamic crusts to these ecosystems?

Question 1 is fundamental to this research, for if N_2 -fixation does not occur the remaining questions are meaningless. Question 2 is based on *a priori* assumptions that were made in the field before any soil analyses were conducted. We assumed that the soil surface cover would affect N_2 -fixation potentials and that soil covered by obvious cryptogams would have the highest potentials. Question 3 states an attempt to identify easily quantifiable soil properties that could be used to estimate N_2 -fixation potential because the acetylene reduction method for estimation of N_2 -fixation potential is labor-intensive. Question 4 addresses the overall importance of cryptogams to the N budget of these recovering ecosystems.

Research Approach

Because of the absence of pre-disturbance data, this research utilized several indirect approaches to address the questions listed above. Relative cryptogamic N_2 -fixation potential was estimated by acetylene reduction assay. Biological N_2 -fixation occurs when the enzyme nitrogenase breaks the N_2 triple bond and reduces atmospheric N to ammonium (NH_4^+). Nitrogenase also preferentially converts acetylene to ethylene in an atmosphere of approximately 10% acetylene. The acetylene reduction assay estimates nitrogenase activity by quantifying the amount of ethylene produced through time. Although the accuracy of potential N_2 -fixation estimates by the acetylene reduction assay has been questioned (Weaver 1986), this analysis should be useful to compare the relative N_2 -fixation potential between sites.

Cryptogamic N contribution can be estimated by means other than N_2 -fixation potentials. Two separate and independent estimates of total cryptogamic N contribution (TCNC) were made based upon total soil N (TN) and stable nitrogen isotope ($\delta^{15}N$) values. The first estimate is based on differences in TN between soils of each of four surface cover types (litter, herbaceous, bare soil, and obvious cryptogams). We assumed that the nitrogen

content of the bare soil represented the nitrogen content of the soil after fire and subsequent soil erosion. The bare soil is used as a standard for comparison because any subsequent inputs of N through wet and dry deposition is assumed to have occurred equally in all soil types. Thus the increase in N in the other soils should be a result of N₂-fixation by nodulated plants and cryptogams. This method yields a potentially conservative estimate of TCNC because any N contribution by non-crystal or free living N₂-fixing organisms occurring in the bare soil is not accounted for in the final estimate.

Stable isotope analysis of soil N can also be used to estimate N inputs. Nitrogen exists as two stable isotopes ¹⁵N and ¹⁴N. The relationship between the isotopes is expressed as a δ¹⁵N value. The δ¹⁵N value of a sample is calculated using the following equation (1):

$$\delta^{15}\text{N} = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000$$

where R_{sample} is the ratio of ¹⁵N:¹⁴N in the sample, and R_{standard} is the ratio of ¹⁵N:¹⁴N in an atmospheric N standard. Sources of N input tend to have a δ¹⁵N near 0 because N₂-fixation does not discriminate between isotopes (Figure 2). The δ¹⁵N of soil N increases through time because biological processes such as N mineralization, nitrification, and denitrification discriminate against ¹⁵N and selectively remove a greater proportion of ¹⁴N (Evans and Ehleringer 1993). As the quantity of residual N decreases, its δ¹⁵N increases. Stated differently, as N losses increase, soil δ¹⁵N increases because processes that lead to N loss will discriminate against the heavier isotope. As N inputs increase, the soil δ¹⁵N will decrease through time because N inputs do not discriminate against ¹⁵N and "recent N" dominates the soil N pool.

A hypothetical soil profile distribution of δ¹⁵N and TN (Figure 3) is based on profiles reported for a juniper/sagebrush ecosystem in southern Utah (Evans and Ehleringer 1993). This profile distribution is based on assumptions that surface N inputs have low δ¹⁵N values, the δ¹⁵N of soil N will increase the longer it remains in the soil, and the age of soil N generally increases with depth.

Surface soil TN and δ¹⁵N values may indicate the recent occurrence of soil erosion (Figure 3). Erosion removes surface soil and its associated N resulting in altered profile N distributions. Eroded surface

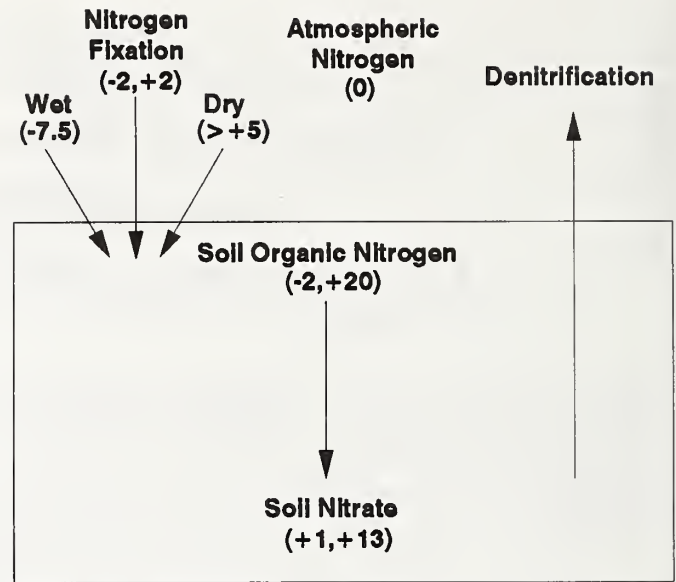


Figure 2.—Conceptual model of ecosystem N and δ¹⁵N dynamics. The values are means or ranges of δ¹⁵N. Nitrogen inputs from N₂-fixation and wet and dry precipitation have a mean δ¹⁵N of zero. Through time the δ¹⁵N of soil organic and inorganic N increases because of processes such as denitrification that discriminate against (leave behind) ¹⁵N.

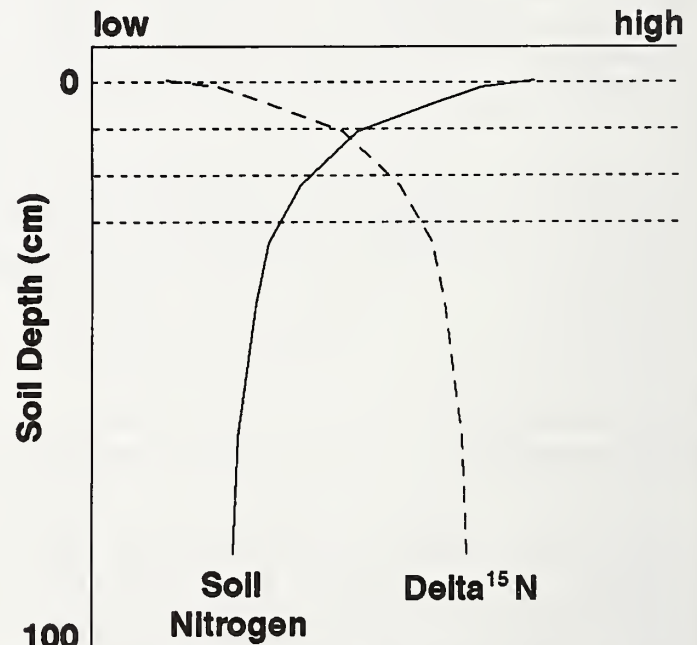


Figure 3.—Hypothetical soil profile distribution of TN and δ¹⁵N based on Evans and Ehleringer (1993). Dashed lines represent potential soil surfaces that would result from soil erosion.

soils should have higher δ¹⁵N and lower TN than undisturbed soils. Comparison of δ¹⁵N of surface soils within or between sites may indicate relative degree of soil loss.

METHODS

Four previously disturbed forest sites in Bandelier National Monument (Figure 4) were chosen as study sites. Sites A, B, and C were located in ponderosa pine forests which burned in the 1977 La Mesa Fire and provide estimates of post-fire cryptogam establishment and potential N inputs. Site A (elev. 8230') was located on Apache Mesa, less than 1 km southwest of the Apache Springs Trailhead. Site B (elev. 7450') was located adjacent to one of Terry Foxx's permanent plots on Escobas Mesa. Sites A and B both have understory vegetation dominated by New Mexico locust (*Robinia neomexicana*), Gambel's oak (*Quercus gambelii*), and sheep fescue (*Festuca ovina*). Site C (elev. 6600') was within the P/J-ponderosa pine ecotone, south of Frijoles canyon and west of the trail that continues to Alamo Canyon. Site C has understory vegetation dominated by mountain muhly (*Muhlenbergia montana*), and junegrass (*Koeleria cristata*). Site D, a P/J woodland (elevation 6390') is east of the Burro trail in the southeastern portion of the Monument. Due to a past history of overgrazing and disturbance by livestock and feral burros (Koehler 1974; Allen 1989), this P/J woodland has very little interspace vegetation and most of the litter is under the canopy of the trees.

Line intercept transects were used to estimate the cover of four surface types: litter, characterized as having greater than 50% dead plant material on the surface; herbaceous vegetation; bare soil; and cryp-

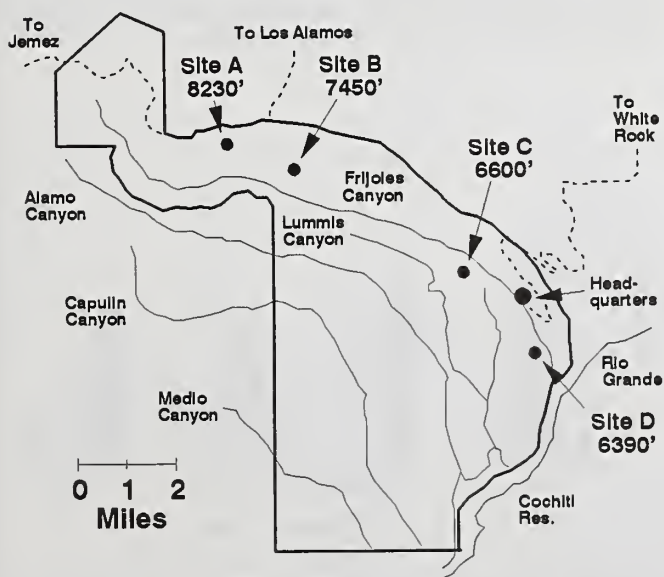


Figure 4.—Location of study sites within Bandelier National Monument, NM.

togamic crust, which was characterized as having greater than 50% recognizable lichen or algal surface crust. Transect data for sites A, B, and C are from previously burned areas only, whereas transect data for site D includes mature pinyon and juniper trees and their associated litter mats. Three, 50 m transects were established within each of the four sites and cover was recorded by centimeter increments along the transects. Within each site, soil surface samples (approx. 3 cm dia. by 3 cm deep) were collected from within areas dominated by each of the four cover types. Soil samples (approximately seven/cover type/site) from all cover type/site combinations were analyzed for total soil N, C, P, and $\delta^{15}\text{N}$. Soil C was estimated by combustion and total P was estimated by Kjeldahl digest. Soil $\delta^{15}\text{N}$ and TN values were provided by Isotope Services, Inc., White Rock, NM. Ratios of elements (C:N, N:P) were calculated from respective analyses. Soils and vegetation transects for sites A, B, C, and D were sampled on 6/18/93, 5/27/93, 5/28/93, and 6/17/93, respectively.

Potential N_2 -fixation in all soil samples was estimated using the acetylene reduction assay. Soil surface samples were incubated under optimal moisture conditions in closed chambers in an atmosphere of approximately 10% acetylene for 48 hrs in the Department of Biology greenhouse on the campus of the University of New Mexico. All soil samples from one habitat type were incubated simultaneously. However, it was not possible to standardize incubation conditions between sites because of the lack of environmental control in the greenhouse. Consequently, comparisons of N_2 -fixation potential between sites are not valid.

The potential N contribution to these forest ecosystems was indirectly estimated using differences in soil TN and $\delta^{15}\text{N}$. These estimates of annual TCNC were calculated using the following equation (2):

$$\text{(TCNC)/cover type} = (\text{TN}_{\text{sample}} - \text{TN}_{\text{bare}}) * (\text{BD}) * (\% \text{ cover}_{\text{sample}}) / 16 \text{ yr}$$

where $\text{TN}_{\text{sample}}$ is the mean TN for the sample soil type (litter, herbaceous, or cryptogamic crust), TN_{bare} is the mean TN for the bare soil type, BD is a constant (3,000) that converts the value to kg ha^{-1} (assuming a bulk density of 1.0 g cm^{-3}), $\% \text{ cover}_{\text{sample}}$ is the % cover of that cover type, and 16 yr is the approximate amount of time since the La Mesa Fire. The sum of the TCNC for each cover type is an estimate of TCNC for a particular site.

The second estimate of cryptogamic crust N contribution is based on differences in $\delta^{15}\text{N}$ between soils of each cover type. The $\delta^{15}\text{N}$ value of a soil is a result of the effects of the fire and erosion, atmospheric and cryptogamic crust N inputs, and subsequent soil processing. Atmospheric inputs and soil processing are assumed to be equal in all soil types. The proportion of soil N (% contribution) for each cover type (X) is determined by the following equation (3):

$$[\delta^{15}\text{N}_{\text{bare}}(1-X)] + [\delta^{15}\text{N}_{\text{cryp}}(X)] = \delta^{15}\text{N}_{\text{sample}}$$

where $\delta^{15}\text{N}_{\text{bare}}$ is the $\delta^{15}\text{N}$ of the bare soil, $\delta^{15}\text{N}_{\text{cryp}}$ is the $\delta^{15}\text{N}$ of N derived from N_2 -fixation by cryptogamic crusts and $\delta^{15}\text{N}_{\text{sample}}$ is the $\delta^{15}\text{N}$ of the sample cover type soil. The TCNC for individual cover types is then determined by the following equation (4):

$$X * (\text{TN}_{\text{sample}}) * (\text{BD}) * (\% \text{cover}) / 15 \text{ yr}$$

where X is the % contribution of cryptogams to the $\delta^{15}\text{N}$ of the cover type soil and the other components are the same as in equation 2. The $\delta^{15}\text{N}$ values of the bare and sample soils are known and the N contributed by cryptogamic N_2 -fixation is assumed to have a $\delta^{15}\text{N}$ of 0. Again, an estimate of site TCNC is generated by summing the TCNC for each cover type.

Within site correlations (Lotus 123 regression routine) were conducted between N_2 -fixation potential and all other measured soil variables.

RESULTS

Above-ground cover estimates of cover categories in each site are shown in Figure 5. Herbaceous cover was greatest in sites A and B. The cover of bare soil and obvious cryptogams was greatest in sites C and D.

In general, soil N, C, P, and N:P (Figures 6, 7, 8, and 9 respectively) were highest in site A and lowest in site D. Soil $\delta^{15}\text{N}$ (Figure 10) was relatively constant in sites A, B, and C but higher and less uniform in site D. C:N ratios (Figure 11) were relatively constant across all sites.

Relative N_2 -fixation potentials for all sites and cover types are shown in Figure 12. For most sites

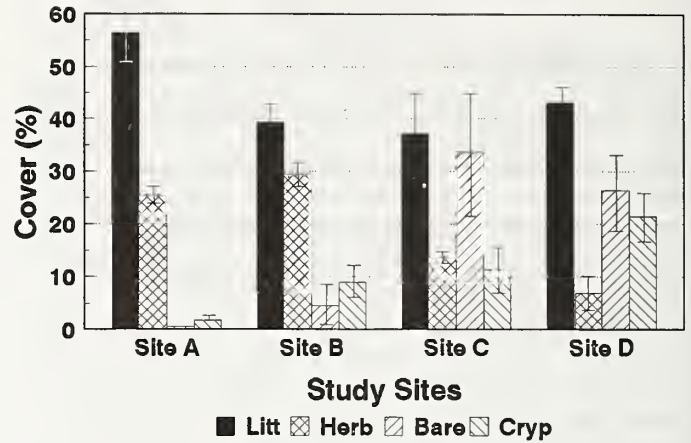


Figure 5.—Mean surface cover of cover types (litter, herbaceous vegetation, bare soil and obvious cryptogams) within each study site.

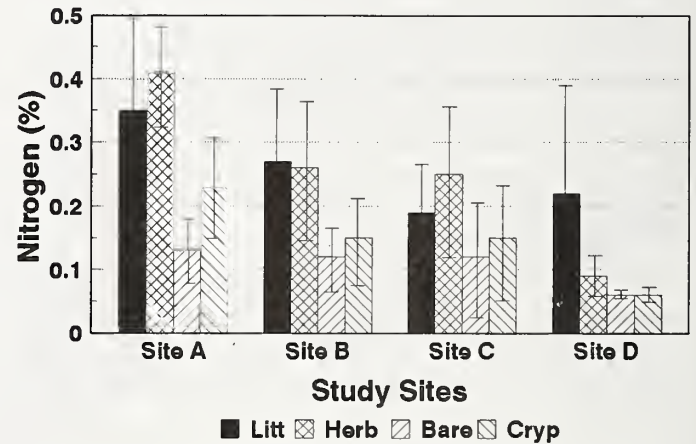


Figure 6.—Mean soil N of cover types (litter, herbaceous vegetation, bare soil and obvious cryptogams) within each study site.

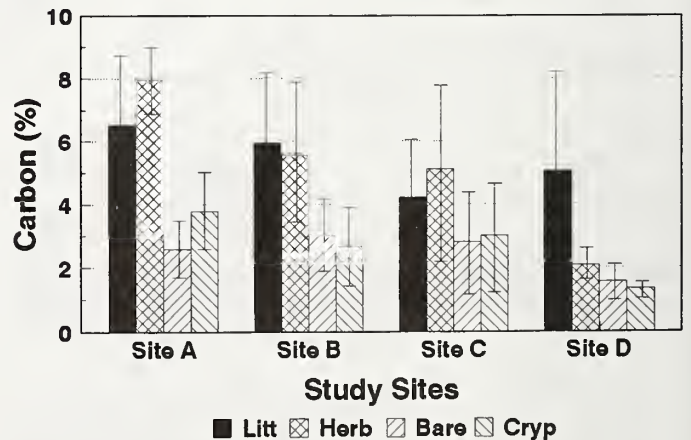


Figure 7.—Mean soil C of cover types (litter, herbaceous vegetation, bare soil and obvious cryptogams) within each study site.

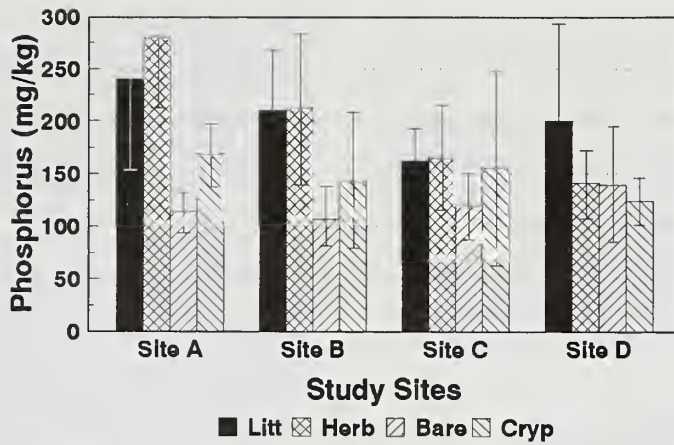


Figure 8.—Mean soil P of cover types (litter, herbaceous vegetation, bare soil and obvious cryptogams) within each study site.

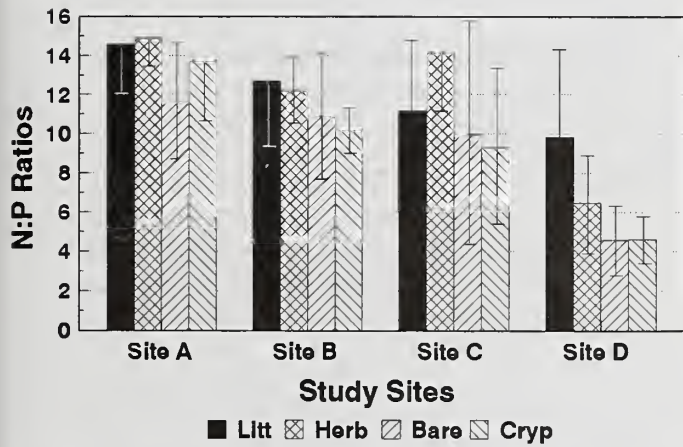


Figure 9.—Mean soil N:P ratios of cover types (litter, herbaceous vegetation, bare soil and obvious cryptogams) within each study site.

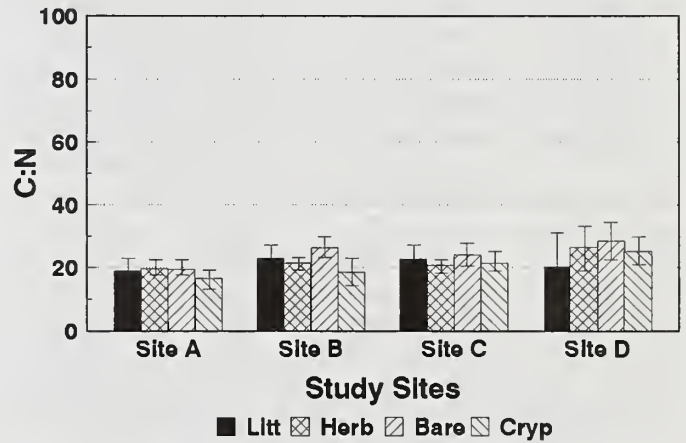


Figure 11.—Mean soil C:N ratios of cover types (litter, herbaceous vegetation, bare soil and obvious cryptogams) within each study site.

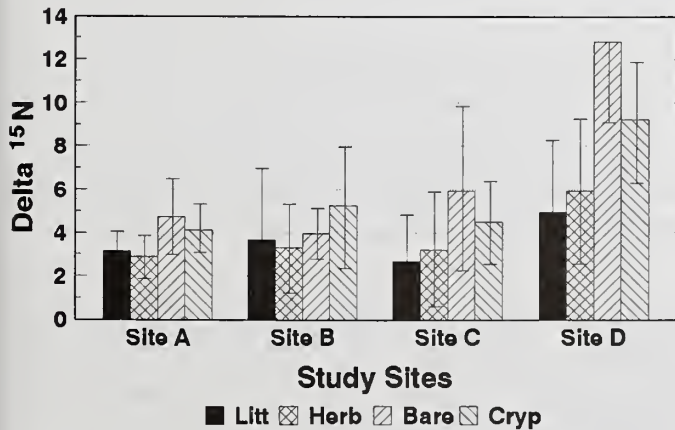


Figure 10.—Mean soil $\delta^{15}\text{N}$ of cover types (litter, herbaceous vegetation, bare soil and obvious cryptogams) within each study site.

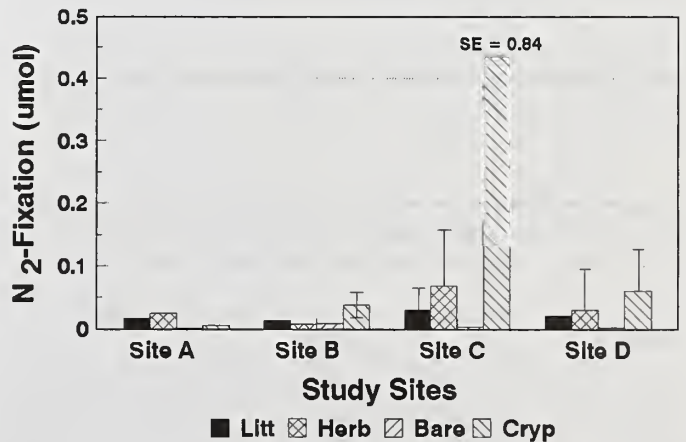


Figure 12.—Total N_2 -fixation (μmol) for cover types within sites. Due to uncontrollable environmental conditions during sample incubation, comparisons should not be made across sites.

the obvious cryptogam cover had the highest potentials, while the bare soil had the lowest potentials.

Within site correlations between N_2 -fixation potential and all other measured soil variables (Table 1) indicated that none of the variables were good indirect estimators of N_2 -fixation potential.

Estimates of annual TCNC for method 1 (TN) and method 2 ($\delta^{15}N$) are shown in Table 2. Values of annual TCNC range from 3.4–25.4 kg ha⁻¹ yr⁻¹.

DISCUSSION

Cryptogamic N Contribution

Two important findings were made with respect to potential N_2 -fixation: 1) N_2 -fixation potential exists in all cover types; and 2) total cryptogam cover may be a poor indicator of the overall importance of cryptogams at these sites. Current cover of cryptogamic crusts may be more sensitive to, or a function of, the amount of bare soil still available for cryptogam establishment following 16 years of ecosystem succession. For example, the relatively high cover of litter and herbaceous vegetation and low cover of cryptogams and bare soil in sites A and B (Figure 5) is probably a result of rapid post-fire recovery because of more mesic conditions at the upper elevations. Although the estimated cover by cryptogams is now low at the upper elevation sites, little is known about cryptogam cover changes in these habitats following the La Mesa Fire (but see W. White, This Volume).

Although no between-site comparisons of N_2 -fixation potential estimates were made, it is possible to compare the relative N_2 -fixation potential of each cover type within the sites (Figure 12). At site A, soils covered by herbaceous vegetation and litter both had higher N_2 -fixation potentials than

obvious cryptogamic crusts, which is the cover type with the highest relative potential at all other sites. Bare soil had the lowest N_2 -fixation potentials except for site B. At this point we do not understand the ecology of cryptogamic organisms well enough to offer an explanation for these results. Undoubtedly, our visual estimates of potential cryptogam activity do not correlate well with what is occurring in the real world. Although necessary information on cryptogam activity is lacking that would permit quantification of current cryptogamic N contributions under field conditions using N_2 -fixation potentials, it is clear that N_2 -fixation is occurring at all sites and in all cover types.

Estimates of total N contribution by soil cryptogamic crusts are remarkably similar between methods and sites (Table 2). However, the total N contribution of cryptogams at the high elevation sites may be greater than at the low elevation sites, despite the discrepancy in cryptogam cover. Because of the more mesic environment, cryptogamic crusts of the upper elevation sites may have longer periods of active N_2 -fixation, which could offset the differences in % cover. The litter and herbaceous cover types, which have highest % cover in sites A and B, are more mesic than the bare soil or obvious cryptogam cover types and may promote even greater cryptogam activity. The total annual N input to comparable sites from wet and dry deposition is approximately 2–4 kg ha⁻¹ yr⁻¹ (Evans and Ehleringer 1993). Rychert and Skujins (1974) estimated cryptogamic N_2 -fixation inputs to Great Basin Desert ecosystems to range from 10–100 kg N ha⁻¹ yr⁻¹. The calculated estimates of annual cryptogamic N-contribution at our study sites are within the range reported by other researchers and well above the estimates for atmospheric N input. Consequently, this is evidence that cryptogamic N_2 -fixation is a very important source of N for these Bandelier sites.

Interestingly, both the lowest and highest estimates of N contribution are from site B. The relatively divergent and extreme estimates at this site may be the result of high N inputs from elk that

Table 1.—Within site correlation coefficients (all cover types) of N_2 -fixation potential against all other measured soil variables.

Variable	Site			
	. A	. B	. C	. D
N	0.37	<0.01	.. 0.08	<0.01
C	0.38	. 0.04	.. 0.08	<0.01
C:N	0.02	. 0.03	<0.01	. 0.03
P	0.38	<0.01	.. 0.06	. 0.01
N:P	0.06	. 0.01	.. 0.09	. 0.03
$\delta^{15}N$	0.02	<0.01	.. 0.01	. 0.08

Table 2.—Estimates of annual total cryptogam N contribution in kg ha⁻¹ yr⁻¹. Calculations based on TN and $\delta^{15}N$ methods.

. Site	Method 1 (TN)	Method 2 ($\delta^{15}N$)
A	24.6	20.2
B	25.4	3.4
C	8.3	11.4
D	14.3	12.6

use this area extensively (Allen, This Volume). The resultant high TN inputs from elk would increase the estimated cryptogam N contribution from method 1, and the high $\delta^{15}\text{N}$ values of the elk-added N would lower the N contribution estimate from method 2, based on differences in $\delta^{15}\text{N}$ values.

Disturbance and Soil Erosion

Soil erosion is a process that removes soil and nutrients from ecosystems and leads to desertification. Lower elevation mesas at Bandelier National Monument were most susceptible to erosion following the La Mesa Fire, probably as a result of lower plant recovery rates (White 1981). Two lines of evidence from this study suggest that greater rates of soil erosion have occurred at the lower elevation P/J woodland site (D), probably because of its relative aridity and disturbance history. First, bare soil comprises 25–35% of the surface in sites C and D (Figure 5). Second, soil TN (Figure 6) and $\delta^{15}\text{N}$ (Figure 9) are lowest and highest, respectively, in site D. This pattern is consistent with removal of N rich, low $\delta^{15}\text{N}$ surface soil and exposure of low N, high $\delta^{15}\text{N}$ subsurface soil (Figure 3). The interspace soils (herbaceous, bare soil and cryptogam cover types) are particularly susceptible to erosion because they are not protected by the tree canopies and their associated litter mats. Stabilization and recovery of these soils could take many years. Evidence from crust removal and reinoculation experiments in Utah suggest that it may take 40–85 years for full recovery of disturbed cryptogamic crusts (Belnap 1993).

CONCLUSIONS

Acetylene reduction assays of surface soils show that the potential for N_2 -fixation occurs in all soils at all sites. The actual N contribution of cryptogamic crusts depends on the abundance and activity of the crust organisms. Actual contributions of N by crusts in the higher elevation sites may be greater than at lower elevations because of more favorable climatic conditions. Although soils with obvious cryptogamic crusts generally had the highest N_2 -fixation potential, this was not always the case. Visual observations of cryptogamic crusts are not reliable estimates of N_2 -fixation potential. None of the soil analyses (TN, TC, C:N, TP, N:P, and $\delta^{15}\text{N}$) were good estimators of N_2 -fixation potential. Estimates of total N contribution by crusts show annual inputs ranging from 3.6–27 kg ha⁻¹ yr⁻¹. These estimates indicate that cryptogamic N_2 -fixation is an important source of N to these post-

disturbance ecosystems. However, without broad scale spatial estimates of all N inputs through time, as well as estimates of disturbance-induced N loss, it is impossible to determine whether or not these forested ecosystems maintain a stable N level. Undoubtedly, recovery from catastrophic disturbances such as the La Mesa Fire or severe overgrazing will require a much greater period of time than recovery from low intensity fires and grazing that were characteristic of ponderosa pine forests and P/J savanna before the arrival of European man.

ACKNOWLEDGEMENTS

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A Survey of Macromycete Diversity in Bandelier National Monument, 1991–1993

Nelson Jarmie^{1,2} and Fran J. Rogers²

Abstract.—This paper reports the progress of an ongoing project to develop an initial inventory of the fungi of the Bandelier area, and describes their relationships with vascular plants and fire ecology. The goal of this ongoing survey has been to collect and identify (at least to genus) as many macroscopic fungi species as possible, and thereby inventory the diversity of such fungi in Bandelier National Monument and adjoining Los Alamos County. The survey covered the three summer seasons of 1991–1993. We collected 836 specimens from a variety of habitats. These were identified as well as possible, recorded in a computer database, dried, and stored, in an herbarium. We found members of 228 species in 118 genera. We were able to identify 95% of the specimens to genus, and 81% to species. In Bandelier alone, we collected 145 specimens in 1991–92 and 270 specimens in 1993, representing at least 74 genera and 93 species. All three basic types of fungi were found: Parasitic, Saprophytic (feeding on dead wood and litter), and Mycorrhizal (in a beneficial symbiosis with a plant). Mycorrhizal fungi compose roughly three fourths of the collection. A variety of sites were studied, with special attention to sites at Bandelier that have burned in recent years, or are planned to be burned soon. The fruitings varied widely (and wildly), making correlation with site location, burns, and other parameters difficult or impossible. The only distinct correlation was with precipitation (and thus elevation). Future needs and possible studies are discussed.

INTRODUCTION

Since the great La Mesa Fire of 1977 in Bandelier much attention has been given to the ensuing course of plant and animal life in that area. Until 1991 however, no studies were conducted on the role of fungi, the third great eukaryotic kingdom of living organisms. This neglect of fungi is common. "Out of sight, out of mind", the fungal vegetative form is most often microscopic and in thin filaments (hyphae), hidden in the soil or in its animal or plant host. Indeed, the study of fungal taxonomy and interrelations with other life forms is perhaps 100 years behind botany and zoology.

Despite our relative ignorance of their affairs, fungi are extraordinarily widespread, diverse, abundant, and ecologically important. Roughly 70,000 species of fungi have been identified out of the one to two million fungal species conserva-

tively estimated to exist (Raven 1994). There are three types of macroscopic fungi (macromycetes): 1) *saprophytic*—consumers of dead, burned, or decaying organic material (these are especially important in breaking down the cellulose and lignin of dead trees); 2) *parasitic*—fungi that feed on living plants, animals or other fungi; and 3) *mycorrhizal*—fungi in mutually beneficial symbiotic relationships with vascular plants, through intimate unions of the fungal hyphae and the feeding rootlets of the vascular plants.

A knowledge of mycorrhizal fungi and their ecological relationships to vascular plants in Bandelier is of special importance in understanding vegeta-

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tion changes since the La Mesa Fire, as mycorrhizal fungi associated with trees and shrubs were the most common type found in this study. The feeding rootlets of most large woody trees are dominated by fungal symbionts (Kendrick 1992), where each rootlet is attached to hundreds or thousands of fungal hyphae. This symbiotic association greatly increases the collection of water and nutrients for uptake by the vascular plant, while in return the fungus receives sugars and other carbohydrates from the tree. The welfare of both the fungi and trees depends upon this obligate relationship, an interdependence which has evolved through the ages. It has been estimated that there are roughly 2500 kg of fungal hyphae per hectare in the soil of a typical forest. The welfare of many species of plants and possibly every vascular plant of Bandelier is intricately bound to an associated fungus, in a beneficial relationship which has co-evolved concurrently with the evolution of the plant species (Kendrick 1992).

No studies of fungi were included in the 1981 Symposium on the La Mesa Fire (Foxy 1984). Given the ecological importance of fungi in forested ecosystems it is essential to begin developing local knowledge about fungi and their ecological roles. This paper reports the progress of an ongoing project to develop an initial inventory of the fungi of the Bandelier area, and describes their relationships with vascular plants and fire ecology.

METHODS

Scope and Range of the Survey

The goal of this ongoing survey has been to collect and identify (at least to genus) as many macroscopic fungi species as possible, and thereby inventory the diversity of such fungi in Bandelier National Monument (BNM) and adjoining portions of Los Alamos County, with special attention paid to Los Alamos National Laboratory (LANL) lands. This survey began in 1991 when Craig Allen of the National Park Service at BNM, in collaboration with Teralene Foxy of the LANL Biological Resource Evaluations Team (LANL Group ESH-20), sponsored this study as part of botanical and zoological surveys of park and Laboratory areas. Most of the inventoried portions of Bandelier are within Los Alamos County, and all of these lands are situated on the Pajarito Plateau on the east flank of the Jemez Mountains in north-central New Mexico.

The request of the sponsors was for a diversity survey—to collect and identify as many different

fungi species as possible. Most of the survey (85%) was done in 1992 and 1993. Broad diversity surveys of fungi are not common in the United States (Nishida et al. 1992; Ammirati et al. 1994), and, as is the case with this report, certain taxa are excluded in the survey.

The objects we collected and cataloged were macroscopic "fleshy" fungi (Figure 1)—fungal fruits of the sexual phase (Teleomorphs) visible to the naked eye in the field (but including hypogeous [underground] species). Almost all the specimens collected and cataloged were in the kingdom Eumycota (Fungi). We found several species of "slime molds" now thought to be in the animal kingdom, as well as a common Juniper rust, and included them in the list for interest. Most mycorrhizal and many saprophytic fungi put up visible fruits making them easier to find and identify. A study of the many species of microscopic fungi (smuts, rusts, mildews, yeasts, blights, and soil fungi, etc.) was not attempted due to the difficulties associated with their identification and our lack of resources, although these fungi are extremely important in the ecology and management of vascular plants (e.g., forest trees and agricultural crops).

In Bandelier we placed special emphasis on collecting in areas burned or scheduled to be burned, particularly in the area of the La Mesa fire of 1977. Burned sites sampled within Bandelier (Figure 2) included: near Juniper and Ponderosa campgrounds; around the park headquarters in Frijoles Canyon; portions of the La Mesa Fire on Burnt Mesa and in the Apache Springs area; and the prescribed burn areas around Corral Hill and near the Dome Road junction with State Highway 4. In Los Alamos National Laboratory we focused on areas where ESH-20 has been conducting botanical and zoological surveys.

Fungal fruiting depends heavily on soil warmth, moisture, and atmospheric humidity. These parameters in the Bandelier/Los Alamos area are in turn dependent on altitude. We searched areas at different altitudes and vegetation zones ranging from 1700 to 2900 m (5500 to 9500 ft) altitude (see Figure 2).

Collection Protocol

We established 45 collection locations in Bandelier and Los Alamos County (Figure 2)—Table 1 gives an abridged list of the Bandelier sites. Vegetation sampling transects of the types commonly used for vascular plants do not work well



Figure 1.—A mycorrhizal fungi, *Amanita muscaria*.

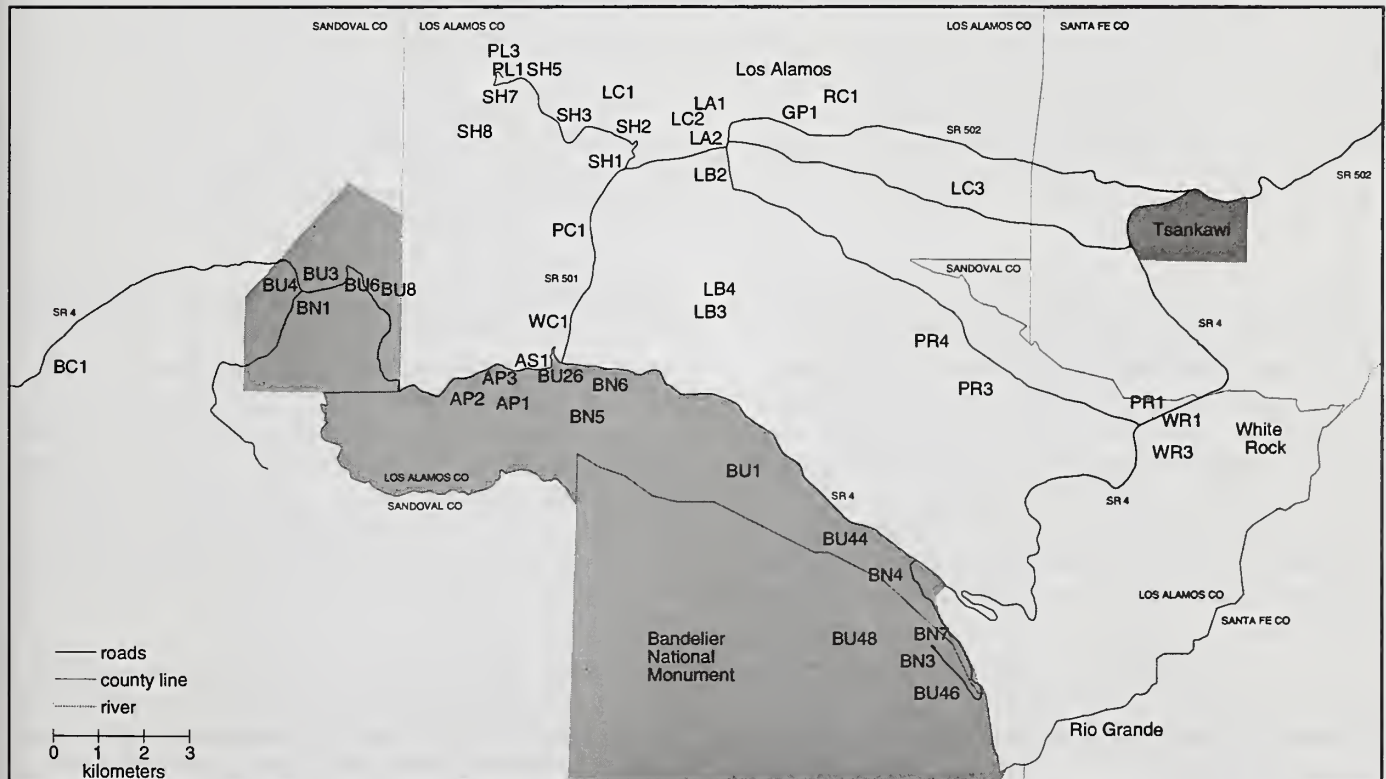


Figure 2.—Location map for collection sites, Bandelier/Los Alamos Fungi Survey. The elevation is lowest along the Rio Grande (lower right) and rises into the mountains at the upper left of the map.

Table 1.—Numbers of taxa of macroscopic fungi found in Bandelier National Monument during the 1993 summer season (No. 1993), compared to the total found in 1991 and 1992 combined (No. 1991/92). The taxa are listed by the area searched. Eight new areas of burn sites were surveyed in 1993. All the new (burn) sites begin with "BU". The "BNM area" codes refer to planned burn units listed in Bandelier's draft Fire Management Plan. Habitat code: MC=Mixed Conifer forest, PP=Ponderosa Pine forest, PJ=Piñon/Juniper woodland, RI=Riparian. NS=Not Surveyed in 91/92.

Site	BNM area	Elevation ft.	Habitat	No. 1991/92	No. 1993	Date last fire yr. or mo./yr.
AP1	UF-23	8444	MC/PP	38	0	not recent
AP2	UF-23	8500	PP	8	0	6/77 in spots
AP3	UF-23	8500	MC	8	3	6/77 in spots
BN1	UF-10	8949	MC	31	1	not recent
BN3	HQ-47	6066	MC/PP/Ri.	11	34	86 & 88 spots
BN6	UH-27	7600	PP	21	30	85 & 77
BU1	UF-35	7200	PP	18	15	6/77
BU3	UF-3	8900	MC	NS	31	10/92 minor
BU4	UF-4	8900	MC	NS	38	87 minor
BU6	UF-6	8900	MC	NS	19	not recent
BU8	UF-8	9100	MC	NS	21	not recent
BU26	UF-26	8150	MC/Ri.	NS	21	93 Spring
BU44	HQ-44	6300	MC/PP/Ri.	NS	22	85 East part
BU46	HQ-46	6000	PP/PJ/Ri.	NS	14	85 in spots
BU48	BW-48	6630	PP/PJ	NS	21	92

Area Place description

- AP1: Apache Springs itself in a little canyon. BNM area UF-23.
 AP2: Apache Springs, Ponderosa Grove to the NE. BNM area UF-23.
 AP3: Woods near Hwy 4 North of Apache Springs. BNM area UF-23.
 BN1: Bandelier, South of intersection of Dome road and Hwy 4: the North tip of BNM area UF-10.
 BN3: Within 400 m of Bandelier Headquarters, BNM area HQ-47.
 BN6: Bandelier, Ponderosa Campground, "Back Gate" BNM area UF-27.
 BU1: Bandelier, "Burnt Mesa" ESH-8 plots BM1, BM2, BM3 La Mesa Fire UF-35.
 BU3: Northeast of intersection of Dome Road and Hwy 4, evidence of mild burn. Not surveyed in 91/92. BNM area UF-3.
 BU4: West of intersection of Dome Road (FR 289) and Hwy 4, BNM area UF-4. Not surveyed in 91/92.
 BU6: South of Frijoles Cr. headwater. BNM area UF-6. Not surveyed in 91/92.
 BU8: East of BU6. Not surveyed in 91/92. BNM area UF-8.
 BU26: Gully southeast of Hwy 4 and Armstead Spring road). Not surveyed in 91/92. BNM area UF-26.
 BU44: Along Frijoles Cr. 2 mile upstream of Ceremonial Cave). Not surveyed in 91/92. BNM area HQ-44
 BU46: Area at and SE of Rainbow House ruin, BNM area HQ-46. Not surveyed in 91/92.
 BU48: Burn area mesa top, South of HQ, between Lummis and Alamo Canyon, BNM Area BW-48. Not surveyed in 91/92.

for fungi, due to the low density and sporadic appearance of fruiting specimens. We informally scanned each collection locality and its environs several times during the season, but our efforts were particularly concentrated on two sets of areas of special interest: 1) recent or planned burn sites in Bandelier; and 2) sites where ESH-20 was conducting botanical studies on Los Alamos National Laboratory lands. Universal Transverse Mercator (UTM) coordinates were determined for each collection site.

Our original goal was to conduct a fruiting density study as is done with vascular plants, using a dedicated plot of ground, with live and dead trees. However, it soon became clear that a "Fickle Fungi Fruiting Factor" exists which results in erratic fruiting of fungi year by year. Given the limits of avail-

able personnel and resources, a meaningful density study proved impossible. In addition, contrary to most plants, the vegetative body of fungi is almost always hidden in the soil or inside living or dead wood. Furthermore, most of the fruits perish rapidly, generally within a few days. The result is that our survey is essentially a "presence log" which simply says: "Yes, this species does exist in this habitat in this location at this time" and includes a subjective statement that it is abundant, common, uncommon, or rare.

We kept field notes, took photographs when possible, and, after identification, dried and preserved many specimens for storage in our fungal herbarium. Several genus specialists have asked for herbarium specimens. Mycologists have visited with us at Bandelier, and others have been avail-

able to us at major statewide or national forays to help with identifications. The primary effort was to identify specimens to genus, because many of the ecological factors (e.g. mycorrhizae) are common to the genus, or even family.

We entered our findings into a relational database (FoxBASE+/Mac) on a personal computer. Each entry record has 34 fields of information and a "memo" field that accepts additional comments. The detailed database will be available as part of a final report (Jarmie and Rogers, in preparation). Each specimen is given an accession number which uniquely identifies its database entry, herbarium position, field notes, etc.

RESULTS

A total of 836 specimens were collected, representing 228 species in 118 genera. Of the total, 96% of the specimens are in the Classes Hymenomycetes and Gastromycetes of the subdivision Basidiomycotina, with the remaining 4% in Orders of the Ascomycotina, an expected proportion. We were able to identify 95% of the specimens to genus, 81% to species. Of the total, we called 51 species "uncommon" and 2 "rare"; use of these adjectives is heavily biased by the observers rapidly developing state of knowledge and level of field experience. More uncommon or rare species may come out of future identifications among the unknown 19% of specimens. We found 34 species new to New Mexico, based upon the state master list of fungi taxa, kept for the New Mexico Mycological Society by R. Bronson. In Bandelier alone we collected 145 specimens in 1991-92 and 270 specimens in 1993. Of these 415 specimens, we identified 94 genera and 137 species. In 1993 alone we identified 74 genera and 93 species.

Table 1 provides a summary of the 1991-1993 fungi collections in Bandelier. Comparison of the sum of specimens collected in 1991-1992 with the 1993 collections demonstrates the erratic nature of fungal fruitings through time. The identification percentages for Bandelier are similar to those given above. Table 2 lists the taxa collected in 1993 at one site (the Bandelier headquarters area) to give an indication of the variety of species present at a locality.

Table 3 presents the species list of all specimens found in Bandelier and Los Alamos County, extracted from our Fungus Registry Database (Jarmie and Rogers, in preparation). The full database includes numerous additional fields, such as location, date collected, habitat, elevation, abundance,

Table 2.—The entire list of taxa collected at the Bandelier Headquarters area (BN3), a typical site, in 1993. The number # before the date is the collection/herbarium accession number.

#	Date	Genus species	Area found
436	8/9/93	Agaricales sp.	BN3
442	8/9	Agaricus campestris	BN3
923	9/17	Agaricus sp.	BN3
858	9/10	Agaricus sp.	BN3
433	8/9	Amanita pantherina	BN3
910	9/17	Amanita vaginata	BN3
911	9/17	Armillaria mellea	BN3
914	9/17	Armillaria mellea grp.	BN3
919	9/17	Armillaria tabescens	BN3
862	9/10	Chroogomphus vinicolor	BN3
864	9/10	Clavariadelphus lovejoyae	BN3
912	9/17	Clavariadelphus truncatus	BN3
915	9/17	Cortinarius sp.	BN3
435	8/9	Cortinarius sp.	BN3
865	9/10	Cortinarius sp.	BN3
443	8/9	Crepidotus applanatus	BN3
861	9/10	Hebeloma sinapizans	BN3
913	9/17	Helvella crispa	BN3
449	8/9	Inocybe albodisca	BN3
859	9/10	Lactarius deliciosus	BN3
837	9/7	Lycoperdon echinatum	BN3
451	8/9	Lycoperdon pyriforme	BN3
434	8/9	Phaeolus schweinitzii	BN3
818	9/7	Phallus impudicus	BN3
821	9/7	Pholiota destruens	BN3
860	9/10	Phyllotopsis nidulans	BN3
440	8/9	Pluteus cervinus	BN3
437	8/9	Polyporus arcularius	BN3
441	8/9	Pycnoporus cinnabarinus	BN3
856	9/10	Russula brevipes	BN3
857	9/10	Stereum complicatum	BN3
863	9/10	Stereum striatum	BN3
439	8/9	Suillus granulatus	BN3
438	8/9	Suillus granulatus grp.	BN3

reliability of identification, identification reference, and whether a herbarium voucher sample exists.

Collections in burn areas sparked an ongoing interest in the taxonomic Class Discomycetes (of subdivision Ascomycotina) whose small members appeared to have a greater density in burned areas; more evident, probably, because of the lack of the usual large mycorrhizal fungi. Typical genera found were Gyromitra, Cudonia, Corirolellus, Scutellinia, Spathularia, Helvella, and Peziza. Again, the erratic fruiting makes correlation difficult. We plan statistical correlation studies in the future with the complete database.

We often felt an aesthetic pleasure, a joy, from walking in the woods and discovering fungi new to us. The AP1 site at Apache Springs in Bandelier was a fungi showcase in 1992. In this moist narrow cleft, surrounded by expanses of drier ponderosa

Table 3.—Species list of fungi collected at Bandelier National Monument and Los Alamos County, 1991-1993. A "T" in the column "bndlr" indicates that a specimen was found within Bandelier, while a "F" denotes a sample collected elsewhere in Los Alamos County. "Year" describes the year of collection, and "ncode" is our accession and herbarium number.

Genus	Species	Family	Order	Bndlr	Year	Ncode
Agaricus	bitorquis	Agaricaceae	Agaricales	F	1991	159
Agaricus	campestris	Agaricaceae	Agaricales	T	1993	442
Agaricus	haemorrhoidarius	Agaricaceae	Agaricales	F	1991	160
Agaricus	pinyonensis	Agaricaceae	Agaricales	F	1993	689
Agaricus	silvicola	Agaricaceae	Agaricales	F	1991	111
Agaricus	xanthodermus	Agaricaceae	Agaricales	F	1991	139
Agrocybe	praecox	Bolbitiaceae	Agaricales	T	1991	166
Amanita	bisporigera	Amanitaceae	Agaricales	T	1991	165
Amanita	caesarea	Amanitaceae	Agaricales	T	1993	455
Amanita	constricta	Amanitaceae	Agaricales	T	1993	824
Amanita	fulva	Amanitaceae	Agaricales	T	1993	417
Amanita	magniverrucata cf.	Amanitaceae	Agaricales	F	1993	930
Amanita	muscaria v. muscar.	Amanitaceae	Agaricales	T	1991	119
Amanita	pantherina	Amanitaceae	Agaricales	T	1993	433
Amanita	vaginata cf	Amanitaceae	Agaricales	T	1993	632
Arcyria	denudata	Trichiaceae	Trichiales	F	1993	933
Armillaria	albolanaripes	Tricholomataceae	Agaricales	F	1993	642
Armillaria	mellea cf.	Tricholomataceae	Agaricales	T	1993	561
Armillaria	straminia cf	Tricholomataceae	Agaricales	F	1993	478
Armillaria	tabescens cf.	Tricholomataceae	Agaricales	T	1993	919
Astraeus	hygrometricus	Astraeaceae	Sclerodermatales	T	1992	344
Auricularia	auricula	Auriculariaceae	Auriculariales	T	1991	134
Auriscalpium	vulgare	Hydnaceae	Aphylophorales	T	1992	202
Battarrea	phalloides	Tulostomataceae	Tulostomatales	F	1991	140
Bisporella	citrina	Leotiaceae	Helotiales	T	1992	388
Bjerkandera	adusta	Polyporaceae	Aphylophorales	T	1993	763
Boletus	barrowsii	Boletaceae	Agaricales	T	1993	807
Boletus	calopus	Boletaceae	Agaricales	F	1993	518
Boletus	chrysenteron cf.	Boletaceae	Agaricales	T	1993	740
Boletus	edulis	Boletaceae	Agaricales	T	1991	118
Boletus	haematinus	Boletaceae	Agaricales	F	1993	651
Boletus	rubripes	Boletaceae	Agaricales	T	1993	771
Caloporus	dichrous	Polyporaceae	Aphylophorales	T	1992	386
Calvatia	gigantea	Lycoperdaceae	Lycoperdales	F	1991	106
Cantharellus	cibarus	Cantharellaceae	Aphylophorales	T	1991	164
Catathelasma	ventricosa	Tricholomataceae	Agaricales	F	1993	900
Ceratiomyxa	fruticulosa	Ceratiomyxaceae	Ceratiomyxales	T	1992	206
Cheimonophyllum	candidissimus	Tricholomataceae	Agaricales	F	1993	409
Chlorociboria	aeruginascens	Dermatiaceae	Helotiales	T	1992	236
Chlorophyllum	molybdites	Lepiotaceae	Agaricales	F	1991	137
Chroogomphus	tomentosus	Gomphidiaceae	Agaricales	F	1993	582
Chroogomphus	vinicolor	Gomphidiaceae	Agaricales	T	1993	862
Clavariadelphus	lovejoyae	Clavariaceae	Aphylophorales	T	1993	864
Clavariadelphus	pistillaris	Clavariaceae	Aphylophorales	F	1993	580
Clavariadelphus	truncatus	Clavariaceae	Aphylophorales	F	1991	110
Clavicornia	pyxidata	Clavariaceae	Aphylophorales	T	1992	232
Clavulina	cristata	Clavariaceae	Aphylophorales	T	1992	226
Clavulina	rugosa	Clavariaceae	Aphylophorales	F	1991	152
Clavulinopsis	corniculata	Clavariaceae	Aphylophorales	T	1992	214
Clitocybe	dealbata	Tricholomataceae	Agaricales	T	1992	306
Clitocybe	dilatata	Tricholomataceae	Agaricales	T	1993	532
Clitocybe	gibba	Tricholomataceae	Agaricales	T	1992	308
Clitocybe	gigantea cf.	Tricholomataceae	Agaricales	T	1993	744
Collybia	dryophila	Tricholomataceae	Agaricales	T	1992	230
Coltricia	perennis	Polyporaceae	Aphylophorales	T	1992	868
Coniophora	puteana	Coniophoraceae	Aphylophorales	T	1992	373
Conocybe	lactea cf.	Bolbitiaceae	Agaricales	F	1993	428
Coprinus	atramentarius	Coprinaceae	Agaricales	T	1993	722

continued

Table 3 (continued).—Species list of fungi collected at Bandelier National Monument and Los Alamos County, 1991-1993. A "T" in the column "bndlr" indicates that a specimen was found within Bandelier, while a "F" denotes a sample collected elsewhere in Los Alamos County. "Year" describes the year of collection, and "ncode" is our accession and herbarium number.

Genus	Species	Family	Order	Bndlr	Year	Ncode
Coprinus	comatus	Coprinaceae	Agaricales	F	1991	163
Coprinus	lagopus cf.	Coprinaceae	Agaricales	T	1993	697
Coprinus	micaceus	Coprinaceae	Agaricales	T	1992	207
Coriolellus	carbonarius	Polyporaceae	Aphyllloporales	T	1992	213
Cortiolopsis	gallica	Polyporaceae	Aphyllloporales	T	1993	822
Cortinarius	alboviolaceus cf.	Cortinariaceae	Agaricales	F	1993	654
Cortinarius	anomalus	Cortinariaceae	Agaricales	T	1993	737
Cortinarius	calochrous	Cortinariaceae	Agaricales	T	1993	540
Cortinarius	glaucopus	Cortinariaceae	Agaricales	F	1991	112
Crepidotus	applanatuscf.	Crepidotaceae	Agaricales	T	1993	443
Crepidotus	herbarum	Crepidotaceae	Agaricales	F	1992	256
Crepidotus	mollis	Crepidotaceae	Agaricales	T	1992	225
Crucibulum	laeve	Nidulariaceae	Aphyllloporales	T	1993	531
Cudonia	circinans	Leotiaceae	Helotiales	T	1992	393
Cyathus	striatus	Nidulariaceae	Aphyllloporales	T	1992	170
Cyptotrama	chrysopeplum	Tricholomataceae	Agaricales	T	1992	371
Cystoderma	amianthinum	Tricholomataceae	Agaricales	T	1992	350
Cystoderma	granulosum	Tricholomataceae	Agaricales	T	1993	828
Dacrymyces	palmatum	Polyporaceae	Aphyllloporales	F	1993	931
Flammulina	velutipes	Tricholomataceae	Agaricales	T	1992	211
Fomitopsis	canjanderi	Polyporaceae	Aphyllloporales	F	1992	341
Fomitopsis	pinicola	Polyporaceae	Aphyllloporales	T	1992	394
Fuligo	septica	Physaraceae	Physarales	T	1993	808
Galerina	autumnalis	Cortinariaceae	Agaricales	T	1992	303
Gamoderma	applanatum	Polyporaceae	Aphyllloporales	T	1992	194
Gautieria	mexicana	Gautieriaceae	Gautieriales	F	1993	934
Geastrum	coronatum	Geastraceae	Lycoperdales	F	1993	686
Geastrum	saccatum	Geastraceae	Lycoperdales	F	1991	156
Geastrum	triplex	Geastraceae	Lycoperdales	T	1992	227
Globifomes	graveolens cf.	Polyporaceae	Aphyllloporales	F	1993	411
Gloeophyllum	sepiarium	Polyporaceae	Aphyllloporales	T	1992	212
Gomphidius	glutinosus	Gomphidiaceae	Agaricales	T	1993	309
Gomphidius	oregonensis	Gomphidiaceae	Agaricales	T	1992	203
Gomphus	bonari	Cantharellaceae	Aphyllloporales	T	1992	316
Gomphus	floccosus	Cantharellaceae	Aphyllloporales	T	1992	229
Guepiniopsis	alpinus	Dacrymycetaceae	Dacrymycetales	F	1992	172
Gymnopolis	sapineus	Cortinariaceae	Agaricales	T	1993	817
Gymnosporangium	speciosus	Pucciniaceae	Uredinales	T	1992	181
Gyromitra	infula	Helvellaceae	Pezizales	T	1992	221
Hebeloma	crustuliniforme	Cortinariaceae	Agaricales	T	1993	778
Hebeloma	sinapizans cf.	Cortinariaceae	Agaricales	T	1993	784
Helvella	acetabulum	Helvellaceae	Pezizales	F	1991	146
Helvella	crispa	Helvellaceae	Pezizales	F	1991	161
Helvella	elastica	Helvellaceae	Pezizales	F	1992	247
Helvella	lacunosa	Helvellaceae	Pezizales	F	1991	149
Hemitrichia	clavata cf.	Trichiaceae	Trichiales	F	1993	603
Heridium	abeitis	Hydnaceae	Aphyllloporales	T	1993	769
Hohenbuehelia	petaloides cf.	Tricholomataceae	Agaricales	F	1993	670
Humaria	hemispherica	Pyronemataceae	Pezizales	T	1992	231
Hygrophoropsis	aurantiaca	Paxillaceae	Agaricales	F	1992	283
Hygrophorus	acutoconica	Hygrophoraceae	Agaricales	T	1993	831
Hygrophorus	chrysodon	Hygrophoraceae	Agaricales	T	1993	698
Hygrophorus	conicus	Hygrophoraceae	Agaricales	T	1992	175
Hygrophorus	marginatus	Hygrophoraceae	Agaricales	T	1993	713
Hygrophorus	pudorinus	Hygrophoraceae	Agaricales	T	1992	235
Hygrophorus	speciosus	Hygrophoraceae	Agaricales	T	1992	354
Hypomyces	chryso-spermum	Hypocreaceae	Sphaeriales	T	1993	853
Hypomyces	hyalinus	Hypocreaceae	Sphaeriales	T	1993	704

continued

Table 3.—(continued) Species list of fungi collected at Bandelier National Monument and Los Alamos County, 1991-1993. A "T" in the column "bndlr" indicates that a specimen was found within Bandelier, while a "F" denotes a sample collected elsewhere in Los Alamos County. "Year" describes the year of collection, and "ncode" is our accession and herbarium number.

Genus	Species	Family	Order	Bndlr	Year	Ncode
Hypomyces	lactifluorum	Hypocreaceae	Sphaeriales	T	1991	101
Inocybe	albodisca cf.	Cortinariaceae	Agaricales	T	1993	449
Inocybe	fastigiata	Cortinariaceae	Agaricales	F	1993	429
Inocybe	lanuginosa	Cortinariaceae	Agaricales	T	1992	305
Inocybe	maculata cf.	Cortinariaceae	Agaricales	F	1993	448
Inocybe	sororia	Cortinariaceae	Agaricales	T	1993	774
Laccaria	amethystina cf.	Tricholomataceae	Agaricales	T	1993	773
Laccaria	laccata	Tricholomataceae	Agaricales	T	1992	310
Lactarius	deliciosus	Russulaceae	Agaricales	T	1992	346
Lactarius	olivaceoumbrius	Russulaceae	Agaricales	F	1993	669
Lactarius	rubriacteus	Russulaceae	Agaricales	T	1993	352
Lactarius	torminosus	Russulaceae	Agaricales	T	1993	634
Lactarius	uvidus	Russulaceae	Agaricales	T	1992	302
Leccinum	aurantiacum	Boletaceae	Agaricales	T	1992	311
Leccinum	insigne	Boletaceae	Agaricales	F	1991	122
Lentinellus	omphalodes cf.	Tricholomataceae	Agaricales	T	1993	781
Lentinellus	ursinus cf.	Tricholomataceae	Agaricales	F	1993	630
Lentinus	ponderosus	Tricholomataceae	Agaricales	F	1992	188
Lenzites	betulina	Polyporaceae	Aphylophorales	T	1992	369
Lepiota	clypeolaria	Lepiotaceae	Agaricales	F	1993	523
Lepiota	cristata	Lepiotaceae	Agaricales	F	1993	524
Lepiota	rhacodes	Lepiotaceae	Agaricales	F	1993	615
Leucopaxillus	amarus	Tricholomataceae	Agaricales	T	1992	299
Leucophleps	spinispora	Leucogastraceae	Leucogastrales	F	1993	937
Lycogala	epidendrum	Reticulariaceae	Liceales	T	1992	208
Lycogala	flavofuscum	Reticulariaceae	Liceales	T	1992	191
Lycoperdon	americanum	Lycoperdaceae	Lycoperdales	T	1992	297
Lycoperdon	echinatum	Lycoperdaceae	Lycoperdales	T	1993	837
Lycoperdon	perlatum	Lycoperdaceae	Lycoperdales	T	1992	224
Lycoperdon	pyriforme	Lycoperdaceae	Lycoperdales	T	1992	304
Marasmius	reades	Tricholomataceae	Agaricales	F	1991	132
Melanoleuca	sp.	Tricholomataceae	Agaricales	T	1992	367
Morchella	augusticeps	Morchellaceae	Pezizales	F	1992	176
Morchella	elata	Morchellaceae	Pezizales	F	1992	177
Morchella	esculenta	Orchellaceae	Pezizales	F	1992	171
Mycena	haemotopus	Tricholomataceae	Agaricales	F	1993	602
Nidula	candida	Nidulariaceae	Nidulariales	T	1991	133
Panaeolus	foenisecii	Coprinaceae	Agaricales	F	1992	183
Panaeolus	retiruges	Coprinaceae	Agaricales	T	1992	218
Peniophora	gigantea	Corticaceae	Aphylophorales	T	1992	351
Peniophora	rufa cf.	Corticaceae	Aphylophorales	F	1993	470
Peziza	repanda	Pezizaceae	Pezizales	T	1993	777
Peziza	succosa	Pezizaceae	Pezizales	T	1992	317
Phaeolus	schweinitzii	Polyporaceae	Aphylophorales	T	1993	434
Phallus	impudicus	Phallaceae	Phallales	T	1993	818
Pholiota	aurivella cf.	Strophariaceae	Agaricales	T	1993	764
Pholiota	destruens	Strophariaceae	Agaricales	T	1992	383
Pholiota	limonella cf.	Strophariaceae	Agaricales	T	1993	559
Pholiota	squarrosa	Strophariaceae	Agaricales	F	1991	155
Phylloporus	rhodoxanthus	Paxillaceae	Agaricales	F	1991	144
Phyllotopsis	nidulans	Tricholomataceae	Agaricales	T	1992	307
Pleurotus	ostreatus	Tricholomataceae	Agaricales	T	1991	136
Pleurotus	sapidus	Tricholomataceae	Agaricales	T	1992	234
Pluteus	cervinus	Pluteaceae	Agaricales	T	1992	204
Pluteus	cervinus v.alba	Pluteaceae	Agaricales	F	1992	291
Polyporus	arcularius	Polyporaceae	Aphylophorales	T	1992	372
Polyporus	badius cf.	Polyporaceae	Aphylophorales	F	1993	407
Polyporus	elegans	Polyporaceae	Aphylophorales	F	1992	360

continued

Table 3.—(continued) Species list of fungi collected at Bandelier National Monument and Los Alamos County, 1991-1993. A "T" in the column "bndlr" indicates that a specimen was found within Bandelier, while a "F" denotes a sample collected elsewhere in Los Alamos County. "Year" describes the year of collection, and "ncode" is our accession and herbarium number.

Genus	Species	Family	Order	Bndlr	Year	Ncode
Polyporus	varius	Polyporaceae	Aphylophorales	F	1993	639
Poria	corticola cf.	Polyporaceae	Aphylophorales	F	1993	444
Poria	spissa	Polyporaceae	Aphylophorales	T	1993	878
Psathyrella	velutina	Coprinaceae	Agaricales	T	1993	546
Pycnoporellus	alboluteus	Polyporaceae	Aphylophorales	F	1992	174
Pycnoporus	cinnabarinus	Polyporaceae	Aphylophorales	T	1992	335
Ramaria	vinosimaculata	Clavariaceae	Aphylophorales	F	1993	652
Rhizopogon	subsalsmonius	Rhizopogonaceae	Hymenogastrales	T	1993	936
Russula	aeruginea	Russulaceae	Agaricales	F	1993	653
Russula	brevipes	Russulaceae	Agaricales	T	1991	117
Russula	emetica cf.	Russulaceae	Agaricales	T	1993	534
Russula	maculata cf.	Russulaceae	Agaricales	T	1993	701
Russula	rosacea cf.	Russulaceae	Agaricales	T	1993	554
Sarcoscypha	coccinea	Sarcoscyphaceae	Pezizales	F	1992	401
Scutellinia	erinaceus cf.	Pyronemataceae	Pezizales	F	1993	685
Scutellinia	scutellata	Pyronemataceae	Pezizales	T	1992	205
Sparassis	crispa	Clavariaceae	Aphylophorales	F	1993	568
Sparassis	radicata	Clavariaceae	Aphylophorales	F	1993	462
Spathularia	flavida	Geoglossaceae	Helotiales	T	1992	301
Spongipellus	pachyodon	Polyporaceae	Aphylophorales	F	1993	426
Steccherinum	ochraceum	Hydnaceae	Aphylophorales	T	1991	135
Stereum	complicatum	Stereaceae	Aphylophorales	T	1993	857
Stereum	hirsutum grp.	Stereaceae	Aphylophorales	F	1992	382
Stereum	striatum	Stereaceae	Aphylophorales	T	1993	863
Stropharia	coronilla	Strophariaceae	Agaricales	T	1992	216
Suillus	granulatus	Boletaceae	Agaricales	T	1992	362
Suillus	lakei	Boletaceae	Agaricales	T	1993	553
Suillus	sibiricus	Boletaceae	Agaricales	F	1993	514
Thelephora	terrestris cf.	Thelophoraceae	Aphylophorales	T	1993	794
Trichaptum	abietinum	Polyporaceae	Aphylophorales	T	1992	399
Tricholoma	sp.	Tricholomataceae	Agaricales	T	1992	389
Tricholomopsis	platyphylla	Tricholomataceae	Agaricales	F	1992	267
Truncocolumella	citrina	Rhizopogonaceae	Hymenogastrales	F	1991	143
Tubifera	sp.	Reticulariaceae	Liceales	F	1993	466
Tulostoma	brumale cf.	Tulostomataceae	Tulostomatales	F	1993	687
Tulostoma	simulans	Tulostomataceae	Tulostomatales	T	1993	829
Tyromyces	guttulatus	Polyporaceae	Aphylophorales	F	1992	190
Volvariella	bombicina	Pluteaceae	Agaricales	T	1993	841
Xeromphalina	campanella	Tricholomataceae	Agaricales	T	1992	219
Xerula	americana	Tricholomataceae	Agaricales	T	1992	258

pine/mixed conifer forest, is a small riparian habitat which provided for a profuse fairyland of mushrooms. There were troops of tiny orange *Xeromphalina campanella* on fallen logs, guarded by flanks of the purpled-pored cups of *Humaria hemisphaerica*, and orange corals (*Clavicornia pyxidata*) amidst red "eye-lash" cups (*Scutellinia scutellata*). We collected 38 species in all from that single site in August/September 1992.

CONCLUSIONS

The main conclusion of our survey is that a broad diversity of macroscopic fungi exist locally.

The contents of our complete database (Jarmie and Rogers—in preparation) provides additional details on this diversity. We collected 836 fruiting bodies belonging to 228 species, 118 genera, 39 families, 12 orders, 5 classes, 2 subdivisions, and 1 division of the kingdom Eumycota (Fungi). The "Fickle Fungi Fruiting Factor" certainly operates in the Jemez Mountains. For example, while only 11 taxa were collected at site BN3 in 1991 and 1992 combined, 34 were found there in 1993 (Table 1, 2); in contrast, at Apache Springs (AP1) this pattern was reversed, with many more species collected in 1991/92 than in 1993 (Table 1). A fruiting of a given species may happen erratically, with a 10 to 15 year

barren interval possible between fruitings (Burdvall 1992). These fluctuations are not well understood. At the least, they are a complex function of rains and rain history, humidity, soil and air contamination, nutrients, length of day, temperature, competition (for nitrogen and other nutrients) with other organisms, and the health of symbiont partner (if there is one). With such variable factors involved we found it difficult to correlate local fruiting patterns with environmental conditions—the only distinct correlation was with precipitation and moist soil conditions.

Thus in general, more fungi and more taxa were seen at the higher, moister elevations, especially in mixed conifer habitats. However, we also observed heavy, intermittent fruiting in typically barren piñon-juniper habitats at lower elevation sites, but usually not until extended rainfall created moist soil conditions for a week or two. Some species, especially in the genera *Agaricus* and *Amanita*, seem to favor piñon-juniper habitats. (Klopatek et al. 1987, 1988). Attempts to make meaningful correlations were again frustrating. For example, 29 specimens were collected from piñon-juniper habitats, but 15 of the specimens could not be reliably identified to species. One identified specimen, *Agaricus pinyonensis*, is known only to occur with piñon-juniper in New Mexico. We also identified *Amanita constricta* that we saw only in the piñon-juniper habitat, yet this species is found mostly under oak or other hardwoods in California (Jenkins 1986).

Apparent symbiotic relationships between trees and fungi were consistently observed. Intensely burned areas where the trees did not survive the 1977 La Mesa Fire lacked the fruits of mycorrhizal fungi. For example, site BN6 (Figure 2), a ponderosa pine grove near "Backgate" (Table 1), produced expected mycorrhizal genera (*Amanita*, *Russula*, *Lactarius*), whereas the nearby site BU1, burned clear of ponderosa pine trees in the La Mesa Fire, displayed none of these genera, or others known to be mycorrhizal.

Fungi species unique to burned habitats, for example *Coriolellus carbonarius*, were found in recently burned areas. There also seemed to be a higher than normal fruiting density of fungi in the class Discomycetes at recently burned sites.

Information gained from an ongoing literature search and from contact with fungi experts seemed at times as important as the survey itself. For example:

1. An obligate mycorrhizal relationship with plants is very common; over 90% of higher plants

have fungal symbionts. Major boreal tree families, such as Pinaceae, are thought to be 100% mycorrhizal (Kendrick 1992). This relationship is an important parameter in forest fires (Dhillion et al. 1987, Pilz and Perry 1983). Mycorrhizal relationships apparently help maintain vascular plant diversity (Grime et al. 1987).

2. A variety of studies provide glimpses of the ecological complexity of fungal activity in soils after fires. For example, an increase in soil temperature results in a decrease in the density of higher fungi, but with an associated increase in bacteria and actinomycetes (Wright and Tarrant 1957). It is apparent that complete studies which include all forms of fungi, bacteria, and other life forms, are necessary to fully understand the ecological interactions of fire and fungi (Moffat 1993, Rose and Hutchins 1988, Wicklow-Howard 1989, Harvey et al. 1976). Local diversity inventories such as the present effort will support more sophisticated fungi-fire research.

3. Tree seedlings used in reforestation must be inoculated with a mycorrhizal partner for survival past one year (Trappe 1977), and there is a succession through time of different symbiotic fungal partners as the trees mature (Visser and Danielson 1990, States 1993).

4. There are subtle factors involved in the ecology of fungi in post-fire environments. For example, in reforestation efforts, attention should be paid to fungal health after inoculation of seedlings; parameters like soil moisture and temperature, and thus time of year and the amount of shade in the area, affect fungal and tree health, with implications for the use of clear-cutting and other forest management techniques (States 1993). Soil nitrogen depletion after fire is an important factor for fungi growth and mycorrhizae (Freeman 1984, see also A.P. Kinzig, and R.H. Socolow 1994).

5. Interesting ecological cycles involving fungi exist, including many that are poorly known. For example, there is a strong relation between ponderosa pine trees, truffles (mycorrhizal Gastromycetes or Discomycetes that are hypogeous—occur underground), and Abert squirrels (*Sciurus aberti*). These truffles exude aromas to attract the squirrels, who dig up and eat these fungi, thereby spreading the spores through their feces, especially to ponderosa pine seedlings which need to be inoculated with these mycorrhizal fungi (Trappe 1977; States et al. 1988). This coevolutionary relationship likely developed over a long time. Near Bandelier headquarters in 1993 an Abert

squirrel noisily scolded us for digging up its truffle dinner from the ponderosa pine needle duff in which it had previously been foraging.

6. In Europe, mycologists have made major fungi diversity surveys for many years, far ahead of American studies, and have charted the changes of fruiting boundaries of various species through time. Detrimental changes in the environment, such as acidic rain, have been correlated with major retreats in the geographic distributions of both fungal species and associated forest plants (Arnolds 1992). Which symbiont partner dies first?

7. In Washington State it has been suggested that there is more commercial value in a possible mushroom harvest than from timber harvests (Molina 1993), a remarkable statement given that this is one of the most productive forestry areas in the world.

Future Possibilities and Considerations

Clearly, more intensive and extensive literature searches would be very productive, as much information on ecological interactions between fungi and fire may already be available in the literature, especially from Forest Service or National Park Service sources.

More focused fungi surveys are needed to use the present resources more efficiently. For example, a few permanently marked plots, 100 to 200 m in diameter, could be set up in key areas and surveyed with higher frequency, in contrast to the current effort to conduct a total diversity study of this whole landscape. Such fungal plot studies could be also be more closely coordinated with other biological surveys.

The fungi database we have developed could be used to decipher additional correlations between local fungal distributions and environmental conditions, such as the associations between intense La Mesa Fire burn sites and certain fungi noted above. For example, it would be useful to compare detailed climatic data (e.g., rainfall patterns) with our fungal fruiting data.

Soil and wood cores could be taken to identify the hyphal vegetative states of fungi using DNA sequence analysis. These new techniques can also help identify single or few celled fungi and bacteria, which are surely very important components of local soil ecosystems. However, such methods are beyond the scope of our current work. To achieve significant additional advances in our knowledge of local fungi diversity and ecology will require

increases in funding and personnel devoted to such work.

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Observations of Arthropod Populations Following the La Mesa Fire of 1977¹

Warren F. Pippin² and Barry Nichols³

Abstract.—Sampling sites were selected in burned and unburned areas where transects for bird surveys had previously been established. Plots were selected randomly in each site and sampled weekly. A 50 m² plot was selected in a severely burned area and an unburned area nearby and observations made on arthropod populations. There were more genera collected in the unburned than the burned areas. Generally, the most common arthropods found in burned and unburned areas were ants and spiders. A New Jersey light trap operated at Ponderosa campground in 1977, before the fire, collected several hundred specimens per trap night. In 1978, the volume of specimens collected in the trap was similar to that collected before the fire. In some areas the drastic reduction in arthropod populations might have had an adverse effect on populations of some insectivorous birds or other animals.

INTRODUCTION

On June 16, 1977, the La Mesa Fire started adjacent to Bandelier National Monument, New Mexico and subsequently swept through a large part of the Monument. The progress of the fire and its ecological aftermath have been extensively documented, providing a framework for investigating fire effects upon arthropod populations.

A general inventory of arthropods that occur on Bandelier had been initiated in May 1977 as part of the VIP program of the NPS. Approximately one month after the fire, it was decided to sample arthropod populations in burned and unburned areas of the Monument, in an effort to document changes, if any, in genus composition and to some extent numbers. Collections were largely confined to macrofauna of the Class Insecta.

MATERIALS AND METHODS

Sampling sites were selected in areas where permanent transects for bird surveys had previously been established by Roland Wauer. These areas are: Frijoles Mesa, pinyon-juniper woodlands; Burnt Mesa, ponderosa-pinyon-juniper woodlands; Escobas Mesa, ponderosa forest; Apache Mesa,

pine-fir-aspen forest; and Frijoles Canyon, riparian habitat (1/2 mile below Upper Crossing).

To sample the arthropod populations in the selected burned and unburned sites, a metal frame was constructed that was large enough to cover an area 1/2 × 1 m. The frame was then thrown in a random manner so it fell within the sample site. The area within the frame was then examined for approximately 15 minutes and all observed arthropods collected and placed in collecting vials containing 70% alcohol. Any flying insects that landed in the sample area were stunned with a fly swatter and collected. The frame was then flipped to cover another 1/2 m and the process repeated. The total area covered for each sample was then 1 sq. meter. Five such paired samples were taken from each site on a weekly basis from July 18–August 26, 1977. Vials containing the samples were labeled and returned to the laboratory for sorting, counting and shipment to specialists for generic determination.

¹Technical editor's note: This paper was presented at the original La Mesa Fire Symposium in October, 1981, and was inadvertently omitted from that symposium proceedings. It is included here to make its findings more generally available.

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Approximately 10 days after the fire was brought under control the principal author, while in a volunteer status, selected two 50 m square plots for observation and collection of arthropod specimens. One plot was in a severely burned area of ponderosa pine-scrub oak near Ponderosa Campground and the other in a similar unburned area approximately 1/2 mile down the fire road toward Frijoles Canyon from Ponderosa Campground. Specimens were collected with a standard insect collecting net and by physical examination of the plots. Collections were made in July 1977 and July 1978.

It was intended to use a 12 volt battery-operated UV light trap in the transect sampling sites in 1977, but unfortunately none became available. A 110 volt New Jersey light trap, borrowed from the U.S. Air Force, was operated 3 nights per week at Ponderosa Campground from May 18–June 24, 1977, prior to the fire and from July 1–Sept. 1, 1977, following the fire. During the summer of 1978 a 12 volt battery-operated light was available and was used to sample night flying insects in the burned and unburned 50 m² plots described above.

RESULTS

Tables 1,2,3,4 and 5 show the relative number of genera collected in each site in the transect areas. As might be expected there were more genera collected in the unburned than the burned areas. For example, Table 1 shows 72 individuals collected from 4 genera in the burned site and 97 individuals belonging to 13 genera in the unburned. (These numbers are indicated in parentheses following the column headings for the table.) The number of individuals did not vary significantly. Generally the most common arthropods found in burned and unburned sites were ants and spiders. The only specimen collected of special interest was one spider, *Robertus* sp. found in a burned area on Escobas Mesa. This is apparently a new record for this genus in New Mexico and may be a new species.

Table 6 shows the result of collections in the burned and unburned 50 m² plots near Ponderosa Campground in July 1977 and 1978. In 1977 the burned area was almost devoid of visual arthropod activity. Four genera, consisting primarily of ants, were collected. The only apparent arthropod life was found under fairly large stones and then only in limited numbers. In 1978, 15 genera were collected in the burned plot. The first insect to appear in any abundance was a species of leafhopper

Table 1.—Arthropod genera collected in burned and unburned areas of Frijoles Mesa.

Burned (72/4) ¹	Unburned (97/13)
Hymenoptera	Hymenoptera
Formicidae	Formicidae
<i>Camponotus</i> sp.	<i>Pheidole</i> sp.
<i>Formica</i> sp.	<i>Camponotus</i> sp.
	<i>Formica</i> sp.
Coleoptera	Coleoptera
Tenebrionidae	Buprestidae
<i>Eleodes</i> sp.	<i>Acmaeocora</i> sp.
Orthoptera	Coccinellidae sp.*
Acrididae	<i>Anatis</i> sp.
<i>Melanoplus</i> sp.	
	Diptera
	Chloropidae
	<i>Hippelates</i> sp.
	Muscidae
	<i>Fannia</i> sp.
	Orthoptera
	Gryllidae
	<i>Gryllus</i> sp.
	Hemiptera-Heteroptera
	Miridae
	<i>Irbisia</i> sp.
	Psyllidae
	<i>Trioza</i> sp.
	Araneida
	Lycosidae
	<i>Lycosa</i> sp.
	Theridiidae
	<i>Theridion</i> sp.
	Chilopoda
	<i>Arenophilus</i> sp.

¹ # of individuals/# of genera.

* Only identified to family.

found on grass. In the unburned plot 24 genera were collected in 1977 and 44 genera in 1978.

A New Jersey light trap operated at Ponderosa Campground in 1977 before the fire collected several hundred specimens per trap night, primarily Lepidoptera, Coleoptera and Diptera. Following the fire collections were reduced an estimated 75%. Collections never reached pre-fire levels by September 1977. No records were kept of actual numbers, except in the case of mosquitoes. It is interesting to note the average number of mosquitoes per trap night was 4 before the fire and 5 after. It was observed that after the fire there was a dramatic reduction in filth fly populations. The numbers remained very low the remainder of the summer.

Table 2.—Arthropod genera collected in burned and unburned areas of Burnt Mesa.

Burned (78/5) ¹	Unburned (91/14)
Hymenoptera	Hymenoptera
Formicidae	Formicidae
<i>Pheidole</i> sp.	<i>Myrmica</i> sp.
<i>Camponotus</i> sp.	<i>Pheidole</i> sp.
	<i>Lasius</i> sp.
	<i>Camponotus</i> sp.
Araneida	
Lycosidae	
<i>Pardosa</i> sp.	
Diplopoda	Hemiptera-Heteroptera
<i>Abacion</i> sp.	Cicadellidae
	<i>Gyponata</i> sp.
	Miridae
	<i>Polymerus</i> sp.
	Nabidae
	<i>Nabis</i> sp.
Chilopoda	Deptera
<i>Arenophilus</i> sp.	Muscidae
	<i>Musca</i> sp.
	<i>Fannia</i> sp.
	Orthoptera
	Acrididae
	<i>Melanoplus</i> sp.
	Coleoptera
	Scarabaeidae
	<i>Polyphaga</i> sp.
	Araneida
	Lycosidae
	<i>Lycosa</i> sp.
	Gnaphosidae
	<i>Gnaphosa</i> sp.
	Diplopoda
	<i>Abacion</i> sp.

¹ # of individuals/# of genera.

In 1978 the volume of specimens collected per trap night was similar to that collected before the fire in 1977. The UV light trap that was operated two nights in July at the burned and unburned plots produced similar catches at each plot, consisting primarily of Lepidoptera in the families Arctiidae, Lasiocampidae, Noctuidae, Sphingidae, Geometridae, Zygaenidae, Pyralidae, Gelechioidea, Notodontidae, and Saturniidae.

SUMMARY AND CONCLUSIONS

Arthropod collections were made in selected sites at Bandelier National Monument, NM, following the intense forest fire that occurred there in 1977. As might be expected there was a reduction in the number of genera in burned as opposed to

Table 3.—Arthropod genera collected in burned and unburned areas of Escobas Mesa.

Burned (51/7) ¹	Unburned (72/13)
Hymenoptera	Hymenoptera
Formicidae	Formicidae
<i>Camponotus</i> sp.	<i>Formica</i> sp.
<i>Formica</i> sp.	<i>Lasius</i> sp.
	<i>Pheidole</i> sp.
Diptera	Diptera
Muscidae	Muscidae
<i>Musca</i> sp.	<i>Fannia</i> sp.
Araneida	Coleoptera
Lycosidae	Carabidae
<i>Lycosa</i> sp.	<i>Harpalus</i> sp.
<i>Robertus</i> sp.	Curculionidae
New record from NM, may be new species.	<i>Thricolepis</i> sp.
Diplopoda	Hemiptera
<i>Abacion</i> sp.	Cicadellidae
	<i>Gyponana</i> sp.
Chilopoda	Miridae
<i>Arenophilus</i> sp.	<i>Psallus</i> sp.
	Araneida
	Lycosidae
	<i>Lycosa</i> sp.
	<i>Pardosa</i> sp.
	Gnaphosidae
	<i>Gnaphosa</i> sp.
	Thomisidae
	<i>Xysticus</i> sp.
	Diplopoda
	<i>Abacion</i> sp.

¹ # of individuals/# of genera.

unburned areas. The number of individual specimens collected did not vary significantly. This may be due to easier visibility for collecting in burned areas. Most of the individual specimens collected in the burned areas were ants and spiders. In severely burned areas, such as the 50 m² plot near Ponderosa Campground, virtually all arthropods were eliminated. One year after the fire the number of genera collected increased, but were below the number of genera collected in the unburned area in 1977. The unburned 50 m² plot was near burned areas and was undoubtedly subjected to heat and smoke. This may account for the small number of fly genera collected in 1977 (3) as opposed to the larger number collected in 1978 (10). Strong fliers may have an opportunity to leave the area or perhaps most were eliminated by heat and smoke.

Light trap collections in 1977 were reduced by almost 75% following the fire and remained low

Table 4.—Arthropod genera collected in burned and unburned areas of Apache Mesa.

Burned (61/8) ¹	Unburned(89/17)
Hymenoptera Formicidae <i>Lasius</i> sp. <i>Camponotus</i> sp.	Hymenoptera Formicidae <i>Myrmica</i> sp. <i>Lasius</i> sp. <i>Camponotus</i> sp.
Coleoptera Carabidae <i>Calosoma</i> sp.	<i>Leptothorax</i> sp.
Diptera Muscidae <i>Fannia</i> sp. Tipulidae <i>Limonia</i> sp.	Coleoptera Chrysomelidae <i>Scelolyperus</i> sp. Curculionidae <i>Gymnetron</i> sp. Cerambycidae <i>Aneflomorpha</i> sp.
Araneida Gnaphosidae <i>Drassodes</i> sp. <i>Haplodrassus</i> sp.	Diptera Sarcophagidae <i>Sarcophaga</i> sp. Muscidae <i>Musca</i> sp. Tachinidae <i>Nowickia</i> sp.
Chilopoda <i>Arenophilus</i> sp.	Hemiptera-Heteroptera Cicadellidae <i>Gyponana</i> sp. Gelastocoridae <i>Gelastocoris</i> sp.
	Orthoptera Gryllidae <i>Gryllus</i> sp. Acrididae <i>Melanoplus</i> sp.
	Araneida Clubionidae <i>Micaria</i> sp. Lycosidae <i>Pardosa</i> sp. Gnaphosidae <i>Gnaphosa</i> sp.

¹ # of individuals/# of genera.

for the remainder of the summer. However, in 1978 the volume of specimens collected was similar to that collected prior to the fire. It appears that night flying insects reappear in burned areas rather quickly, especially where there are "islands" of unburned areas scattered throughout the burned

Table 5.—Arthropod genera collected in burned and unburned areas of Frijoles Canyon.

BURNED (59/7) ¹	UNBURNED (93/19)
Hymenoptera Formicidae <i>Camponotus</i> sp. <i>Formica</i> sp.	Hymenoptera Formicidae <i>Formica</i> sp. <i>Camponotus</i> sp. <i>Crematogaster</i> sp. <i>Leptothorax</i> sp.
Hemiptera-Heteroptera Cicadellidae <i>Cicadula</i> sp.	Hemiptera-Heteroptera Lygaeidae <i>Lygaeus</i> sp. Cicadellidae <i>Cicadula</i> sp.
Coleoptera Scarabaeidae <i>Aphodius</i> sp.	Miridae <i>Labops</i> sp.
Araneida Lycosidae <i>Pardosa</i> sp. Thomisidae sp.* <i>Xysticus</i> sp.	Coleoptera Chrysomelidae <i>Scelolyperus</i> sp. Curculionidae <i>Apion</i> sp.
Chilopoda <i>Arenophilus</i> sp.	Diptera Muscidae <i>Musca</i> sp. Tachinidae <i>Peleteria</i> sp.
	Lepidoptera Geometridae <i>Glena</i> sp.
	Araneida Lycosidae <i>Lycosa</i> sp. <i>Pardosa</i> sp. Theridiidae <i>Theridion</i> sp. Agelenidae <i>Agelenopsis</i> sp. Salticidae <i>Pellenes</i> sp. Gnaphosidae <i>Zelotes</i> sp. <i>Gnaphosa</i> sp.

¹ # of individuals/# of genera.

* Only identified to family.

areas. Ground inhabiting species and weak fliers appear to return more slowly.

In some areas the drastic reduction in arthropod populations might have an adverse effect on populations of some insectivorous birds or other animals, especially those with highly specific diets.

Table 6.—Arthropod genera collected in burned and unburned plots near Ponderosa Campground in 1977 and 1978.

Burned		Unburned (continued)	
1977 (4) ¹	1978 (15)	1977 (24) ¹	1978 (44)
Hymenoptera Formicidae <i>Formica</i> sp. <i>Pheidole</i> sp.	Hymenoptera Formicidae <i>Formica</i> sp. <i>Pheidole</i> sp.	Elateridae <i>Melanotus</i> sp. Buprestidae <i>Acmaeodera</i> sp. Ptinidae <i>Ptinus</i> sp.	Coleoptera Scarabaeidae <i>Diplotaxis</i> sp. <i>Cheiroplatys</i> sp. Cerambycidae <i>Cosmosalia</i> sp. <i>Anastrangalir</i> sp.
Diptera Tachinidae <i>Peleteria</i> sp.	Hemiptera-Heteroptera <i>Cicadellidae</i> sp.	Diptera Calliphoridae <i>Phormia</i> sp. Bombyliidae <i>Poecilanthrax</i> sp. Muscidae <i>Fannia</i> sp.	Lycidae <i>Dietyopterus</i> sp.
Araneida Lycosidae <i>Pardosa</i> sp.	Diptera Muscidae <i>Fannia</i> sp. Tachinidae <i>Peleteria</i> sp. <i>Sitophaga</i> sp. Sarcophagidae <i>Ravinia</i> sp. <i>Sarcophaga</i> sp. Syrphidae <i>Blera</i> sp.	Hymenoptera Vespidae <i>Vespula</i> sp.	Elateridae <i>Melanotus</i> sp. Melandryidae <i>Eustrophinus</i> sp. Buprestidae <i>Acmaeodera</i> sp. Chrysomelidae <i>Pyrrhalta</i> sp. Ptinidae <i>Ptinus</i> sp.
	Coleoptera Coccinellidae <i>Anatis</i> sp. Buprestidae sp.*	Orthoptera Acrididae <i>Melanoplus</i> sp. <i>Dissosteria</i> sp.	Diptera Calliphoridae <i>Phormia</i> sp. Culicidae <i>Aedes</i> sp. Bombyliidae <i>Poecilanthrax</i> sp. Sarcophagidae <i>Ravinia</i> sp. <i>Sarcophaga</i> sp. Mycetophilidae <i>Mycetophila</i> sp. Tachinidae <i>Peleteria</i> sp. Muscidae <i>Fannia</i> sp. Phoridae <i>Phora</i> sp. Tipulidae <i>Tipula</i> sp.
	Orthoptera Acrididae <i>Melanoplus</i> sp. <i>Dissosteria</i> sp.	Araneida Lycosidae <i>Lycosa</i> sp. <i>Pardosa</i> sp. Gnaphosidae <i>Zelotes</i> sp. <i>Gnaphosa</i> sp.	
	Araneida Lycosidae <i>Pardosa</i> sp. Gnaphosidae <i>Gnaphosa</i> sp.		
	Unburned		
1977 (24) ¹	1978 (44)		
Hymenoptera Formicidae <i>Pheidole</i> sp. <i>Lasius</i> sp. <i>Formica</i> sp. <i>Camponotus</i> sp.	Hymenoptera Formicidae <i>Conomyrma</i> sp. <i>Pheidole</i> sp. <i>Liometopum</i> sp. <i>Lasius</i> sp. <i>Formica</i> sp. <i>Camponotus</i> sp.		Hymenoptera Megachilidae <i>Megachile</i> sp. Vespidae <i>Polistes</i> sp. Sphecidae <i>Sphex</i> sp. Apidae <i>Bombus</i> sp. Ichneumonidae <i>Gelis</i> sp. Neuroptera <i>Raphidia</i> sp.
Hemiptera-Heteroptera Cicadellidae <i>Gyponana</i> sp. <i>Exitianus</i> sp. Aphididae <i>Cinara</i> sp. Miridae <i>Phytocoris</i> sp. Nabidae <i>Nabis</i> sp.	Hemiptera-Heteroptera Cicadellidae <i>Gyponana</i> sp. <i>Ballana</i> sp. Aphididae <i>Dactynotus</i> sp. <i>Cinara</i> sp. Psyllidae <i>Trioza</i> sp. Miridae <i>Psallus</i> sp. <i>Digiognathus</i> sp.		Orthoptera Acrididae <i>Melanoplus</i> sp. <i>Dissosteria</i> sp.
Coleoptera Scarabaeidae <i>Cheiroplatys</i> sp. Lycidae <i>Dietyopterus</i> sp.			Araneida Lycosidae <i>Lycosa</i> sp. <i>Pardosa</i> sp. Gnaphosidae <i>Gnaphosa</i> sp.

¹ # of genera.

* Only identified to family.

A Comparison of Ground-Dwelling Arthropod Assemblages Among Different Habitats Resulting from the 1977 La Mesa Fire

David C. Lightfoot¹

Abstract.—This study was conducted to determine whether or not post-fire habitats resulting from the 1977 La Mesa Fire support different assemblages of ground-dwelling arthropods. Four principal post-fire vegetation habitats were identified: 1) ponderosa pine forest, 2) ponderosa pine savanna, 3) Gambel oak thickets, and 4) open grasslands. Ground-dwelling arthropods were sampled from each of the four habitats during the summer of 1993. Numerically important arthropod groups found in the samples included spiders, harvestmen, bristletails, crickets, fungus beetles, rove beetles, ground beetles, and darkling beetles. Total arthropod abundances were significantly different among the four habitats, and changed through the summer. Total species diversity differed little among the habitats. Each arthropod group was significantly more abundant in one or two habitat types, and the different arthropod groups had dissimilar abundance patterns among the habitats. These findings are consistent with other studies of post-fire patterns of ground-dwelling arthropod assemblages, and have important implications for differences in decomposition and nutrient cycling rates among habitats, and food resource availability to vertebrate animal predators in those habitats.

INTRODUCTION

The effects of fires on forest arthropods are not well known, especially in the mid-elevation ponderosa pine forests of the Southwest (Wright & Baily 1982). Most studies of arthropod responses to forest fires elsewhere have focused on relatively short-term post-fire recovery or recolonization. Such studies have found that some ground-dwelling soil and litter arthropods may survive fires, depending on burn intensity (Buck 1979, Majer 1984, Abbott 1984), while others recolonize intensely burned areas from surrounding unburned or less intensely burned forest (Touyama et al. 1989, Buck 1979). Recovery of soil and litter inhabiting arthropods after forest fires is generally about five years (Wright & Baily 1982). Actual recovery times will vary with forest type, and the intensity and extent of fires.

Post-fire ground-dwelling arthropod assemblages in forest ecosystems exhibit consistent pat-

terns of various arthropod species and taxonomic groups occurring in different post-fire habitats (Majer 1984, Touyama et al. 1979, Harris & Whitcomb 1974, Richardson & Holliday 1982, Dindal & Metz 1977). Such variation in relative abundances of different arthropod taxa may result from dissimilar recolonization rates (Touyama et al. 1989, Abbott 1984), or from preferences for different habitats resulting from post-fire vegetation recovery (Richardson & Holliday 1982, Dindal & Metz 1977).

In June of 1977 the La Mesa Fire burned approximately 15,000 acres of ponderosa pine forest in the Jemez Mountains of north-central New Mexico (Foxy 1981a). Studies on vegetation (Potter & Foxy 1984), birds (Wauer & Johnson 1984) and small mammals (Guthrie 1984) have shown that the La

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Mesa Fire had significant effects on the resident flora and fauna. Pippin and Nichols (This Volume) sampled arthropods in burned and unburned areas immediately after, and up to one year after the fire. They found reductions in diversity and abundance of arthropods immediately after the fire, and some increases within one year. The greatest reductions in arthropods were in severely burned locations. Nothing is known about the long-term effects of the La Mesa Fire on invertebrates.

Invertebrates are important components of forest ecosystems (Mattson 1977), yet little is known about the taxonomic composition and ecology of invertebrates of ponderosa pine forests of the Southwest. Existing literature on forest insects focuses on plant-feeding insects associated with dominant tree species (Furniss & Carolin 1977). Relatively little is known about ground-dwelling arthropods in coniferous forests.

The goals of this research project were to sample ground-dwelling macro-arthropods from major post-fire habitats resulting from the 1977 La Mesa Fire to: 1) determine the taxonomic composition of ground-dwelling arthropods in the La Mesa Fire area, 2) determine whether or not total arthropod abundance and species diversity differed among post-fire habitats, and 3) to identify which taxonomic and trophic groups were numerically dominant in the different post-fire habitats.

METHODS

This research project was conducted in the north-central portion of the La Mesa Fire, on Apache Mesa and Escobas Mesa, near Ponderosa Campground (Figures 1 & 2). The sampling was performed for a five-month period from late May through early November of 1993. Four vegetation types were identified as major physical habitats resulting from different fire intensities during the La Mesa Fire, and subsequent post-fire vegetation recovery. These four habitat types included 1) intact ponderosa pine forest that was exposed to low-intensity ground fire, and most of the trees survived the fire, 2) ponderosa savanna that resulted from moderately burned ponderosa forest, where some trees survived the fire, 3) Gambel oak thickets that have expanded into areas where all pine trees were killed by intense fire, and 4) open grassland areas that were also intensely burned, and all ponderosa pine trees killed.

Ground-dwelling arthropods were sampled from the four habitats by the use of pitfall traps

(Southwood 1978). Pitfall traps used in this study consisted of steel cans measuring 4.5 inches deep, and 3 inches in diameter. Each can was buried in the soil with the open tops flush with the ground surface. Each open can contained one 10 oz. plastic cup, which was half-filled with propylene glycol. A 6-inch diameter, 3/8-inch thick plywood cover was placed over each trap, supported on four 3.5-inch nails, to protect the traps from weather.

Pitfall traps were placed in at least two locations in each of the four habitat types (Figure 2). Each of the site locations were selected subjectively to represent the major post-fire habitat types in the La Mesa Fire burn area. Traps were placed randomly at each location, for a total of ten traps representing each habitat type. Traps were randomly located at each site by utilizing random compass directions and random distance measures. All traps at each site were located at least 20 meters apart.

The contents of the pitfall traps were collected once every 4–8 weeks. The contents of the traps were collected by removing each 10 oz. plastic cup, pouring the contents through a wire-mesh strainer, and transferring the contents to glass vials containing ethyl alcohol. Each vial was labelled with the site name, the trap number and the date of collection. The propylene glycol was placed back into each cup, with more added as needed, and each cup was then placed back into the can from which it came for continued trapping. All traps were collected within a several day time period. All of the traps were collected four times during the summer and autumn, 1) mid-July or early summer (sampling period: June, mid-July), 2)

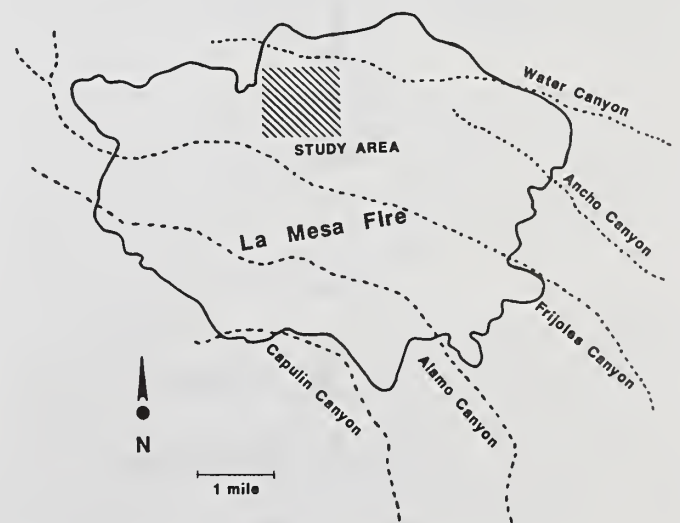


Figure 1.—Location of arthropod study area within the 1977 La Mesa Fire.

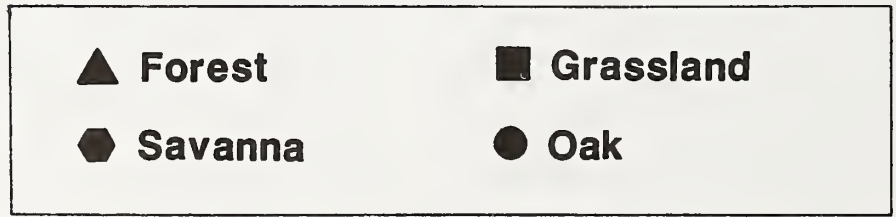
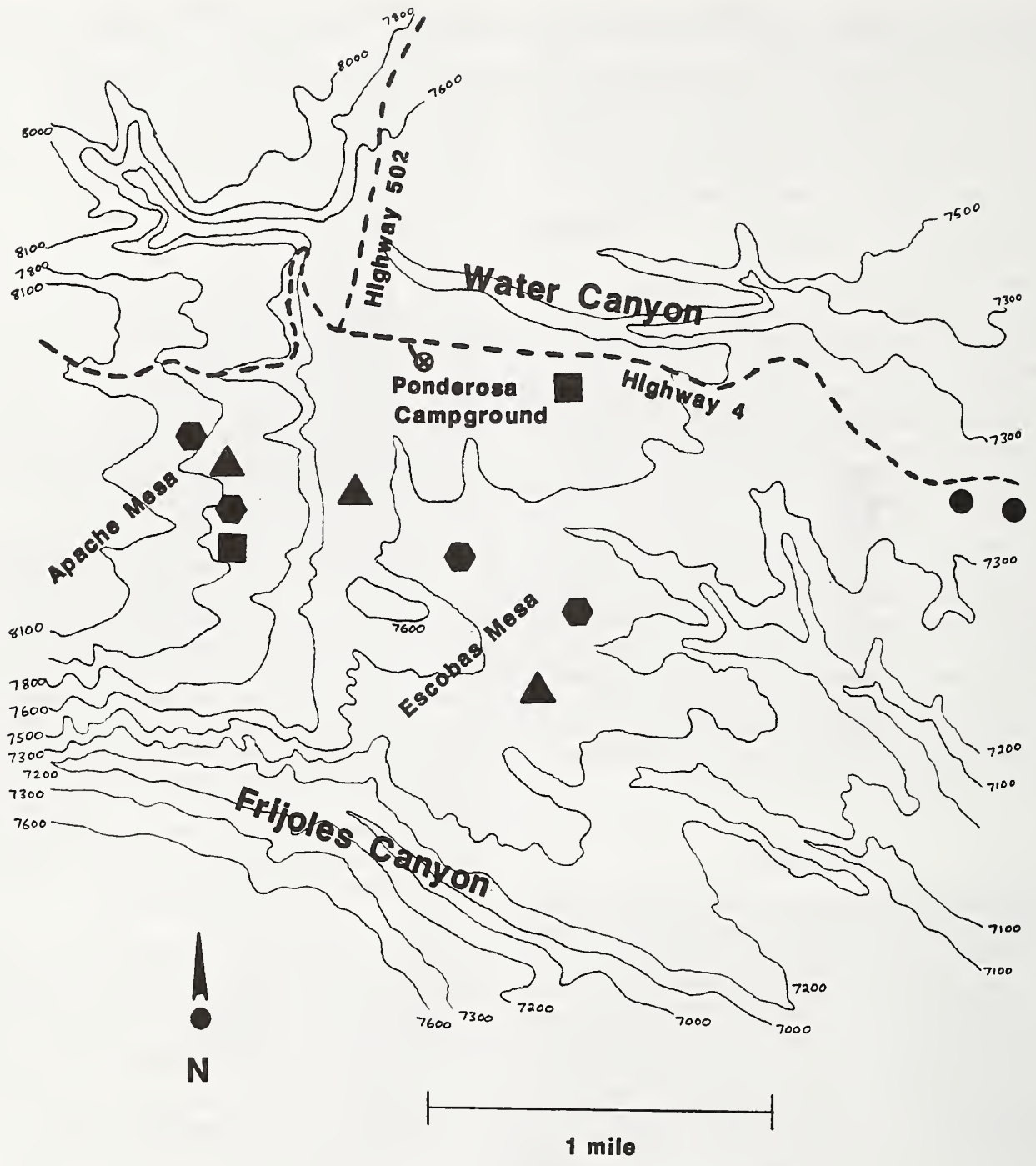


Figure 2.—Locations of arthropod pitfall trapping sites representing post-fire ponderosa pine forest, ponderosa pine savanna, Gambel oak thickets, and grassland habitats.

mid-August or mid-summer (sampling period: late July-early August), 3) early October or late summer (sampling period: late August-early October), and 4) mid-November or autumn (sampling period: mid-October-mid-November).

The labelled vials with the trap contents were taken to a laboratory at UNM where the arthropods from each vial were sorted, identified, and counted. Count data of individuals representing each species, for each date were entered onto data sheets. Only ground-dwelling or ground-surface active arthropods that are appropriately captured by pitfall traps were considered. Such target groups included ground-dwelling spiders, centipedes, millipedes, beetles, crickets, and others. Non-target, or typically non-ground-dwelling arthropods such as flies, were not recorded. Although ants are ground-dwelling arthropods, their populations are not adequately sampled by pitfall traps, and ants were not included in this study.

Many of the arthropods could not be identified to the species, genus, or in some cases family level at the time that samples were sorted and tabulated. Such species were assigned alpha-numeric codes as operational taxonomic units (OTU'S) or morpho-species. Each code consisted of two characters for classification to the order, family, genus, and species ranks. If the name of a particular rank was known, the first two letters of that name was used for that level of the code. If the name was not known, a numeric value was used, and ascending numeric values were used for additional unknown taxa of that rank. Taxonomic classification of insects to the order and family level corresponds to Arnett (1985). Taxonomic classification of non-insect arthropods to the class, order, and family levels corresponds to Borror et al. (1981).

A reference collection of voucher specimens of all species or OTU's was assembled. Those species that were not initially identified are in the process of being identified by experts of the particular taxonomic groups. OTU codes will then be changed to the actual species codes as the identifications are completed.

A data book of taxonomic codes was maintained, as well as data books for the species count data. All data read from data books were entered into a computer spreadsheet database. Various sorting routines were used to visually error-check the data within the spreadsheet.

Data analysis was performed with SAS (SAS Institute 1990) analytical software. Means of arthro-

pod count data were generated by PROC MEANS (SAS Institute 1990) to provide graphs of mean counts for the arthropods. Univariate analysis of variance (ANOVA) was performed on the data with PROC GLM (SAS Institute 1990) to provide tests for differences in arthropod abundances among the four habitats on different dates. The numerically important taxonomic groups of arthropods were identified and separate ANOVA tests were performed for each group. Duncan's multiple range test was used to determine which mean values from each habitat were significantly different between each other. The arthropod count data were log-transformed for the ANOVA tests.

PROC CANDISC (SAS Institute 1990) multivariate canonical discriminant analysis (Manly 1986) was used to test for differences among the habitats based on the combined variances from the major arthropod taxonomic groups, and to determine which arthropod groups were the best discriminators between the four habitats. Separate analyses were run for each of the sampling dates. The arthropod count data were log-transformed for the canonical discriminant analysis.

RESULTS

Many types of ground-dwelling arthropods were collected in the pitfall traps, including spiders, harvestmen, centipedes, millipedes, jumping bristletails, crickets, and several families of beetles. Many micro-arthropods such as mites and springtails were also common in the traps but they were not included in the analysis because they are more appropriately sampled by other techniques, and because of their small size they were difficult to identify to morphospecies or OTU's.

The arthropod groups that were most numerous and most consistently encountered in samples, were spiders, harvestmen, bristletails, crickets, fungus beetles, rove beetles, ground beetles, and darkling beetles (Table 1). Individuals of those taxonomic groups were consistently numerous in traps from most of the four habitats.

Total numbers of all ground-dwelling arthropods peaked during early to mid-summer (June to mid-July) in the two non-forest habitats, and in mid-summer (late-July through August) in the two forest habitats. There were significantly more arthropods in the oak habitat during the early summer than in the other three habitats (Figure 3). In mid-summer there were significantly fewer arthropods in the grassland habitat than in the

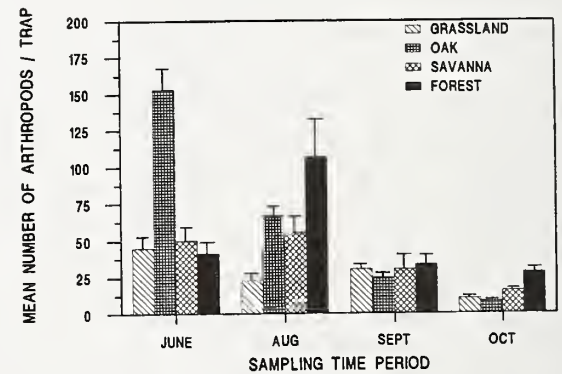
Table 1.—Major taxonomic arthropod groups sampled from pitfall traps in all four habitats.

Arthropod group	Important taxa	Trophic status
spiders (Araneae)	Clubionidae	predators
	Dictynidae	predators
	Gnaphosidae	predators
	Lycosidae	predators
	Thomisidae	predators
harvestmen (Opiliones)	two species	predators
bristletails (Microcoryphia)	<i>Mesomachilis leechi</i>	detritivores
	<i>Machilinus aurdantidicus</i>	detritivores
camel crickets (Gryllacrididae)	<i>Ceuthophilus utahensis</i>	detritivores
	<i>Ceuthophilus pallidus</i>	detritivores
	<i>Styracosceles neomexicanus</i>	detritivores
	several species	detritivores
fungus beetles (Cryptophagidae)	several species	predators
rove beetles (Staphylinidae)	several species	predators
ground beetles (Carabidae)	<i>Synchus dubius</i>	predators
	<i>Cimindis punctiger</i>	predators
	<i>Carabus taedatus</i>	predators
	<i>Eleodes extricata</i>	detritivores
darkling beetles (Tenebrionidae)	<i>Eleodes nigrinus</i>	detritivores
	<i>Eleodes planipennis</i>	detritivores

other habitats. In late summer (late August-early October) there was no significant difference in arthropod abundances among the four habitats, and in autumn (mid-October-mid November), there were significantly more arthropods in the forest habitat than the others. There was an overall trend for decreasing numbers of arthropods from early summer to autumn in the non-forested habitats, with similar declines observed after mid-summer in the forest and savanna sites (Figure 3).

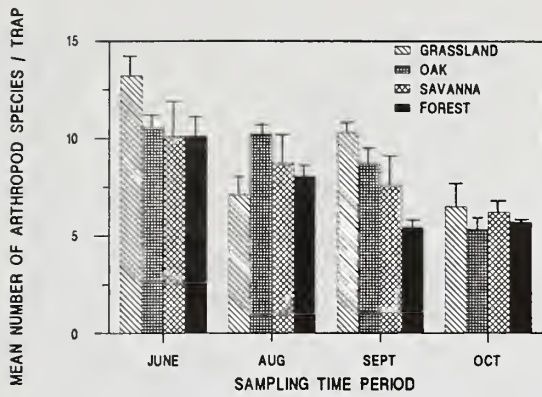
Species diversity, or total numbers of species of ground-dwelling arthropods (i.e., species richness), did not differ significantly among habitats in early summer. In mid-summer, the oak habitat had significantly more species than the grassland, but neither were significantly different from the forest or savanna (Figure 4). In late summer, the grassland and oak habitats had significantly more species than the forest, and the grassland also had significantly more species than the savanna. There was no significant difference in species diversity among habitats in autumn. There was an overall trend for decreasing species diversity from early summer to autumn (Figure 4).

Spider abundance was not significantly different among the four habitats in early summer (Figure 5). In mid-summer, spiders were significantly less abundant in the forest habitat than the oak, but neither habitat was significantly different from the savanna or grassland. In late summer, spiders were significantly less abundant in the forest habitat than the other three. In autumn, spiders were significantly more abundant in the grass habitat than



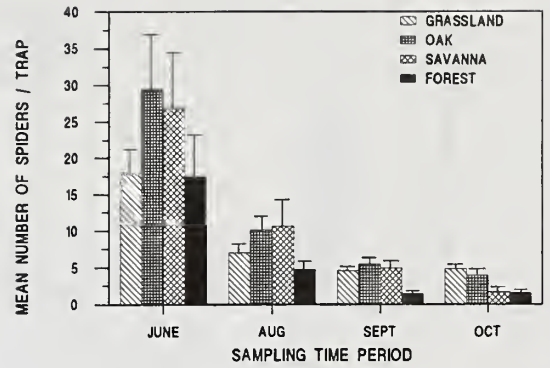
Arthropod Group	Time Period	ANOVA Pr.>F	Sign. @0.05	Duncan Groupings high \bar{x} → low \bar{x}
All individuals	June	0.0001	Yes	<u>O</u> S G F
	Aug.	0.0003	Yes	<u>F</u> <u>O</u> S G
	Sept.	0.8172	No	G F S O
	Oct.	0.0001	Yes	<u>F</u> S G O

Figure 3.—Graph of mean numbers and standard errors of all ground-dwelling arthropods per trap from each of the four post-fire habitats, and at different times of the season (June=early summer, Aug.=mid-summer, Sept.=late summer, and Oct.=autumn). ANOVA results testing differences between habitats are given below. Duncan groupings provide comparisons of each habitat (F=forest, G=grassland, O=oak, S=savanna). Letters not underscored by the same line are significantly different.



Arthropod Group	Time Period	ANOVA Pr.>F	Sign. @0.05	Duncan Groupings high \bar{x} -> low \bar{x}
All species	June	0.1670	No	<u>G O F S</u>
	Aug.	0.0586	No	<u>O S F G</u>
	Sept.	0.0092	Yes	<u>G O S F</u>
	Oct.	0.6149	No	<u>G S F O</u>

Figure 4.—Graph of mean numbers and standard errors of all arthropod species per trap from each of the four post-fire habitats, and at different times of the season (June=early summer, Aug.=mid-summer, Sept.=late summer, and Oct.=autumn). ANOVA results testing differences between habitats are given below. Duncan groupings provide comparisons of each habitat (F=forest, G=grassland, O=oak, S=savanna). Letters not underscored by the same line are significantly different.



Arthropod Group	Time Period	ANOVA Pr.>F	Sign. @0.05	Duncan Groupings high \bar{x} -> low \bar{x}
Spiders	June	0.3036	No	<u>O S G F</u>
	Aug.	0.1124	No	<u>O S G F</u>
	Sept.	0.0014	Yes	<u>O G S F</u>
	Oct.	0.0256	Yes	<u>G O F S</u>

Figure 5.—Graph of mean numbers and standard errors of spiders per trap from each of the four post-fire habitats, and at different times of the season (June=early summer, Aug.=mid-summer, Sept.=late summer, and Oct.=autumn). ANOVA results testing differences between habitats are given below. Duncan groupings provide comparisons of each habitat (F=forest, G=grassland, O=oak, S=savanna). Letters not underscored by the same line are significantly different.

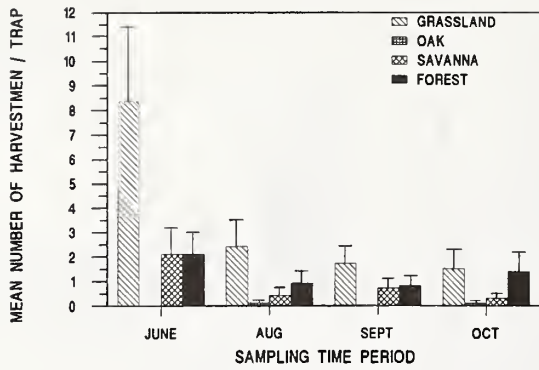
the forest or savanna. Overall spider abundance decreased from early summer to autumn (Figure 5).

Harvestmen were significantly more abundant in early summer in the grassland habitat (Figure 6). In mid-summer, harvestmen were significantly more abundant in the grassland habitat than the oak and savanna, but numbers were not significantly different between grassland and forest, or between forest, savanna, and oak. In late summer, harvestmen were significantly more abundant in the grassland than the oak habitat, but counts from both habitats were not different from forest and savanna. There were no significant differences in the abundances of harvestmen among habitats in autumn. Overall harvestmen abundance was high in the grassland in early summer but varied little thereafter, and

remained relatively constant through the seasons in the other habitats (Figure 6.)

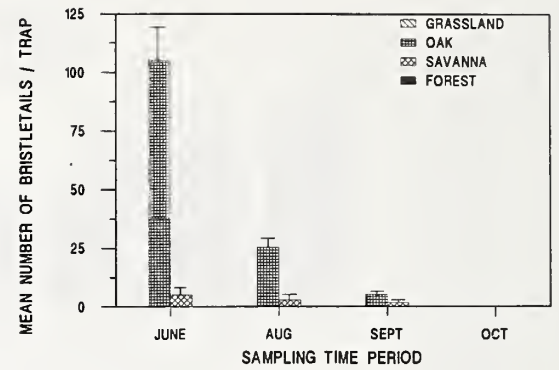
Bristletails were significantly more abundant in traps from the oak habitat in early summer, mid-summer, and late summer (Figure 7). In early and mid-summer, bristletails were significantly more abundant in the savanna sites than the grassland and forest sites where bristletail numbers were near zero throughout the sampling period. In autumn bristletail abundances were near zero, and there were no significant differences in bristletail abundance among habitats. In the oak and savanna habitats, bristletail abundances were high in early summer and declined through the seasons to near zero by autumn (Figure 7).

Cricket abundance did not differ significantly among the four habitats at any time of the season



Arthropod Group	Time Period	ANOVA Pr.>F	Sign. @0.05	Duncan Groupings high \bar{x} -> low \bar{x}
Harvestmen	June	0.0039	Yes	<u>G</u> S F O
	Aug.	0.0412	Yes	<u>G</u> F S O
	Sept.	0.0382	Yes	<u>G</u> F S O
	Oct.	0.1214	No	G F S O

Figure 6.—Graph of mean numbers and standard errors of harvestmen per trap from each of the four post-fire habitats, and at different times of the season (June=early summer, Aug.=mid-summer, Sept.=late summer, and Oct.=autumn). ANOVA results testing differences between habitats are given below. Duncan groupings provide comparisons of each habitat (F=forest, G=grassland, O=oak, S=savanna). Letters not underscored by the same line are significantly different.



Arthropod Group	Time Period	ANOVA Pr.>F	Sign. @0.05	Duncan Groupings high \bar{x} -> low \bar{x}
Bristletails	June	0.0001	Yes	<u>O</u> S F G
	Aug.	0.0001	Yes	<u>O</u> S F G
	Sept.	0.0001	Yes	<u>O</u> S G F
	Oct.	0.1347	No	O G F S

Figure 7.—Graph of mean numbers and standard errors of bristletails per trap from each of the four post-fire habitats, and at different times of the season (June=early summer, Aug.=mid-summer, Sept.=late summer, and Oct.=autumn). ANOVA results testing differences between habitats are given below. Duncan groupings provide comparisons of each habitat (F=forest, G=grassland, O=oak, S=savanna). Letters not underscored by the same line are significantly different.

(Figure 8). Overall cricket abundance was greatest during mid-summer.

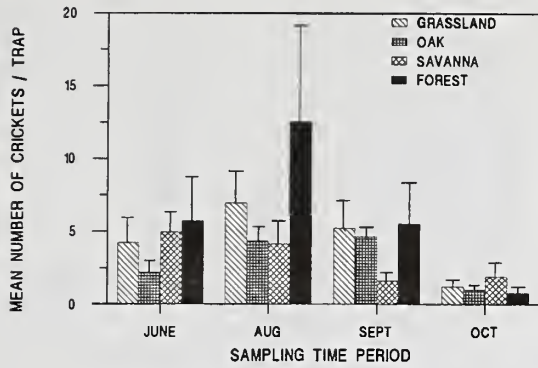
Fungus beetles were significantly more abundant in the forest and savanna habitats than the grassland or oak habitats in early summer, and mid-summer (Figure 9). In late summer, the numbers of fungus beetles did not differ significantly among the four habitats. In autumn, fungus beetles were significantly more abundant in the forest habitat than the other three. Overall fungus beetle abundance peaked during the mid-summer period (Figure 9).

Rove beetles were significantly more abundant in the forest habitat in early summer and autumn, and the forest and savanna habitats in mid-summer and late summer (Figure 10). Overall rove beetle abundance tended to increase through the seasons (Figure 10).

Ground beetles were significantly more abundant in the oak habitat in early summer and mid-summer (Figure 11). There was no significant difference in ground beetle counts among the four habitats in late summer and autumn. Overall ground beetle abundance was greatest during the mid-summer period, and declined to low levels by autumn (Figure 11).

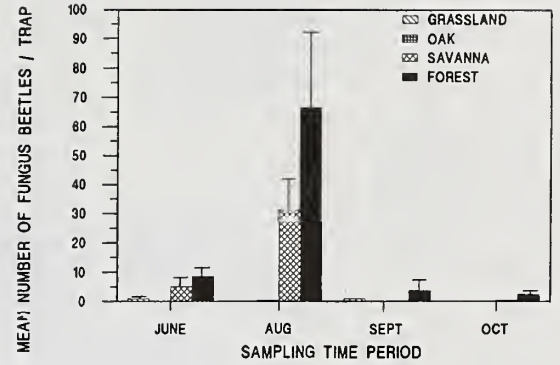
Darkling beetles were significantly more abundant in the grassland habitat in early summer, and the oak habitat in mid-summer (Figure 12). There was no significant difference in darkling beetle abundance among the four habitats in late summer or autumn. Overall darkling beetle abundance was greatest in early summer, and declined through the rest of the season (Figure 12).

Multivariate canonical discriminant analysis of differences among habitats based on abundance



Arthropod Group	Time Period	ANOVA Pr.>F	Sign. @0.05	Duncan Groupings high \bar{x} -> low \bar{x}
Crickets	June	0.7739	No	<u>S F G O</u>
	Aug.	0.8414	No	<u>G O F S</u>
	Sept.	0.1650	No	<u>O G F S</u>
	Oct.	0.8014	No	<u>S G O F</u>

Figure 8.—Graph of mean numbers and standard errors of crickets per trap from each of the four post-fire habitats, and at different times of the season (June=early summer, Aug.=mid-summer, Sept.=late summer, and Oct.=autumn). ANOVA results testing differences between habitats are given below. Duncan groupings provide comparisons of each habitat (F=forest, G=grassland, O=oak, S=savanna). Letters not underscored by the same line are significantly different.



Arthropod Group	Time Period	ANOVA Pr.>F	Sign. @0.05	Duncan Groupings high \bar{x} -> low \bar{x}
Fungus Beetles	June	0.0340	Yes	<u>F S G O</u>
	Aug.	0.0001	Yes	<u>F S O G</u>
	Sept.	0.5830	No	<u>F G S O</u>
	Oct.	0.0015	Yes	<u>F S O G</u>

Figure 9.—Graph of mean numbers and standard errors of fungus beetles per trap from each of the four post-fire habitats, and at different times of the season (June=early summer, Aug.=mid-summer, Sept.=late summer, and Oct.=autumn). ANOVA results testing differences between habitats are given below. Duncan groupings provide comparisons of each habitat (F=forest, G=grassland, O=oak, S=savanna). Letters not underscored by the same line are significantly different.

data for the major taxonomic arthropod groups resulted in overall significant differences among habitats, at all four times of the season (Table 2a-d).

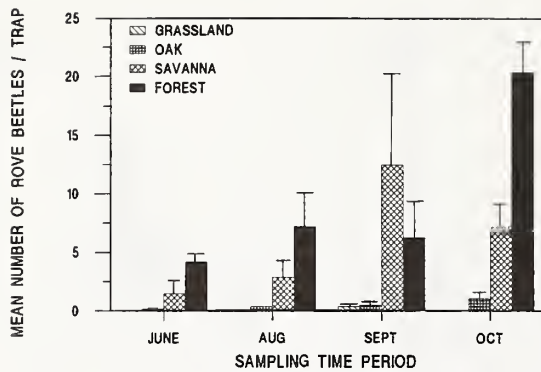
Examination of standardized canonical coefficients for each of the arthropod groups revealed that bristletails, ground beetles, fungus beetles and rove beetles contributed to the discrimination of habitats in early summer and mid-summer (Table 2a-d). Bristletails, spiders, ground beetles, and crickets accounted for the discrimination of habitats in late summer, and rove beetles and fungus beetles accounted for most of the discrimination in autumn (Table 2a-d).

Graphical plots of canonical variate scores for individual traps from each habitat type based on canonical scores for the first two discriminant functions, illustrate the discrimination of the four habi-

tats based on abundances of the major arthropod groups (Figure 13a-d). The scores for traps from forest, grassland, and oak habitats were very different from each other at each sample period. Scores for savanna traps tended to be intermediate between those of the other three habitats, although they were most similar to the forest habitat (Figure 13a-d).

DISCUSSION

Results of this study reveal that there were significant differences in overall abundances of ground-dwelling arthropods among the four habitat types, and differences in the abundances of the major taxonomic arthropod groups among the four habitats. Significantly higher numbers of all arthro-

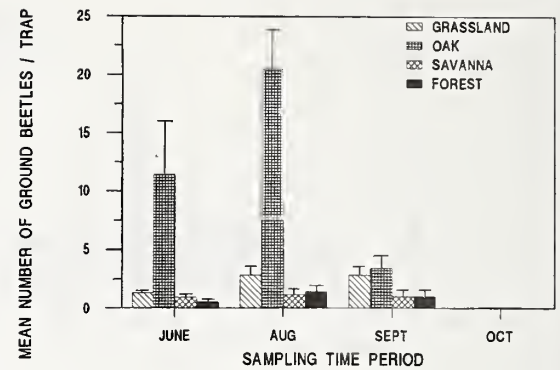


Arthropod Group	Time Period	ANOVA Pr.>F	Sign. @0.05	Duncan Groupings high \bar{x} -> low \bar{x}
Rove Beetles	June	0.0001	Yes	<u>F</u> S O G
	Aug.	0.0047	Yes	<u>F</u> S O G
	Sept.	0.0456	Yes	<u>S</u> F G O
	Oct.	0.0001	Yes	<u>F</u> S O G

Figure 10.—Graph of mean numbers and standard errors of rove beetles per trap from each of the four post-fire habitats, and at different times of the season (June=early summer, Aug.=mid-summer, Sept.=late summer, and Oct.=autumn). ANOVA results testing differences between habitats are given below. Duncan groupings provide comparisons of each habitat (F=forest, G=grassland, O=oak, S=savanna). Letters not underscored by the same line are significantly different.

pod individuals in the oak habitat in early summer, forest, oak, and savanna in mid-summer, and forest in autumn may be attributed to high numbers of particular major taxonomic groups in those habitats at those times of the season. During those time periods, the oak habitat was dominated by bristletails, spiders, and ground beetles, and the forest and savanna habitats were dominated by fungus beetles, and rove beetles. Harvestmen and darkling beetles were most abundant in grassland habitats, but since the numbers of those arthropods were low relative to the other arthropod groups the grassland sites had consistently low overall arthropod abundances.

Total arthropod species diversity did not change much among the four habitats, even though abundances of various arthropod groups did. Such re-



Arthropod Group	Time Period	ANOVA Pr.>F	Sign. @0.05	Duncan Groupings high \bar{x} -> low \bar{x}
Ground Beetles	June	0.0001	Yes	<u>O</u> G S F
	Aug.	0.0001	Yes	<u>O</u> G F S
	Sept.	0.1048	No	<u>G</u> O S F
	Oct.	0.6017	No	<u>S</u> O F G

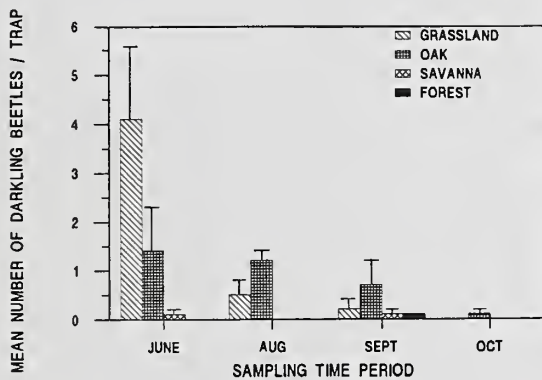
Figure 11.—Graph of mean numbers and standard errors of ground beetles per trap from each of the four post-fire habitats, and at different times of the season (June=early summer, Aug.=mid-summer, Sept.=late summer, and Oct.=autumn). ANOVA results testing differences between habitats are given below. Duncan groupings provide comparisons of each habitat (F=forest, G=grassland, O=oak, S=savanna). Letters not underscored by the same line are significantly different.

sults indicate that the different groups contributed differentially to the total numbers of species in each habitat. Thus, species composition changed between the habitats, but overall species richness or diversity did not.

Seasonal trends in total arthropod abundance reflected the seasonal trends in the abundances of the individual major taxonomic groups. Bristletails, spiders, harvestmen, and darkling beetles were all most abundant in early summer, with declining populations through the season to autumn. Such a pattern probably reflects the life-history patterns of these arthropods. Bristletails, spiders, and harvestmen all reproduce once a year, with juveniles present in the spring and early summer, maturing to adults by mid-summer. Adults and juveniles of these arthropods occur in the same habitats. Many

juvenile bristletails, spiders, and harvestmen were present in the early summer. Mortality among juveniles over time may account for the seasonal decline in these arthropods. In contrast, darkling beetles have distinct larval and adult stages, where the larvae live in the soil and are not caught in pitfall traps, and adults are active on the ground surface, and are caught in pitfall traps. All darkling beetles captured were adults. The seasonal pattern in darkling beetle abundance indicates that adult activity is greatest in the early summer for the three dominant species of *Eleodes*.

Crickets, fungus beetles, and ground beetles were most abundant in the middle of the summer. Perhaps the activity of these insects is synchronous with the summer rainy season. Rove beetles were most abundant late in the summer. Most of the species of rove beetles found in the traps were very small, indicating that they probably feed on micro-



Arthropod Group	Time Period	ANOVA Pr.>F	Sign. @0.05	Duncan Groupings high \bar{x} → low \bar{x}
Darkling Beetles	June	0.0007	Yes	<u>G O S F</u>
	Aug.	0.0001	Yes	<u>O G F S</u>
	Sept.	0.4662	No	<u>O G S F</u>
	Oct.	0.4635	No	<u>O G F S</u>

Figure 12.—Graph of mean numbers and standard errors of darkling beetles per trap from each of the four post-fire habitats, and at different times of the season (June=early summer, Aug.=mid-summer, Sept.=late summer, and Oct.=autumn). ANOVA results testing differences between habitats are given below. Duncan groupings provide comparisons of each habitat (F=forest, G=grassland, O=oak, S=savanna). Letters not underscored by the same line are significantly different.

Table 2.—Results of canonical discriminant function analysis for arthropod taxonomic group data among four habitats.

a. Sample Period: June (early summer)			
Overall Multivariate F test (Pr.>F): 0.0001			
Discriminant Functions:	1	2	3
Significance (Pr.>F):	0.0001	0.0001	0.0632
Eigenvalue:	14.99	5.99	0.56
Cumulative variance:	69%	97%	100%
Standardized Canonical Coefficients			
Darkling Beetles	0.39	0.50	0.86
Ground Beetles	0.91	0.69	0.89
Fungus Beetles	0.06	-1.08	0.12
Rove Beetles	-0.13	-1.60	1.20
Spiders	0.12	0.08	-0.96
Crickets	-0.18	0.23	-0.59
Harvestmen	0.29	0.91	0.67
Bristletails	3.11	-1.46	0.25
b. Sample Period: August (mid-summer)			
Overall Multivariate F test (Pr.>F): 0.0001			
Discriminant Functions:	1	2	3
Significance (Pr.>F):	0.0001	0.0003	0.4119
Eigenvalue:	13.59	1.98	0.22
Cumulative variance:	86%	99%	100%
Standardized Canonical Coefficients			
Darkling Beetles	0.31	-0.42	0.25
Ground Beetles	1.26	-0.27	0.78
Fungus Beetles	0.44	1.16	-0.09
Rove Beetles	0.25	0.74	0.54
Spiders	-0.29	0.07	-0.78
Crickets	0.20	-0.12	0.07
Harvestmen	-0.55	-0.21	-0.08
Bristletails	2.61	0.91	-0.54
c. Sample Period: September (late summer)			
Overall Multivariate F test (Pr.>F): 0.0001			
Discriminant Functions:	1	2	3
Significance (Pr.>F):	0.0001	0.0527	0.2410
Eigenvalue:	2.89	0.76	0.36
Cumulative variance:	72%	91%	100%
Standardized Canonical Coefficients			
Darkling Beetles	0.15	0.01	-0.01
Ground Beetles	0.07	1.16	-0.19
Fungus Beetles	-0.24	0.15	-0.20
Rove Beetles	-0.27	-0.76	0.63
Spiders	0.67	0.67	0.55
Crickets	0.16	-1.02	-0.60
Harvestmen	-0.44	0.41	0.14
Bristletails	1.16	-0.64	0.11
d. Sample Period: October (autumn)			
Overall Multivariate F test (Pr.>F): 0.0001			
Discriminant Functions:	1	2	3
Significance (Pr.>F):	0.0001	0.0383	0.2941
Eigenvalue:	12.27	0.96	0.32
Cumulative variance:	90%	98%	100%
Standardized Canonical Coefficients			
Darkling Beetles	-0.90	-0.12	0.70
Ground Beetles	0.17	-0.36	0.26
Fungus Beetles	0.44	1.06	0.56
Rove Beetles	2.76	-1.11	0.32
Spiders	0.62	0.05	0.65
Crickets	-0.07	-0.60	-0.18
Harvestmen	0.43	1.30	0.25
Bristletails	-0.16	-0.49	0.88

arthropods such as springtails and mites. Springtail and mite populations probably increase following summer rains, providing increased food resources for rove beetles late in the season.

The relatively high numbers of bristletails, spiders, and ground beetles in the oak habitat indicates that some features of the environmental char-

acteristics of those habitats are more favorable to these three arthropod groups. An important feature of the oak habitats that is different from the other three habitats is the oak leaf litter that covers the ground in the Gambel oak thickets. This oak leaf litter apparently provides a favorable food resource for bristletails in the early summer. The large numbers of bristletails in the oak leaf litter may in turn

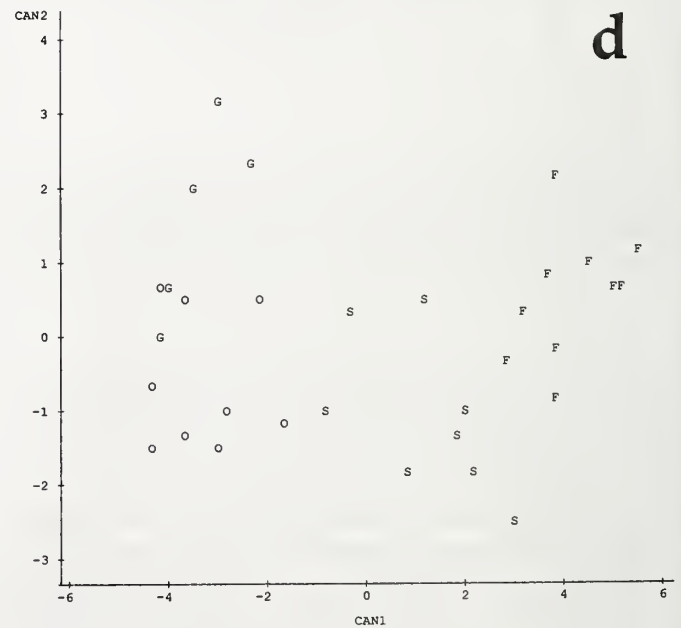
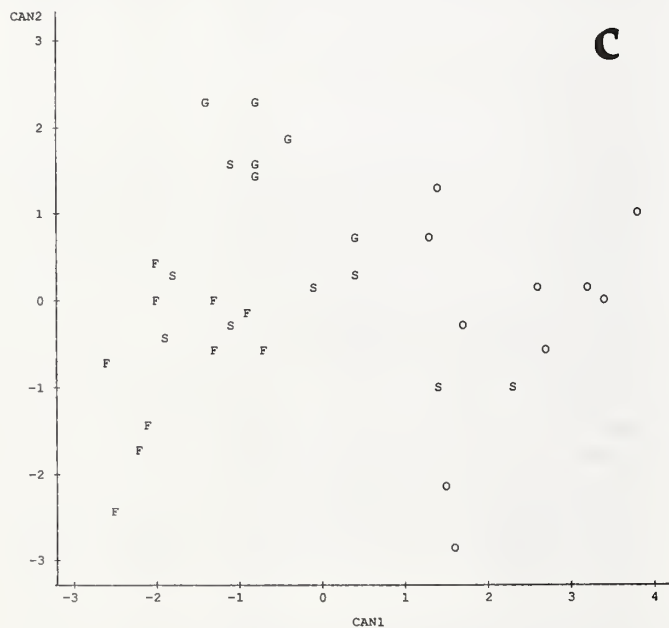
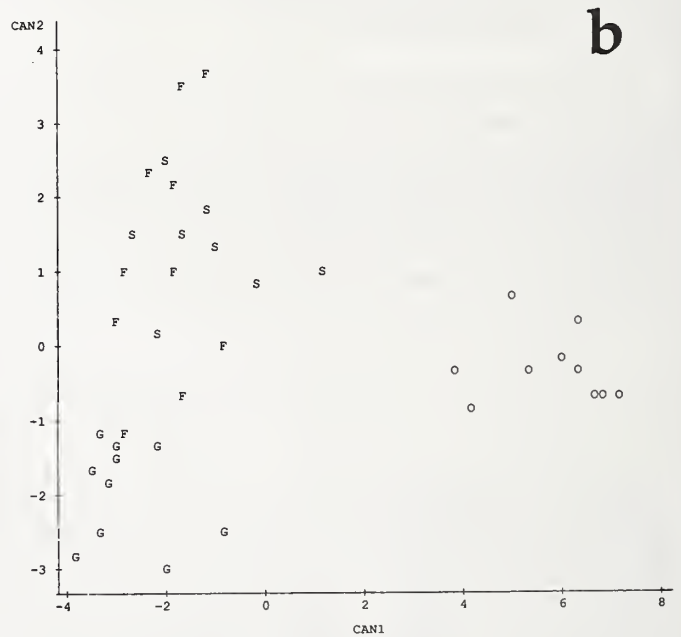
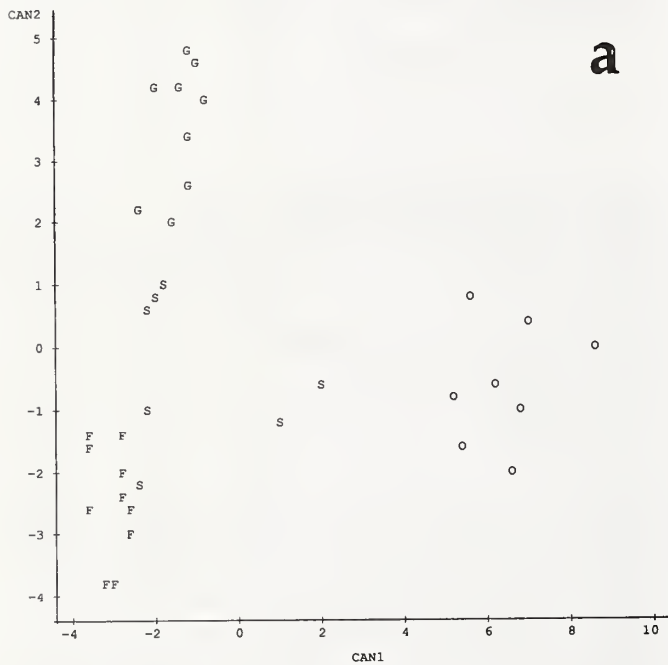


Figure 13a-d.—Plots of canonical variate scores for traps from each habitat from each of the sampling dates (a. June=early summer, b. Aug.=mid-summer, c. Sept.=late summer, and d. Oct.=autumn).

support large populations of predators such as spiders and ground beetles.

Fungus beetles and rove beetles are typically abundant in forest litter. The relatively high numbers of fungus and rove beetles from the forest and savanna habitats in this study is consistent with known habitat preferences for these beetles.

Darkling beetles and harvestmen were most abundant in the open grassland habitats. The most common species of darkling beetle, *Eleodes extricatus*, is usually found in open piñon-juniper woodlands, as are the harvestmen. The open vegetation canopy of the grassland areas may provide a habitat similar to the open piñon-juniper habitats found at elevations slightly below the La Mesa Fire area. Such open canopy habitats are apparently preferred by these arthropods.

Results from this study demonstrate that different burn intensities from the La Mesa Fire did change the composition of ground-dwelling arthropods occurring in four post-fire vegetational habitat types. These findings are consistent with other studies of post-fire responses of ground-dwelling arthropods in forest ecosystems (Harris & Whitcomb 1974, Abbott 1984, Majer 1984, Touyama et al. 1989). Pippin and Nichols (This Volume) found immediate reductions in arthropod diversity and abundances apparently caused by mortality from the La Mesa Fire. In contrast, this study was conducted 16 years after the La Mesa Fire, and the differences found in arthropod assemblages between post-fire habitats are probably due to arthropod preferences for different habitats resulting from differences in post-fire vegetation, not post-fire recolonization of areas where the pre-fire arthropod fauna was destroyed or altered by the fire. Other studies of arthropod response to forest fires have found that several years after fires, different species or groups of arthropods are found in different post fire habitats as a result of habitat selection (Harris & Whitcomb 1974, Dindal & Metz 1977).

Implications of these findings at the La Mesa Fire are pertinent to ecosystem processes where arthropods probably regulate rates of decomposition of ground-level vegetation litter. Detritivores such as bristletails, crickets, and darkling beetles probably have major roles in nutrient cycling in forest ecosystems, and predators such as spiders and ground beetles may have important roles regulating populations of detritivores. Different taxonomic groups of detritivores and predators in the four habitats reveals that the trophic structure varies between each habitat, and thus the decomposi-

tion processes and rates are also likely to differ. For example, Springett (1979) found that post-fire effects on detritivore arthropods led to changes in litter decomposition rates. Any future studies on decomposition and nutrient cycling in post-burn habitats of the La Mesa Fire should be concerned with differences in arthropod trophic groups.

Different assemblages of ground-dwelling arthropods with dissimilar seasonal abundance patterns in the four post-fire habitats reveal that food resources to higher level vertebrate predators are not the same among the four habitats. Ground-level foraging animals such as small mammals, birds, and reptiles and amphibians, will encounter different prey items and prey abundances among the four post-fire habitats. Changes in arthropod prey composition will probably have important implications to the foraging strategies, and perhaps species composition of vertebrate predators in different post-fire habitats in the La Mesa Fire area.

Ground-dwelling arthropods are important components of forest ecosystems as regulators of nutrient cycling, and as food resources for higher trophic level consumers (Mattson 1977). Future studies of forest ecosystem processes or biological community dynamics in the La Mesa Fire area should address the roles and attributes of these animals relative to the study questions.

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Elk Response to the La Mesa Fire and Current Status in the Jemez Mountains

Craig D. Allen¹

Abstract.—Faunal remains in local archeological sites and historic information suggest that elk populations in the Jemez Mountains were low from ca. 1200 A.D. through ca. 1900 A.D., when they were extirpated from this region. Elk were reintroduced to the Jemez country in 1948 and 1964–1965, and their population apparently grew exponentially, reaching 1000 animals in the 1970's and about 7000 by 1991.

Elk populations in Bandelier National Monument and adjoining areas increased rapidly after the 1977 La Mesa Fire. Winter use by elk in the La Mesa Fire area, centered on Bandelier, grew from about 100 animals in 1978 to around 1500 elk by 1992. The dramatic increase in the Bandelier elk herd (an annual growth rate of 21.3% and a 3.6 year population doubling time) was due in part to the creation of about 6000 hectares of grassy winter range in and around the park by the La Mesa Fire. Some of this local population increase reflects concentration of elk into this favorable wintering habitat from surrounding portions of the Jemez Mountains.

Existing data are inadequate to determine whether elk populations are still growing rapidly in the Jemez Mountains. While annual aerial surveys since 1990 in Bandelier reveal no clear population trend, a variety of observations demonstrate increasing elk use of lower elevation areas. Negative resource impacts from today's high elk populations are beginning to be widely noted across the Jemez Mountains, especially in high-use portions of the Bandelier National Monument area. Affected resources range from plant communities to soils and even archeological sites. Given the large uncertainties associated with the current data on elk populations, care should be taken to avoid further population increases until the resource impacts of this new phenomenon (large numbers of elk) can be identified, desirable population levels identified (based to a significant degree upon ecological information and resource carrying capacities, as well as social considerations), and appropriate cooperative management strategies implemented.

INTRODUCTION

The habitat changes associated with the La Mesa Fire have benefited some species, prominently including elk. This paper reviews elk response to the La Mesa Fire, and provides an overview of the past and current status of this species in the southeastern Jemez Mountains.

Prehistoric Elk Abundance

Rocky Mountain elk (*Cervus elaphus nelsoni*) are considered native to the Jemez Mountains (Bailey 1931). Figure 1 shows a prehistoric elk petroglyph,

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Figure 1.—Prehistoric elk petroglyph, White Rock Canyon near Bandelier National Monument. Horizontal scale is 10 cm long with 1 cm subdivisions, while the vertical rod is divided into 25 cm sections. Photograph by Betty Lillienthal, ARMS Site Files collection, Laboratory of Anthropology, Santa Fe, New Mexico.

etched into a basalt boulder in White Rock Canyon near Bandelier National Monument. Elk were present here into the late 19th Century, but by 1906 they had probably been eliminated from the Jemez country (Bailey 1931:40).

There is no evidence that elk were ever abundant during prehistoric or historic times in the Bandelier area. Table 1 displays a compilation of ungulate faunal remains recovered from 45 local archeological sites (Allen—in review), almost all dating to before 1500 A.D. Out of a total of 218 ungulate individuals which were determined to species (based upon a total of 646 identified bones), only three individual elk were determined (based upon nine identified elk bones); eight of these elk bones date from the late 1800's, while the ninth was a 15th Century bone tool which might easily have been imported. While deer remains dominate local archeological faunal assemblages, bighorn sheep, pronghorn, and even bison remains exceed those of elk. (Since bison were absent from the local fauna their remains were presumably traded into the

Bandelier area from the Great Plains to the east.) Kay (1990) reviews various factors that could bias the relative proportions of faunal remains excavated from archeological sites (e.g., differential preservation or field disposal of bone from larger ungulates by butchering at the kill site), concluding that these processes would not unduly discriminate against the presence of elk materials. If true, the paucity of local elk remains suggests low elk populations in and around today's Bandelier National Monument during the main period of prehistoric occupation (roughly 1200–1500 A.D.).

The large sample of excavated faunal remains (at least 226 ungulate individuals) from nearby Arroyo Hondo (Lang and Harris 1984), outside Santa Fe, similarly shows few elk remains (Table 1). The absence of any elk remains during the period of peak human population suggests that ancestral Puebloan peoples may have eliminated local elk populations (Lang and Harris 1984:49).

Indeed, a strong case has recently been made for prehistoric aboriginal control of elk numbers across

Table 1.—Ungulate remains recovered from archeological sites in and around the Jemez Mountains.

	Minimum Number of Individuals					
	Deer	Elk	Bighorn	Antelope	Bison	Ungulate
Jemez Mts. (45 sites)	154	3	30	24	7	58
Arroyo Hondo (Santa Fe)	157	6	—	56	7	213
Total	311	9	30	80	14	271

	Number of Identified Specimens (Minimum Estimate)					
	Deer	Elk	Bighorn	Antelope	Bison	Ungulate
Jemez Mts. (45 sites)	515	9	32	24	66	1,126
Arroyo Hondo (Santa Fe)	300	9	—	77	11	568
Total	815	18	32	101	77	1,694

widespread portions of the western U.S. and Canada (Kay 1990 and 1994, Martin and Szuter—in review). Kay (1994) bases his “aboriginal overkill” hypothesis of elk population control on various factors which also would have applied to Southwestern Pre-Columbian peoples, including: 1) the efficiency of Native American predation, which included cooperative hunting, use of dogs, food storage, ability to switch to non-ungulate foods, and various effective hunting techniques (such as running down elk in deep snow); 2) optimal-foraging studies which suggest that elk would have been a preferred prey species; 3) low elk numbers in the ungulate species remains found in archaeological contexts compared with the ratios of present ungulate communities; 4) the high numbers of Native Americans which were present in many areas before Old World diseases drastically reduced the aboriginal populations; 5) a presumed lack of effective Native American conservation practices; and 6) synergism between human and carnivore predation in suppressing prey populations.

Focused more specifically on the Southwest, Osborn (1993) reviews rationales for high levels of ungulate utilization by prehistoric Native Americans, suggesting that the stereotype of the Anasazi-Hohokam-Mogollon peoples as farmers understates the importance of big game food resources, and thus hunting, in their subsistence patterns. Certainly crossing the mesas of the Bandelier area during Anasazi times would have required running a gauntlet of protein-hungry, crop-defending humans. Overall, it is plausible to envision that elk numbers in the Jemez Mountains area were suppressed by the large numbers of ancestral

Puebloans who inhabited this region after circa 1200 A.D.

Historic Elk Abundance

Historic documents further suggest low elk populations in the Jemez Mountains area since Anglo-American contact. In the 1880’s Adolph Bandelier attributed the local scarcity of game, including elk, to Native American hunting (Bandelier 1892:141). Henderson and Harrington (1914:3) state that for the overall American Southwest: “A study of the literature of early exploration does not indicate general distribution of vast herds of antelope, elk, and deer—and especially this is true of elk”. More particularly, by the latter half of the 1800’s elk were certainly scarce in the Jemez Mountains area (Henderson and Harrington 1914:2–3), becoming extinct around the turn of the century. It is curious that the grassy, fire-maintained, open forests which characterized much of the Jemez landscape in earlier centuries apparently supported so few elk. Perhaps the pre-1880 recurrence of landscape-wide fires across the Jemez Mountains every 20 or so years (Allen et al. 1995, Touchan et al., This Volume) contributed to the effects of human and wild carnivore predation to constrain elk populations by occasionally imposing limited forage availability across broad portions of their mountain refuges, forcing more elk down into areas where human hunting pressures were greater. In any event, by the time of Vernon Bailey’s biological surveys of the Jemez area in 1904 and 1906 elk were apparently extirpated. As he stated (Bailey 1931:40):

In 1906, the writer saw a fair-sized elk horn in a good state of preservation on the fence at a Mexi-

can ranch near Jemez Hot Springs, and was told that it was picked up on Cebolla Creek in the central part of the Jemez Mountains. He could get no records of elk in the Jemez Mountains in recent years, but has no doubt that they once covered these mountains, which are in close connection with the San Juan Range.

Overall, the available evidence suggests that since the La Mesa Fire the Jemez Mountains population of reintroduced elk has grown to levels far greater than anything known since at least A.D. 1200.

ELK POPULATION TRENDS IN THE JEMEZ MOUNTAINS

Reintroduction and Population Growth

In 1948 the New Mexico Game and Fish (NMGF) Department released 21 cows/calves and 7 bulls of *Cervus elaphus nelsoni*, from Yellowstone National Park, into the Jemez Mountains in "the Clear Creek area" on the south side of the San Pedro parks (letter of 19 Dec., 1961, from NMGF Director Fred Thompson to Bandelier National Monument). Bandelier's 1948 "Annual Wildlife Report" estimates a population of 5 elk in the park, noting:

This is the first report of elk on the Bandelier area. In early May of this year 28 elk were introduced to the higher Jemez (m)ountains to the north and east (sic—should be west) of the monument by the State Fish and Game Department. On July 9 the tracks of a bull and cow elk were observed on trails in the upper portions of Bandelier (*author's note*: likely on the mesa south of Upper Crossing at about 2200 m elevation, given the different park boundary of that time). On September 15 four bulls were seen in the lower end of Alamo Canyon near our southern boundary. We shall watch with keen interest the activities of these newcomers during the winter months (S. Keefe, 25 Sept., 1948, report on file at Bandelier National Monument).

By 1961 NMGF estimated a population of at least 200 elk in the Jemez Mountains, all descendants of the 28 founders (letter of 19 Dec., 1961, from NMGF on file at Bandelier). Yet from 1948–1965 elk were rarely seen in Bandelier, with park population estimates ranging from 0 to 6 individuals (incomplete set of annual wildlife reports on file at Bandelier). The park apparently did not provide particularly good elk habitat at that time, despite

the increased protection that it offered from poaching and other human disturbances. In 1964–1965 another 58 elk from the Jackson Hole area were released into the mountains of Los Alamos County adjacent to Bandelier (White 1981).

The elk population in the Jemez Mountains (delineated as Unit 6 by NMGF) has apparently exhibited exponential population growth over at least portions of the past 47 years (Figure 2). If the population grew from 28 elk in 1948 to 200 animals in 1961, this represents a 16.3% annual increase and a 4.6 year doubling time. By 1989 the Unit 6 elk herd had grown to an estimated level of roughly 6000–8000 individuals, with about 3500 elk summering on the Baca Location (R. Isler, NMGF—1989 personal communication); this remains the range of "official" NMGF population estimates (L. Fisher—1995 personal communication). However, note that a long-time Unit 6 wildlife officer has consistently estimated only 3500–5000 elk in the Jemez area for the period 1990–1995 (P. Cassidy—1995 personal communication). For the time period 1948–1992, given the increase from the original 28 planted elk to an estimated 7000 elk, the calculated annual growth rate for the Jemez elk herd is 13.4%, with a doubling time of 5.5 years. If the elk population is assumed to have grown from 200 animals in 1961 to the median NMGF estimate of 7000 animals in 1992, this indicates a 12.2% annual population growth, with a doubling time of 6.0 years. This large population growth occurred despite significant increases in permitted elk hunting in Unit 6 since 1980 (Table 3).

Rapid growth of elk populations has also occurred in the state as a whole. By 1910 all elk populations in New Mexico were considered extirpated (Bailey 1931:40–44, Findley 1987:141–142), probably due to uncontrolled hunting and competition for herbaceous forage with domestic livestock. Rocky Mountain elk reintroductions into New Mexico began in 1911 (Bailey 1931:41). Elk populations grew to estimated statewide population levels of 32 in 1911 (Bailey 1931:41), "about 60" in 1912 (Findley 1987:142), 126 in 1914 (compiled from Bailey 1931:41), 750 in 1923 (Findley 1987), 680 in 1926 (Ligon 1927:71), between 3500 (Bryant and Maser 1982) and "perhaps 4000" (Findley 1987) in 1934, "almost 11,000" in 1967 (Findley 1987), and 10–12,000 elk by 1976 (Bryant and Maser 1982). The 1992 population was estimated to be 40,000 elk (D. Weybright, NMGF—1992 personal communication). If there were 10,800 elk in 1967 and 40,000 in 1992, this would indicate a 5.4% annual growth rate and a 13.2 year doubling time over this period.

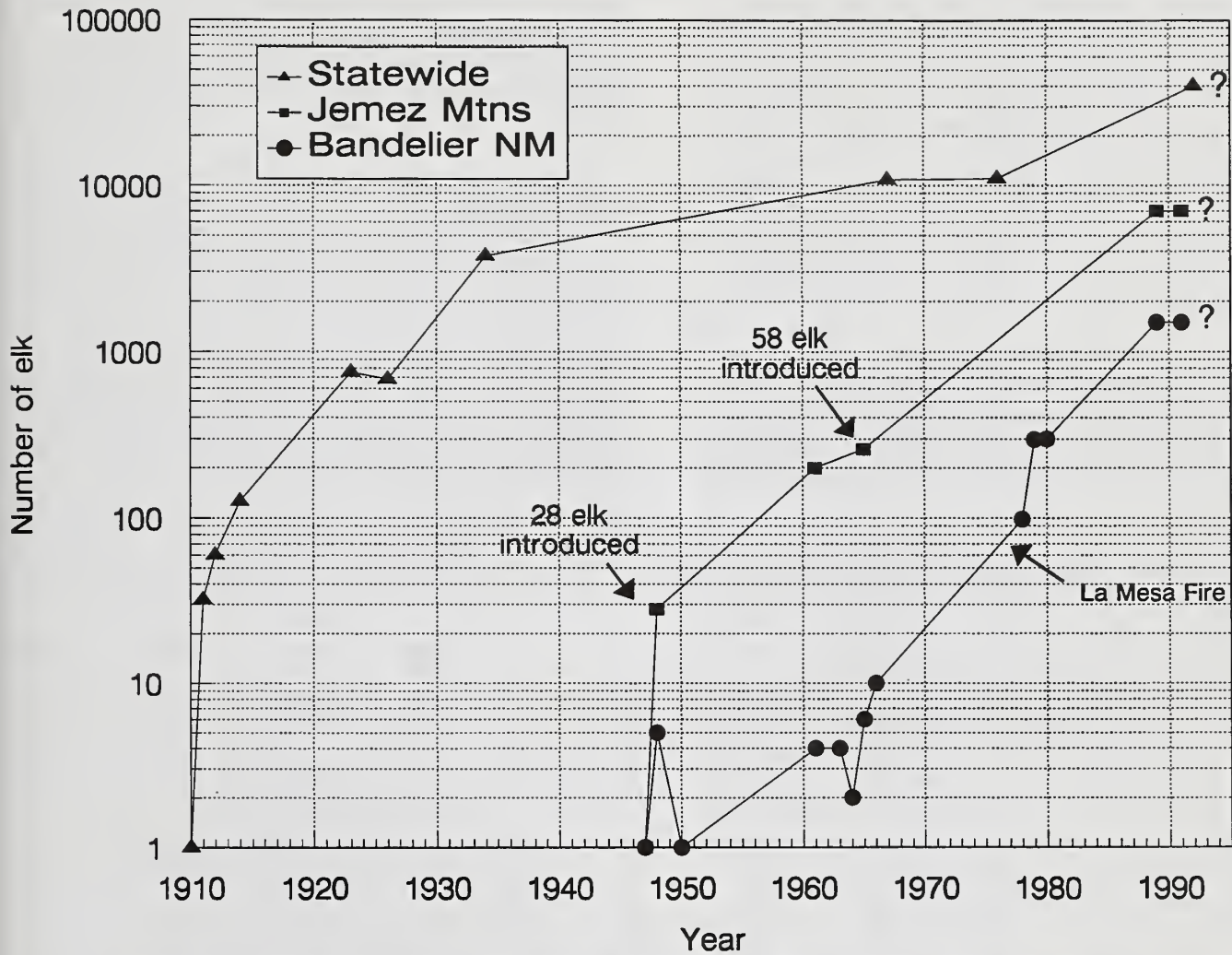


Figure 2.—Estimated changes in elk populations in New Mexico (“Statewide”), the Jemez Mountains, and Bandelier National Monument. Note the logarithmic scale on the y-axis.

Alternatively, if we assume 11,000 elk in 1976 and still 40,000 in 1992, this translates into a 8.4% annual growth rate and a 8.6 year doubling time for the period 1976–1992. It is thought by NMGF that the total number of elk in New Mexico has increased little, if at all, since 1992 because of high harvest levels (L. Fisher—1995 personal communication). Statewide, the annual (legal) elk harvest has increased from about 2800 in 1985 to 11,000 in 1993, with a concurrent increase in cow elk taken from 800 to 5,000 (L. Fisher—1995 personal communication).

Uncertainties in Elk Population Data

It is difficult to accurately determine elk population parameters in forested, montane wildlands like the Jemez Mountains. While aerial surveys are

widely used, results are biased by numerous factors including speed and height of flight, transect width, terrain, variation in observers and pilots, time of day, snow conditions, and low elk sightability in many forested habitats (Caughley 1974, Davis and Winstead 1980, Samuel et al. 1987, Kie 1988). The probability of sighting elk in the Rocky Mountains is quite variable and usually less than 50% (Bear et al. 1989). During winter surveys bulls are typically alone or in small bachelor groups which are relatively hard to spot from the air compared to the larger cow/calf bands, introducing another bias. Thus NMGF estimates of elk populations in particular areas (like Unit 6) are rather imprecise, inasmuch as they are largely based upon limited, non-systematic, aerial surveys and the field impressions of local wildlife officers.

These same sampling biases also affect recent aerial surveys at Bandelier (Table 2, Figure 3), despite efforts to minimize these effects through relatively intensive and spatially systematic flights with experienced NMGF observers. Bandelier's annual survey counts have averaged 70% of the total elk surveyed by NMGF in Unit 6 since 1990 (range = 46% to 98%, Table 2), reflecting the relative intensity of the park's surveys (as well as the easily visible concentrations of elk in the open burn areas). These annual park flights have also maintained relatively consistent spatial coverage between years across the La Mesa Fire area. However, significant portions of the park have remained unsurveyed in these efforts, including the Sandoval County portions of the upper Frijoles watershed and the deep and extensive canyon systems. Also,

even in the surveyed areas the flight pattern intensity is inadequate to fully cover the complicated terrain—about 1/3 of the surface area of these “surveyed” uplands is likely missed in any given year.

Note that the “percent of total elk counted which were not classified” (into gender or age classes) is over 50% for most of the recent Bandelier surveys (Table 2). This is because large herds of 100–200+ individuals are typically encountered in the La Mesa Fire area (Figure 3), and it is hard to accurately classify such big groups. Since these large unclassified groups are usually cow/calf herds, the true ratio of bulls to cows in Bandelier is likely lower than presented in Table 2, while the true ratio of calves to cows is uncertain.

Table 2.—Winter aerial count data, elk, Bandelier National Monument.

Year	# ELK	% ?	% #6	Bull: COW	♂	♀	:JUV	JUV: ADUL	# MIN	E/M
1984	345	0	—	.03	19	100	50	.42	52	6.6
1985	281	0	66	.21	52	100	67	.44	?60	?4.7
1987	395	0	66	.25	38	100	63	.46	87	4.5
1990	504	.80	83	.80	93	100	29	.15	93	5.4
1991	907	.42	98	.26	41	100	38	.27	138	6.6
1992a	777	.63	—	.43	59	100	38	.24	79	9.8
1992b	867	.65	82	.45	62	100	38	.24	155	5.6
1993	499	0	47	.15	25	100	29	.23	214	2.3
1994	939	.71	66	.31	40	100	45	.32	200	4.7
1995	548	.62	46	.20	43	100	66	.46	115	4.8

Explanation of Headings (from left to right):

YEAR = year of helicopter survey (precise dates listed below)

1984 = 2/2/84

1985 = 1/7/85

1987 = 1/23/87

1990 = 1/31/90

1991 = 1/28/91

1992a = 2/11/92 (first 79 minutes)

1992b = 2/11/92 (all 155 minutes, last 76 minutes spent in low-elevation, piñon-juniper woodlands)

1993 = 2/1/93 (note that much of this flight time was spent over low-elevation, barren, piñon-juniper woodlands where few ungulates were observed)

1994 = 2/17/94 (little snow cover)

1995 = 2/7/95 (little snow cover)

ELK = total # elk counted

% ? = percent of the total elk counted which were not classified

% 6 = percent of the total elk surveyed by NMGF in Unit 6

BULL:COW = ratio of adult male to non-juvenile female (cow) elk

♂ = number of adult and yearling males per 100 cows

♀ = number of cow elk, standardized at 100

:JUV = number of calves per 100 cows

JUV:ADUL = ratio of juveniles to adult elk

MIN = number of flight minutes spent counting ungulates

E/M = number of elk counted per minute of flight counting time

Elk Mortality

Estimates of elk mortality by NMGF are also beset with large uncertainties, since they are primarily derived from voluntary mail-return surveys of hunter success. Uncertain biases and low return rates plague such surveys; e.g., statewide survey return rates since the mid-1980's range from 25–33% (L. Fisher—1995 personal communication). A possible, cost-effective, remedy is to utilize telephone surveys, which can provide more comprehensive and accurate results (Steinert et al. 1994).

Results from mail-in surveys since 1988 in Unit 6 suggest that the success rates of bow hunters have hovered around 20%, rifle success rates around 30%, and private land hunter success rates between 65% and 80%. The surveys indicate that about 1000 elk are killed by state-regulated hunters each year in Unit 6 (Table 3). Poaching and roadkills are estimated to annually kill an additional 200 and 100

elk, respectively, in Unit 6 (P. Cassidy—1993 personal communication), but substantive corroborating data are lacking. Mortality rates from other causes (e.g., natural predation, disease) are unknown. Take of elk on Native American lands (e.g., the local pueblos of Santa Clara, San Ildefonso, Cochiti, Zia, and Jemez) is unregulated by the State of New Mexico and currently unassessed by NMGF. Overall, the data currently available to NMGF do not allow precise determination of ongoing elk population status or trends at local or regional scales.

Elk populations in the Bandelier area may have high survival rates, facilitating rapid population growth. White (1981) presented local survival data on 28 radio-collared elk for the period spanning early 1978 to May 1980. Sixteen elk were collared in early 1978 and 12 in early 1979. Twelve of 13 calves survived at least through the first year after being collared (in winter)—the one death was apparently caused by lightning. Twenty-three of 28 total elk lived through the first year of monitoring, while 13 of 16 survived at least 25 months. Of the 28 collared elk, 22 were still alive in May 1980. Causes of mortality were legal hunting (2), poaching (2), lightning (1), and malnutrition (1). One of the collared females has been seen repeatedly in Bandelier as late as the winter of 1993–94, demonstrating local survival in the wild for at least 15 and one-half years. Note that legal harvest of elk has increased markedly since the White study ended (Table 3).

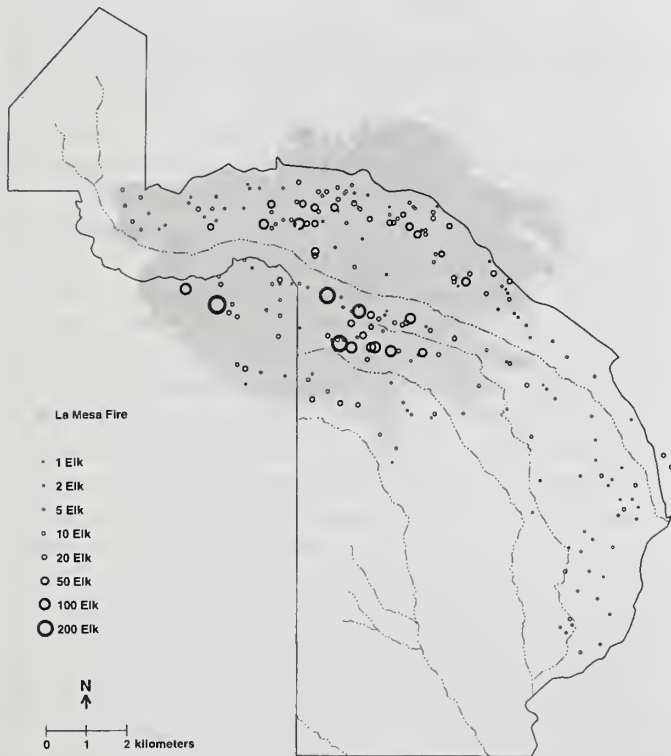


Figure 3.—Aerial survey observations of elk at Bandelier National Monument, 1990–1995, excluding 1993. Each point represents an observation in a particular year. The solid line represents the park boundary, dashed lines major canyon drainages. Adjoining lands include the Santa Fe National Forest (west, southeast, and north), Los Alamos National Laboratory (northeast), the Baca Ranch (northwest), and Cañada de Cochiti (south). The northwestern and southwestern portions of the park were essentially not surveyed in these years.

Table 3.—Harvest history of elk in the Jemez Mountains (Unit 6). Data from New Mexico Department of Game and Fish, extrapolated from mail-in survey estimates of hunter success. Data for 1987 are not available. Explanation of headings: # HUNT = # of licensed hunters, TOTAL = Total # elk legally killed by hunters; ♂ = # male elk legally killed by hunters; ♀ = # female elk legally killed by hunters.

YEAR	# HUNT	TOTAL	♂	♀
1981	44	39	39	0
1982	1716	286	271	15
1983	1953	290	265	25
1984	2125	526	358	168
1985	2017	379	350	29
1986	2262	416	354	62
1987	—	—	—	—
1988	2635	728	515	213
1989	3053	855	540	315
1990	3172	1086	622	464
1991	3392	1029	640	389
1992	3178	1000	676	324
1993	2535	968	587	381
1994	3223	1458	771	688

White's biotelemetry study (1981) also showed that most of the collared elk were part of a population that was relatively immune to hunting mortality because of the geography of local land ownerships. These elk largely summered (and calved) in the high elevation forests and meadows of the Baca Ranch, moving to wintering areas on Bandelier and Los Alamos National Laboratory (LANL). Elk are protected from public hunting across this 65,000 ha expanse of connected lands, although several hundred elk permits are issued to the Baca Ranch each year. It is presumed that a large portion of the current, larger elk population in the Bandelier area continues to follow this seasonal migration pattern, which provides year-round access to the security, food and water supplies, and cover that elk need.

Differences between aerial survey data collected in February 1995 from Bandelier (Table 2) and the rest of Unit 6 (L. Fisher—1995 personal communication) hint at either the coarse resolution of these data, or perhaps mortality differences between subpopulations in this unit. While the Bandelier survey noted 548 elk (62% not classified), the surveys outside Bandelier counted 656 animals, with only 15% not classified (as there were no big groups of 100+ elk). The bull:cow:calf ratios differed markedly between Bandelier, at 43:100:66, and the rest of Unit 6 at 28:100:37. If these values accurately describe the sampled elk "populations", they suggest that bulls are more heavily harvested and reproductive success is lower outside the relative protection offered to the Bandelier/Los Alamos/Baca Ranch population. Alternatively, differences in these values between populations might simply reflect sampling problems.

The most important natural predator of elk in the Jemez Mountains, the gray wolf (*Canis lupus*), was eliminated from the area by the mid-20th Century (Brown 1988). People have also made attempts to reduce local populations of another elk predator, the mountain lion (*Felis concolor*) (Allen 1989:153), although Bandelier certainly harbors a number of lions today, as tracks and droppings are commonly found (S. Fettig—unpublished data). Without their primary natural predator (wolves), New Mexico elk populations must ultimately be limited by either human hunting or by starvation/disease types of mortality when habitat resource limits are exceeded.

There are practical limits to the number of elk that can be harvested from Santa Fe National Forest lands (the primary public hunting grounds in Unit 6). In areas of high road density, use of ve-

hicles by road hunters scare the elk into less accessible portions of Forest Service land (where fewer hunters venture) or onto protected areas, such as Bandelier National Monument and LANL lands, and hunter success is limited. So, while reducing open road density improves the quality of elk habitat (and hunting success), it reduces the number of hunters who are willing to access the roadless areas, especially as horses, carts, or snowmobiles become nearly essential to pack kills out to the nearest road.

Overall, the existing data, as well as much anecdotal information, suggests that elk populations in the Jemez Mountains, as in much of New Mexico, are still expanding their distribution, and perhaps their numbers. The spread and exponential increase of New Mexico elk populations through circa 1990 (Figure 2) indicates that hunting harvests were conservative enough to allow elk populations to grow markedly, as intended by NMGF to restore elk to its native range in New Mexico. Population trends in the 1990's are not yet clear.

RESPONSE OF ELK TO THE LA MESA FIRE

The area around Bandelier and Los Alamos National Laboratory was the focus of much research on elk immediately after the 1977 La Mesa Fire. Studies conducted locally included radiotelemetry research on 30 collared elk (White 1981, White 1983), changes in utilization and migration patterns, including information from 70 permanent pellet transects (Conley et al. 1979), diets and physiologic response to differing diets (Rowland et al. 1983, Weber et al. 1984), and radionuclide concentrations in elk tissues (Meadows and Salazar 1982, Meadows and Hakonson 1982). These studies found that: 1) in the Jemez Mountains elk were primarily grazers, although they also used woody browse species (Rowland et al. 1983, Wolters, This Volume); 2) local elk use was concentrated on non-forest or early successional forest areas, prominently including about 50 ha affected by two wildfires in the early 1950's just above West Jemez Road (White 1981:3); and 3) in the Jemez Mountains most elk spent the majority of the year at upper elevations, especially on the Baca Ranch, with the bulk of the population seasonally migrating to lower elevation sites as needed to avoid deep winter snows.

Since the 1977 La Mesa Fire the population of the Bandelier area elk herd has increased dramatically (Figure 2), due to intrinsic population increase

combined with in-migration to about 6000 ha. of fire-created, grassy winter range. Conley et al. (1979) estimated that less than 100 elk wintered on Bandelier in 1977–78, and 296 in 1978–79. In 1979–80 an estimated 200–400 elk wintered in the La Mesa Fire area (Rowland et al. 1983). Wintering populations on Bandelier and adjacent LANL and Santa Fe National Forest lands were estimated in 1989 to be 1000–2000 individuals (R. Isler, New Mexico Dept. of Game and Fish—1989 personal communication). Annual helicopter counts in Bandelier since 1990 similarly suggest that on the order of 1500 elk now regularly winter on Bandelier and the adjoining portions of the La Mesa Fire area, since about 500 to over 900 animals were being counted in 1–3 hours of flight time (Table 2). If there were 100 elk wintering in the Bandelier area in 1978 and 1500 elk in 1992, this indicates an annual growth rate of 21.3%, and a 3.6 year doubling time!

Some of this rapid population increase undoubtedly reflects concentration of animals into this favorable wintering habitat. Recent aerial surveys clearly show that winter elk use is generally focused on the La Mesa Fire area (Figure 3). Protection from human disturbance and the availability of needed food resources are likely key factors behind these winter elk concentrations. The fire converted dense, monotypic ponderosa pine forests into a more productive and diverse mosaic of grassland, shrubland, and forests, resulting in a corresponding diversity of herbaceous and woody food available for elk to incorporate into their eclectic diets (see Rowland et al. 1983, Wolters—This Volume). Also, the moderate elevations of the La Mesa Fire area (between 2000 and 2600 m) apparently provide a locally optimum balance between vegetation that is sufficiently productive to be attractive and winter snow conditions which allow elk to access their potential food.

However, an exception to this pattern of concentrated elk use occurred during the winter of 1992–1993 (Figure 4). Interspersed snow and rain storms created dense, icy snowpack conditions which apparently restricted elk utilization of the grassy La Mesa Fire burn area that winter (cf. Lyon and Ward 1982:471). As a result, many fewer elk were observed in the burn area that winter (Figure 4, Table 2). Also, the large herds of 100+ animals which have been evident every other year (Figure 3) were absent during the 1993 survey, which allowed all surveyed animals to be classified that year. While total elk numbers were apparently depressed in Bandelier that winter as more elk dispersed to ad-

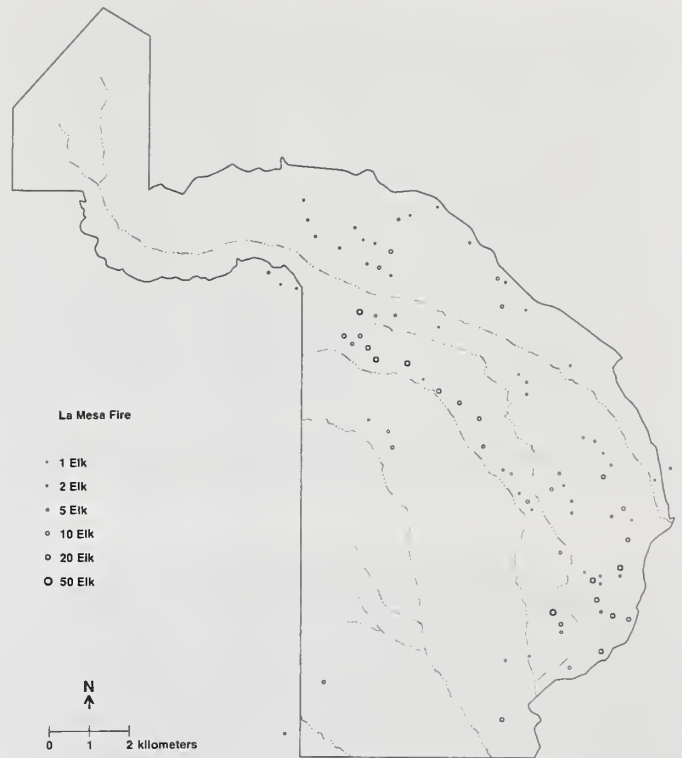


Figure 4.—Aerial survey observations of elk at Bandelier National Monument, 1993. The solid line represents the park boundary, dashed lines major canyon drainages. The linear-bounded, northwestern portion of the park was not surveyed.

joining lands, elk use was observed to be particularly widespread and relatively abundant across lower elevation portions of the park (Figure 4).

At the time of the initial post-La Mesa Fire studies, elk populations on Bandelier were relatively small and only used the burn area in the winter, but the attractiveness of the burn for elk and the potential for rapid population growth were apparent. For example, White (1981) predicted that:

The habitat created by the La Mesa fire and the use of this habitat by elk may cause a future overpopulation of elk. Problems related to overpopulation include damage to vegetation, which increases soil erosion, and an increase in accidents between elk and automobiles. Because neither Bandelier National Monument nor the Laboratory allows public hunting on their lands, elk populations will be difficult to control. The hunting pressure necessary to control elk herds often drives them to the refuges provided by Bandelier and the Laboratory.

The natural plant succession that will occur on the La Mesa burn also may lead to elk over-

population and to the subsequent problem of elk-damaged vegetation. Early successional stages are preferred by elk for wintering habitat, as demonstrated by the response of radio-collared animals to the fire habitat. A population increase probably will result. However, later successional stages (that is, as a ponderosa pine forest replaces the present grass cover) will not be beneficial to elk. Therefore, any population increase caused by the currently available food supply on the La Mesa burn may lead to an overpopulation at later stages when less food is available.

Unfortunately, but not surprisingly, these predictions are becoming reality in the Bandelier area.

RECENT ELK-RELATED OBSERVATIONS IN THE BANDELIER AREA

While there is no doubt that the local elk herd has grown rapidly during the last three decades, existing data are inadequate to accurately determine the current population trend. As described above, recent aerial surveys at Bandelier are beset by high levels of uncertainty. In particular, the large percentage of unclassified animals in most recent surveys (up to 80% unclassified—see Table 2) and the lack of any measures of variance reduces the reliability of any conclusions derived from these data. The large interannual variability in some observed survey parameters (e.g., the bull:cow ratio) further suggests cautious use of these values. Still, inasmuch as these are the best local data available, some survey results are worth reporting, along with a variety of other elk-related observations from this area.

In the period 1990–1995, winter juvenile:adult ratios in Bandelier elk averaged 0.28, with a range from 0.15 to 0.46 (Table 2). These values suggest that significant population growth may be continuing, unless adult mortality rates are greater than seems likely for this relatively well-protected (i.e. little-hunted) subherd. Indeed, true juvenile:adult ratios may be even higher, given that large cow:calf herds could not be classified in most years. There is also a trend of increasing juvenile:adult ratios since 1993 at Bandelier. However, the implication of these ratios for elk population growth is uncertain without better mortality data.

Deep or icy winter snowpacks, or unusually cold weather, can act as a check to elk populations by causing them to expend more energy to move and dig for food, and by forcing them to lower eleva-

tions where food may be less plentiful or they are more subject to human disturbance. However, the burgeoning of the local elk population has occurred despite greater than average snowpack conditions most winters since the La Mesa Fire, including the record snowfall winter of 1986–87 (Bowen 1990:150, unpublished data on file at Bandelier) and the icy snows of 1992–1993 (personal observation). This suggests that snow conditions in the Jemez Mountains will seldom serve to directly reduce current elk population levels. Indeed, most winters some elk are able to stay at relatively high elevations throughout the winter, e.g., elk typically use south-facing slopes winter-long in the Valle San Antonio area (P. Cassidy—personal communication).

All local observers agree that over the past several years more elk are wintering farther down the mesas of the Pajarito Plateau. Moreover, in recent years resident populations have developed at lower elevations. In Bandelier, the aerial surveys conducted each winter since 1990 typically find groups of elk all the way down to the Rio Grande (Figures 3 and 4). Indeed, the 2/1/93 aerial survey found the largest groups of elk at low elevations in piñon-juniper woodland, with groups as large as 18 animals observed along the Rio Grande (Figure 4). Elk have been year-round residents on Burnt Mesa since at least 1989, when cow and calf groups were repeatedly observed by archeologists working in that area. In early 1991, certainly for the first time in over 100 years, elk began to utilize the open headquarters area of Frijoles Canyon on winter evenings. Elk were first heard bugling in piñon-juniper areas near Juniper Campground in fall of 1991 (personal observation). Elk sign (tracks, droppings) are now seen year-round throughout the park, including low-elevation woodlands and canyons. Adjoining Bandelier's south boundary, cow and calf elk have been observed year-round in the Cañada de Cochiti area in and downstream of Dixon's orchards (elevation <1740 m) since summer of 1992.

Similarly, Santa Fe National Forest staff have observed signs of expanding range and increasing elk impact in the Jemez Mountains (personal communications with M. Orr, Española District biologist, and J. Elson, Forest Range/Wildlife staff officer), including: heavy browsing on New Mexico locust, aspen stems, and Gambel's and wavyleaf oak; barking of aspen stands; and intense grazing pressure on moist montane meadows throughout the Jemez Mountains (see Wolters, This Volume). Concentrated grazing by wintering elk certainly occurs on the USFS portions of the La Mesa Fire

burn adjoining Bandelier (Figure 3), although determination of elk grazing effects is confounded in many areas by the presence of cattle, especially in moist meadows and riparian settings. Greater year-round use of lower elevation areas is being observed throughout much of the Forest, and elk have recently colonized the Caja del Rio area, opposite the Rio Grande from Bandelier. For example, on 5/24/95 two cow elk were seen along the Rio Grande about 2 km south of the mouth of Frijoles Creek, across the river from Bandelier on Forest Service land (S. Fettig—personal communication). While definite elk effects are certainly observed in a number of particular areas, the extensiveness of negative impacts is unknown and available evidence does not show that elk populations are currently pushing against some sort of ecological carrying capacity all across the Jemez Mountains.

Los Alamos National Laboratory biologists have also observed recent increases in elk numbers and spread of elk-use areas within LANL (personal communications with T. Foxx and J. Biggs). There is ample evidence of elk in all Technical Areas, with year-round use seen throughout the Lab since the early 1990's. Elk with calves are now observed in summer at Mesa del Buey and in lower Pajarito Canyon (near White Rock). Elk tracks are observed all the way down to the Rio Grande in the TA-33 area. Overflight prohibitions have precluded aerial survey efforts to date, but it is apparent that large numbers of elk winter on LANL lands, which include a portion of the La Mesa Fire area immediately north of Bandelier. The western lands of San Ildefonso Pueblo, which adjoin LANL, White Rock, and the detached Tsankawi Unit of Bandelier, also receive considerable winter use by elk. Elk have been causing damage to yards in the White Rock townsite for a number of years (at least throughout the 1990's), causing conflict between people who like to feed the elk and those who dislike the harm to their property.

Contamination of elk by radioactive materials at LANL has received study, with conclusions to date indicating little cause for concern (Meadows and Salazar 1982, Meadows and Hakonson 1982, Fresquez et al. 1995-a). However, recent findings of high levels of strontium-90 (Fresquez et al. 1995-b) in a preferred browse species (rabbitbrush), and the small sample sizes of elk tissue sampled in the past, suggests the potential for unassessed elk (and deer) contamination problems.

Elk have become an important traffic hazard in Los Alamos County (Burns 1992), as night-time

drivers commonly encounter elk along local highways. The Los Alamos Police Department recorded at least 51 car accidents involving elk, and 54 with deer, between January 1990 and February 1995 (Gonzales et al. 1995). At least 29 additional accidents were recorded during this time period as "animal", most of which likely involved elk or deer. These encounters account for about 6% of all accidents in Los Alamos County (Los Alamos Police Dept.—unpublished data). While two-thirds of elk-related accidents occurred in fall or winter, this hazard is now present year-round and affects roads through low-elevation woodlands. Regrowth of trees and shrubs near the road in the 1977 fire area is decreasing visibility and further increasing the hazard of collisions with animals.

Resource Impacts in the Bandelier Area

As large herbivores, elk can play a key role in structuring local ecosystems (Kay 1990, 1994). Thus the recent increases in elk numbers and range are having a number of effects on local resource values. For example, elk use of the La Mesa Fire area is so ubiquitous that it is difficult to find upland areas that have not been recently affected by elk-mediated transfers of nutrients, as evidenced by the fecal pellet groups of elk (see C. White, This Volume).

Many examples of elk impacts on Bandelier vegetation have become apparent. For example, the shattered rosettes of *Yucca baccata* found across local piñon-juniper woodlands each spring indicate one food preference of wintering elk. Intensive elk browsing has largely destroyed aspen (*Populus tremuloides*) reproduction from upland portions of the La Mesa Fire (e.g., Apache Mesa, Mesa del Rito) and the headwaters of the Frijoles watershed, while mature aspen trees are heavily barked in many areas (cf. Allen 1989:136-138). Photographs taken from permanent points in open grasslands on Cerro Grande reveal that clumps of the shrub *Holodiscus dumosa* were browsed back severely between October 1983 and October 1992. In the prime elk wintering areas of the La Mesa Fire, browsing effects are evident on a variety of shrubs, including New Mexico locust (*Robinia neomexicana*), various oak (*Quercus*) species, and especially the small buckbrush (*Ceanothus fendleri*), which in particular is severely browsed. The uniformly mowed tops of young locust sprouts indicates that elk browsing is currently a major factor slowing the still-rapid spread of locust clones across wide portions of the 1977 burn. Elk buckbrushes are also somewhat slow-

ing tree re-establishment into the La Mesa Fire burn area (cf. Allen 1989:137).

Moist meadows in Bandelier are being kept in an early seral stage by excessive elk use (see Wolters, This Volume). Similar impacts are apparent in nearby portions of the Jemez Mountains, where elk and cattle combine to overgraze many meadows (personal observation). Portions of the grassy La Mesa Fire burn area are also being utilized heavily by elk (e.g., Escobas Mesa, see Wolters, This Volume). The initial post-fire flush of high plant productivity has passed, and vegetational succession has begun to return many La Mesa Fire areas back to pine forests again, which will support fewer elk. These observations imply increasing pressure through time on other elk-favored vegetation types in Bandelier if elk populations remain at or exceed current levels.

Severe erosion problems exist in Bandelier's piñon-juniper woodlands (Allen 1989:165–167), and park resource managers are concerned that increasing elk utilization of these areas may exacerbate these erosion problems by reducing already stressed herbaceous ground cover in the interspaces between the small trees. By their sheer numbers and large food intake requirements (on the order of 10 to 25 pounds of forage per day per adult elk [Nelson and Legee 1982:363]), elk grazing could easily have negative impacts on woodland conditions analogous to the well-documented effects of smaller feral burros in Bandelier from ca. 1930–1980 (Koehler 1974, Earth Environmental Consultants 1974, USDI National Park Service 1976, Potter and Berger 1977). Any similar increases in soil erosion from LANL lands might lead to increased runoff of radioactive materials, such as depleted uranium, which is a widespread surface soil contaminant in some woodland areas of LANL (Becker 1992).

Because local archeological sites are primarily found in woodland areas this erosion is also a major cultural resource problem at Bandelier, as about 70% of archeological sites within Bandelier are being damaged by soil erosion (Head 1992). Bandelier has been testing methods for increasing herbaceous ground cover in eroding woodland areas (Chong 1994; unpublished data on file at Bandelier), which are largely in remote portions of the Bandelier Wilderness that would be attractive wintering habitat for elk if adequate food existed. Thus concern exists that the potential for successful erosion control will be set back by the attraction of more elk to the treatment areas.

Elk are large animals—the mean weight of 5 local adult females was 233 kg (513 lb) (Meadows and Hakonson 1982), and adult males of Rocky Mountain elk typically weigh over 300 kg (Peek 1982). The concentrated hoof action of large numbers of these heavy animals is also starting to damage park resources. Ongoing revegetation research in piñon-juniper woodlands (Chong 1994, B. Jacobs—personal communication) reveals that by spring elk hoofprints can cover most of the bare ground surface between woodland trees. Similarly, recent surveys have found that numerous archeological sites within Bandelier are being damaged by trampling from large ungulates, mostly elk (Figure 6). New elk trails continue to emerge in various parts of the park, from mesatops to steep canyon walls.

Water sources, which are relatively scarce in higher elevation areas of the Jemez Mountains, are being degraded in portions of the park and nearby areas by heavy elk use. Some small ponds display elk-trampled margins, wallows, and highly turbid water (personal observation). These scarce waters are ecologically important for reasons which may be compromised by elk-induced changes in water quality, (such as the breeding of amphibians). I have observed various places where elk have turned small seeps into wallows, such as sites located west of Corral Hill, near the headwaters of Frijoles Creek, and at the base of the Cañada Bonito grassland.

Elk may compete with mule deer in various ways (Nelson 1982:425; Lyon and Ward 1982:464). While deer populations in many parts of New Mexico have been depressed in recent years, Bandelier has exhibited relatively high deer populations for several decades (Allen 1989:132–134, Table 4), probably because it offers a fairly secure refuge from poaching as well as legal hunting. Eberhardt and White (1979) demonstrated that LANL deer occupied consistent home ranges year-round, although this was prior to the recent buildup of elk numbers. Aerial surveys in Bandelier since 1990 provide indications that mule deer numbers may be in decline (Table 4), although cautious interpretation is required due to the large and unquantified uncertainties associated with these data. The spatial distributions of elk and deer revealed by the winter aerial surveys (compare Figures 3 and 5) suggest that deer are largely excluded from zones of high elk density in the La Mesa Fire area. Heavy elk use of the La Mesa Fire area may be reducing winter deer utilization of this relatively desirable grass and shrub-rich zone, forc-

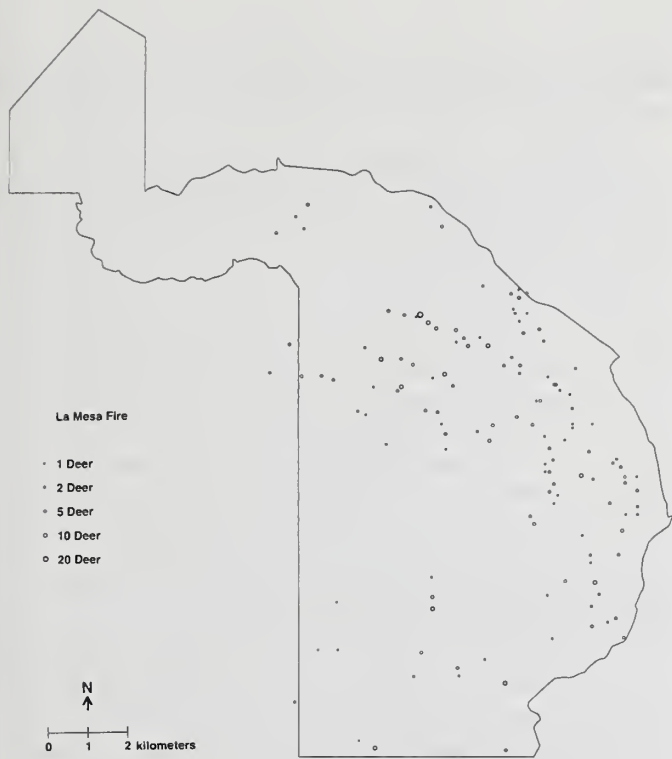


Figure 5.—Aerial survey observations of deer at Bandelier National Monument, 1990–1995. Each point represents an observation in a particular year. The solid line represents the park boundary, dashed lines major canyon drainages. The linear-bounded, northwestern portion of the park was not surveyed.

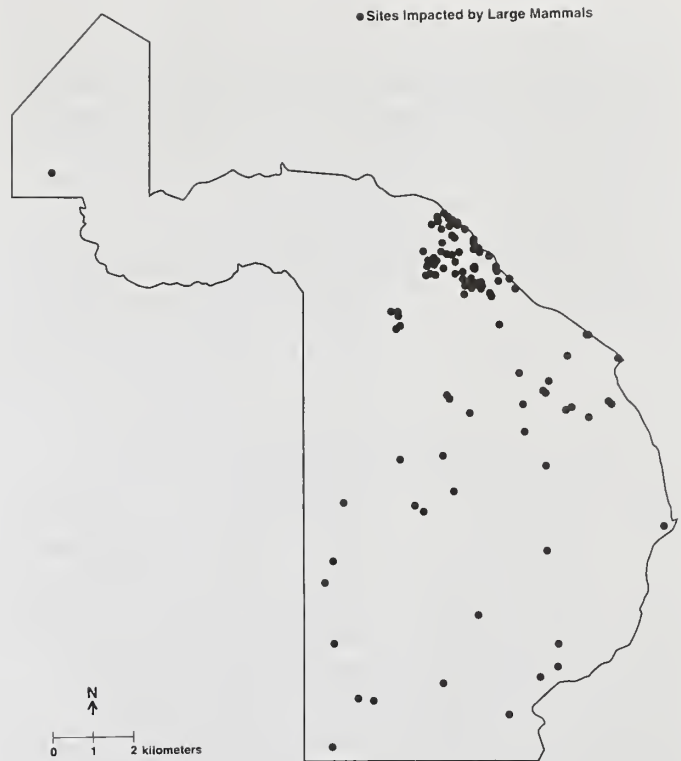


Figure 6.—Archeological sites impacted by elk or deer at Bandelier National Monument, based upon post-1986 surveys of about 44% of the park (unpublished data on file at Bandelier).

ing the deer to occupy less productive areas downslope in piñon-juniper woodlands and thereby diminishing their winter survival and subsequent reproductive success.

CONCLUDING THOUGHTS

Overall wintering conditions for elk will likely improve across the Jemez Mountains during the coming decade. Land management agencies will create more grassy winter ranges at moderate to low elevations through ongoing "ecosystem management" efforts to reduce forest and woodland densities with large-scale prescribed burns and understory thinning projects. As a result, there will continue to be potential for further elk population increases in Unit 6.

On the other hand, large portions of the La Mesa Fire burn area may become less desirable habitat for elk as vegetational succession proceeds. Many open grassland patches are rapidly turning into shrub thickets, and ponderosa pine regeneration is

Table 4.—Winter aerial count data, deer, Bandelier National Monument.

YEAR	# DEER	♂:	♀	:JUV	D/M
1984	24	19	100	50	0.46
1985	18	160	100	100	20.3
1987	121	46	100	70	1.4
1990	156	25	100	55	1.68
1991	161	26	100	68	1.16
1992a	53	32	100	57	0.67
1992b	78	26	100	56	0.50
1993	137	24	100	48	0.64
1994	79	7	100	77	0.40
1995	46	9	100	65	0.40

Explanation of Headings (from left to right):

YEAR = year of helicopter survey (precise dates in Table 2)

DEER = total # deer counted

♂ : = number of adult and yearling males per 100 non-juvenile female deer

♀ = non-juvenile female deer, standardized at 100

:JUV = number of juveniles per 100 non-juvenile female deer

D/M = number of deer counted per minute of flight counting time

well established across extensive areas. While elk herbivory is modulating the successional pathway of much of the burn area, it will not prevent open grasslands from returning to forests which will support fewer elk. Still, park prescribed burning programs (Lissoway 1995) and other vegetation management efforts (Sydoriak 1995) are expected to maintain or develop herbaceous understories throughout the park, so ample elk wintering habitat should continue to be available in the park.

There are multiple indications that excessive conservatism should be avoided in managing the overall population of elk in Unit 6. Current elk populations are apparently larger than anything known for at least the past 800 years. Various signs of elk-induced resource stress are becoming apparent, and the potential for elk-related conflicts between land managers has been increasing. With the probability of further improvements in winter ranges and the demonstrated high reproductive potential of cow-dominated elk populations, elk numbers could rise even further. Major data uncertainties preclude precise knowledge of elk population dynamics, including responses to management actions such as hunting. Recent growth in elk numbers has coincided with the anomalously wet period of the past 18 years (Grissino-Mayer 1995, Allen—in review). Current concerns over elk effects on other resources will become more urgent when the next extended dry spell hits New Mexico, as drought will highlight elk impacts on vegetation and competition with livestock on public and private lands. Overall, prudence suggests limiting further growth in Unit 6 elk populations until some of these issues are resolved. In this light, the higher harvest levels estimated for Unit 6 in 1994 (Table 3) are encouraging.

The New Mexico Game and Fish Department has recently been soliciting comments from the public and various interest groups in an effort to develop a formal "Long Range Plan for the Management of New Mexico's Elk". The October 1995 draft of this document (NMGF 1995) opens with the stated goal "(T)hat hunters and interested individuals enjoy high levels of elk recreational opportunities and experiences". These social considerations are certainly important. However, the single-species focus on recreational considerations presented by this document, to the near-exclusion of ecological information or wider resource management issues, is worrisome. Elk management needs to be considered within broader contexts of **both** societal and ecological issues, otherwise unnecessary conflicts could develop with various land

managers in New Mexico who have overriding management objectives which may be inconsistent with high elk numbers.

The NMGF draft management plan seems cautious in its formulation of elk-related issues (NMGF 1995). It states that the main problems specific to Unit 6 are (sic):

1) "Poor quality winter ranges cause elk to concentrate on National Park, National Laboratory, Tribal, and private lands creating difficulty in attaining hunt objectives and trespass problems"; and 2) "Divergent management objectives of New Mexico, Los Alamos National Labs and Bandelier National Monument, and the Baca Location hampers effective elk management".

The draft plan suggests that the primary strategies to resolve these problems are to:

1) "Develop cooperative agreements with public land agencies and affected agencies and individuals to enhance winter habitat on public lands"; and 2) "Develop cooperative management agreements with the Baca Location, Los Alamos National Labs and Bandelier National Monument to meet joint objectives".

These are important issues and strategies to pursue, especially the emphasis on cooperative interactions among local land managers. In addition, at least two key questions must be thoroughly addressed if the proposed cooperative agreements are to be successful: 1) What ecological considerations (and tradeoffs) should be included in determining elk-related management goals? 2) Given overall social and ecological considerations and trade-offs, what are appropriate target numbers of elk, both overall and for particular portions of Unit 6?

Bandelier is just beginning to quantitatively document the impacts of elk grazing to park resources and review the options which may be available for controlling excessively large in-park populations. A number of research needs have been identified to address elk-related issues at Bandelier (Sydoriak 1995), including needs for better data on population dynamics, seasonal use of habitats across landscape gradients, "migration" corridors, effects of elk use on herbaceous vegetation and soil surface conditions, and possible development of carrying capacity indicators. However, it is already apparent that novel management actions may be required **within** Bandelier to prevent excessive elk impacts to various park resources unless adequate control is also applied to overall elk population numbers in the Jemez Mountains.

How will local elk populations be limited? Perhaps some combination of public and private hunting similar to the current mix will be adequate to control elk numbers, although the geography of Bandelier-area land ownerships certainly increases the difficulties in managing local elk populations. To date the Baca Ranch has supported high elk numbers for reasons ranging from aesthetic appreciation of free-ranging herds of these magnificent animals to the favorable economics of their trophy elk hunting business (where more elk means a larger pool from which to select high-value bulls). While the current seasonal migration patterns of local elk have yet to be fully determined, it is clear that many elk move directly from the Baca to the security of Bandelier and LANL in the fall, avoiding any exposure to public hunting pressure. This obviously creates population control challenges, as hunting on Bandelier is expressly prohibited by Code of Federal Regulations (CFR), Title 36, Part 2, Section 2.1 (preservation of natural resources), Section 2.2 (wildlife protection), and Section 2.4 (weapons, traps, etc.). Opening the park to public hunting would require an act of Congress, and direct reductions by park or NMGF staff for management purposes would be controversial and require substantial NEPA documentation and public review. However, there may be other ways to reduce the sense of security elk currently experience in Bandelier that could decrease the attractiveness of the park as wintering habitat.

In conclusion, the habitat changes initiated by the La Mesa Fire have supported the recent development of a large elk population in the Bandelier area. Such high elk numbers are apparently an ecologically novel situation, and many signs of elk-related resource stress are becoming apparent. The Bandelier area elk population is inextricably linked to the overall status of elk in the Jemez Mountains. Large uncertainties and data gaps cloud our understanding of current elk population dynamics in Unit 6. Care should be taken to avoid further increases in Jemez Mountains elk numbers until the resource impacts of this historically unprecedented phenomenon (high elk numbers) can be identified, desirable population levels agreed upon (based to a significant degree upon ecological information and resource carrying capacities, as well as social considerations), and appropriate cooperative management strategies determined and implemented.

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Elk Effects on Bandelier National Monument Meadows and Grasslands

Gale L. Wolters

Abstract.—This study was designed to quantify current vegetation composition and determine forage production, use, and preference by elk on a seasonal basis on two Bandelier National Monument habitat types—mesa grasslands and montane meadows. In 1993, the mesa grassland habitat, created by the 1977 La Mesa Fire, was dominated by sheep fescue and other grasses. Montane meadows were dominated by low to mid-seral introduced species such as Kentucky bluegrass, white clover, and common dandelion. Kentucky bluegrass provided over twice as much cover and total plant cover was about 40% greater on a portion of one meadow protected from grazing by elk for several years. The change in species composition and litter, after a few years protection from elk, suggest montane meadows may respond rapidly to reduced elk grazing pressure. Annual production averaged about 1,600 and 1,000 kg/ha on montane meadows and grassland sites, respectively. Utilization averaged about 50% on the meadows and only about 25% on the grasslands. Warm season grasses such as blue grama, little bluestem, spike muhly, and Arizona three-awn were the principal forage species consumed on grassland sites while Kentucky bluegrass, beauty cinquefoil, and bedstraw were the most common species consumed by elk on montane meadows.

INTRODUCTION

Wintering Rocky Mountain elk (*Cervus elaphus nelsoni*) population in Bandelier National Monument was estimated at less than 100 in 1977–78 and 296 in 1978–79 (Conley and Sivinski 1979) one to two years after the La Mesa Fire. Elk populations increased dramatically after the fire and the current population of wintering elk is estimated to be 1,000 to 2,000 (Allen this volume). White (1981) alerted public land managers of the potential for elk overpopulation and habitat destruction in the Jemez Mountains. Allen also notes several soil erosion problems in Bandelier's pinyon-juniper woodlands (*Pinus edulis*, *Juniperus monosperma*) erosion, damage to most Bandelier archeological sites, degradation of high elevation water sources, browsing damage to particular plant species, and over utilization of the La Mesa Fire grasslands; all of the resource impacts are attributed to or exacerbated by increasing numbers of elk. Apparent over utilization has also been observed on adjacent Forest

Service-administered montane meadows jointly grazed by elk and domestic livestock (Jerry Elson—1991 personal communication).

The objectives of this study are to quantify current vegetation composition and determine forage production, use, and preference by elk on a seasonal basis. The current data set represents preliminary findings from a 3-year study.

STUDY AREA

The study was designed to quantify herbage use by elk on two habitat types in Bandelier National Monument. Initially, the study was designed to quantify herbage use by cattle and elk on key montane meadow habitats in mixed conifer forest vegetation zone. Study sites on Bandelier National

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Monument were selected in 1992 as control sites (no cattle use) for sites grazed by livestock on the Santa Fe, Carson, and Gila National Forests. Because both wild and domestic ungulates spend a disproportionate amount of time foraging on montane meadow vegetation, mountain meadows were selected for study as areas where competition, overuse, or conflicts in use would most likely occur first. The following year, study objectives were broadened to include the grassland habitat type in Bandelier National Monument which was created by the 6,180 ha 1977 La Mesa Fire. These lower elevation grasslands occurring on mesas in the midst of the ponderosa pine (Table 1) vegetation zone have since become an important elk winter range area.

Three montane meadow sites were selected for study (Figure 1). The meadow study sites, characteristic of Bandelier National Monument meadows, were dominated by Kentucky bluegrass, common dandelion, and white clover, and all appeared to be heavily grazed by elk. Ski Park site was located approximately 200 m northeast of the intersection of NM Highway 4 and St. Peters Dome Road at an elevation of 2,730 m, Frijoles Canyon site was approximately 300 m downstream from NM Highway 4 along the east fork of Rito de los Frijoles at 2,650 m, and the Weather Station site was located approximately 500 m north of the intersection of NM Highway 4 and the Los Alamos/Sandoval County boundary at an elevation of 2780 m (Fig. 1). The Weather Station site, was later added to the

Table 1.—Scientific and common names of all plants that were encountered at the mesa grassland and montane meadow study sites, and in fecal pellets.

Scientific Name	Common Name	Scientific Name	Common Name
<i>Achillea lanulosa</i> Nutt.	western yarrow	<i>Juncus</i> spp.	rush
<i>Agropyron smithii</i> Rydb.	western wheatgrass	<i>Juniperus monosperma</i> (Engelm.) Sarg.	one-seed juniper
<i>Agropyron subsecundum</i> (Link) Hitchc.	bearded wheatgrass	<i>Machaeranthera canescens</i> (Pursh) Gray	hoary aster
<i>Agropyron trachycaulum</i> (Link) Malte	slender wheatgrass	<i>Muhlenbergia montana</i> (Nutt.) Hitchc.	mountain muhly
<i>Allium cernuum</i> Roth	nodding onion	<i>Muhlenbergia wrightii</i> Vasey	spike muhly
<i>Andropogon gerardii</i> Vitman	big bluestem	<i>Penstemon strictus</i> Benth.	Rocky Mtn. penstemon
<i>Andropogon scoparius</i> Michx.	little bluestem	<i>Phalaris arundinacea</i> L.	reed canary grass
<i>Androsace</i> spp.	rock jasmine	<i>Phleum alpinum</i> L.	alpine timothy
<i>Antennaria rosulata</i> Rydb.	pussytoes	<i>Phleum pratense</i> L.	blue timothy
<i>Aristida arizonica</i> Vasey	Arizona three-awn	<i>Pinus edulis</i> Engelm.	pinyon
<i>Artemisia ludoviciana</i> Nutt. subsp. <i>ludoviciana</i>	Louisiana wormwood	<i>Pinus ponderosa</i> Dougl. ex Laws.	ponderosa pine
<i>Artemisia ludoviciana</i> subsp. <i>redolens</i> (Gray)	Keck sagebrush	<i>Poa fendleriana</i> (Steud.) Vasey	mutton grass
<i>Blepharoneuron tricholepis</i> (Torr.) Nash	pine dropseed	<i>Poa pratensis</i> L.	Kentucky bluegrass
<i>Bouteloua gracilis</i> (H.B.K.) Lag.	blue grama	<i>Poa palustris</i> L.	fowl grass
<i>Bromus carinatus</i> Hook. & Arn.	California brome	<i>Potentilla hippiana</i> var. <i>diffusa</i> Lehm.	horse cinquefoil
<i>Campanula rotundifolia</i> L.	bluebell	<i>Potentilla pulcherrima</i> Lehm.	beauty cinquefoil
<i>Carex</i> spp.	sedge	<i>Pseudocymopterus montanus</i> (Gray)	Coult. & Rose mountain parsley
<i>Ceanothus fendleri</i> Gray	fendler buckbrush	<i>Pseudotsuga menziesii</i> (Mirb.) Franco	Douglas-fir
<i>Cerastium arvense</i> L.	starry cerastium	<i>Quercus gambelii</i> Nutt.	gambel oak
<i>Cirsium neomexicanum</i> Gray	lavender thistle	<i>Rosa fendleri</i> Crep.	Fendler rose
<i>Cirsium parryi</i> (Gray) Petrak	Parry thistle	<i>Rudbeckia hirta</i> L.	black-eyed-susan
<i>Chrysopsis villosa</i> (Pursh) Nutt. ex DC.	hairy goldaster	<i>Salvia subincisa</i> Benth.	sage
<i>Cowania mexicana</i> D.Don	Mexican cliffrose	<i>Senecio biglovii</i> Gray var. <i>biglovii</i>	bigelow groundsel
<i>Danthonia parryi</i> Scribn.	Parry oatgrass	<i>Silene laciniata</i> Cav.	Mexican silene
<i>Epilobium angustifolium</i> L.	blooming Salley	<i>Sphaeralcea fendleri</i> A. Gray	Fendler globemallow
<i>Equisetum arvense</i> L.	common horsetail	<i>Sporobolus cryptandrus</i> (Torr.) Gray	sand dropseed
<i>Erigeron formosissimus</i> Greene	itchy fleabane	<i>Stipa lettermanii</i> Vasey	Letterman needlegrass
<i>Erigeron divergens</i> Torr. & Gray	spreading fleabane	<i>Taraxacum officinale</i> Weber	common dandelion
<i>Festuca ovina</i> L.	sheep fescue	<i>Thermopsis pinetorum</i> Greene	Piney golden pea
<i>Fragaria americana</i> (Porter) Britt.	wild strawberry	<i>Thamnosma texana</i> (Gray) Torr.	Texas desert-rue
<i>Galium stellatum</i> Kell	bedstraw	<i>Tragopogon dubius</i> Scop.	golden salsify
<i>Geranium richardsonii</i> Fisch. & Traut	Richardson geranium	<i>Tridens pilosus</i> (Buckl.) Hitchc.	hairy tridens
<i>Grindelia aphanactis</i> Rydb.	gumweed	<i>Trifolium repens</i> L.	white clover
<i>Hordeum brachyantherum</i> Nevski	meadow barley	<i>Verbascum thapsus</i> L.	miners candle
<i>Hymenoxys richardsonii</i> (Hook.) Cockrell	pinque	<i>Vicia americana</i> Muhl. var. <i>americana</i>	American vetch
<i>Iris missouriensis</i> Nutt	Rocky Mountain iris	<i>Vicia pulchella</i> H.B.K.	sweetclover
<i>Janusia gracilis</i> Gray	slender janusia		

study when it was noted that a portion of this meadow had been protected from grazing by elk since about 1989 by a 2 m high chain link fence enclosure of a 10 X 10 m area.

Two mesa grassland sites (Southwest and East), typical of the upland grasslands created by the La Mesa Fire, were located about 1 km east/southeast of Ponderosa Campground on Bandelier National Monument (Figure 1). Elevations of the grassland sites were approximately 2,270 m. These grassland sites were dominated by sheep fescue, little bluestem, mountain muhly, and spike muhly.

METHODS

Botanical composition of the study sites were determined by the canopy-coverage method (Daubenmire 1959) during the late summers of either 1992 or 1993. Botanical composition of each study site was determined by estimating cover class by species in 20- x 50-cm plots at 2 m intervals along two, 100 m, permanent transects for a total of 100 plots per site. Transects were established to bisect representative areas of the study sites. Frequency was calculated from species presence in the one hundred 20- x 50-cm plots. The common and scientific nomenclature of all plant species found in this study are listed in Table 1.

Forage production and utilization were estimated on all grassland and montane meadow sites except the Weather Station site. Production and utilization estimates were made on portions of the study site judged to be representative of the area.

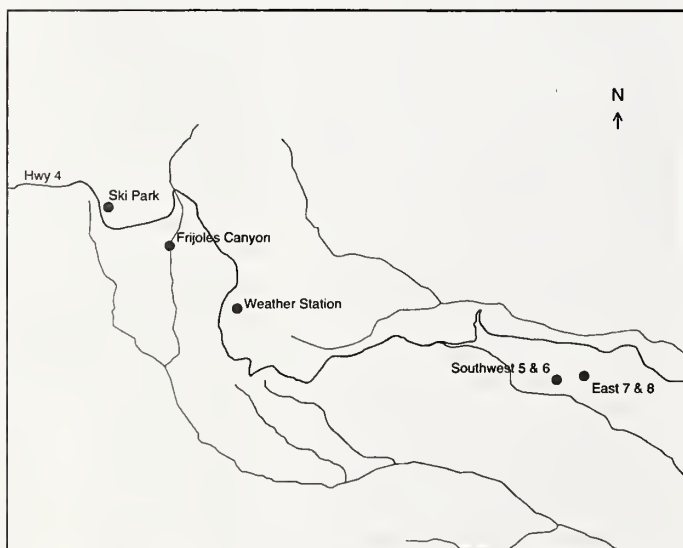


Figure 1.—Location of study sites in Bandelier National Monument.

Forage production and utilization were determined on 18 grazed and 18 protected 0.5 m² quadrats on each study site using the double sampling procedure described by Wilm et al. (1944). We estimated forage on all grazed and protected quadrats and we randomly selected 6 (1 from each series of 3 quadrats) grazed and 6 protected quadrats for clipping. Regression analysis was used to correct estimated values based upon clipped weight of herbage. Production estimates on ungrazed "protected" areas were made inside 7.3- X 7.3-m fenced enclosures (at the two primary meadow sites) or under 1.2- X 1.2-m cages (at the two mesa grassland sites) that prevented forage consumption by elk or deer. Forage utilization was determined on adjacent grazed areas by estimating residual forage and then subtracting the residual estimates from the production estimates. Production and utilization estimates were made 28 October 1992, and 1 July, and 27 October 1993 on montane meadow sites and 24 March and 25 October 1993 on the grassland sites.

Elk pellet groups on permanently marked 100- X 1-m transects were counted each time production and utilization estimates were made. The permanently marked botanical composition transects served as one side of each pellet group transect. Three or 4 sample pellets from each pellet group were collected during every count. The fecal material was evaluated by microhistological analysis (Sparks and Malachek 1968) at the University of Arizona Range Utilization Laboratory to determine seasonal composition of elk diets.

Sorensen's Index of Similarity (SPCC) (Mueller-Dombois and Ellenberg 1974) was used to estimate the similarity of species presence among seasons and past use. Quantitative comparisons of species cover by use and elk diet by season were made using Czekanowski's Coefficient of Similarity (CZC) (Grieg-Smith 1983).

RESULTS

Cover and Frequency

Sheep fescue was the most common plant species on the La Mesa Fire grassland sites in 1993, accounting for 20% ground cover (Table 2). Little bluestem, mountain muhly, western wheatgrass, spike muhly, and big bluestem were also common and accounted for 1 to 5% of the total cover. Combined grasses accounted for 36% of the cover. Grasses exhibited a uniform distribution over the

study area. For example, sheep fescue occurred in nearly 90% of the sample plots while little bluestem and western wheatgrass occurred in 35 and 41% of the plots, respectively. As cover of other species diminished so did their relative frequencies.

Forbs did not contribute substantially to the total plant cover on the grassland sites. Composites were the most common broadleaved herb group, accounting for over 70% of the forb cover; hairy goldaster was the most common composite. American vetch was another prominent forb. Woody plants (browse) accounted for about 4% of the cover with fendler buckbrush, gambel oak, and Louisiana wormwood being the most common.

Table 2.—Percent cover and frequency of plants on La Mesa Fire grassland sites.

Lifeform/species Other factors	% Cover	% Frequency
GRAMINOIDS		
Sheep fescue	20.3	89.0
Little bluestem	5.5	34.5
Mountain muhly	3.3	18.5
Western wheatgrass	3.0	41.0
Spike muhly	2.2	14.5
Big bluestem	1.1	2.5
Pine dropseed	.1	2.0
Blue grama	.1	2.0
Arizona three-awn	.1	1.5
Kentucky bluegrass	.5	3.0
<i>Subtotal</i>	36.2	
FORBS		
Hairy goldaster	.6	3.5
Other forbs	.7	18.5
American vetch	.4	9.5
Spreading fleabane	.3	12.0
Pussytoes	.2	2.5
Hoary aster	.1	2.5
Lavender thistle	.1	1.5
Pinque	T ¹	1.5
Golden salsify	T	1.0
Western yarrow	T	.5
Miners candle	T	.5
<i>Subtotal</i>	2.4	
BROWSE		
Fendler buckbrush	2.2	9.5
Gambel oak	1.4	2.0
Louisiana wormwood	.3	3.5
Fendler rose	.2	1.5
Ponderosa pine	T	1.0
<i>Subtotal</i>	4.1	
TOTAL PLANT	42.7	
Litter	36.2	99.5
Moss	2.3	27.5
Rock	2.0	13.0
TOTAL SOIL		83.2
BARE TOTAL	16.8	

¹ T signifies less than 0.05 percent cover.

Plant litter covered 36% of the soil surface, and litter was present on nearly every sample plot. Decadent down logs and sloughed bark remaining from trees killed by the La Mesa Fire accounted for a substantial portion of the litter on the grassland sites. Rock and moss were also present on the soil surface and combined accounted for 4.3% ground cover on the La Mesa study sites. Bare soil was exposed on less than 17% of the surface area.

In July of 1977, less than a month after the La Mesa Fire, about 45,500 kg of grass seed was aeri-ally applied to almost the entire burn area (Table 3). Sixteen years after aerial seeding, the grasslands created by the La Mesa Fire retained little resemblance to the applied seed mixture. Sheep fescue was the only seeded species present in substantial amounts, although western wheatgrass was also widespread. Slender wheatgrass and sand dropseed were either not present or were present in insignificant amounts. These data are consistent with earlier findings by Potter and Foxx (1986) who documented initial reseeding success for slender wheatgrass but observed that it was declining in cover in 1985 while sheep fescue increased in cover.

Kentucky bluegrass, white clover, and common dandelion were the dominant plant species on Bandelier Monument montane meadow study sites (Table 4). These three species combined produced over 50% of the ground cover and each species occurred in over 90% of sample plots, indicating widespread uniform distribution. Fowl grass, California brome, slender wheatgrass, western yarrow, itchy fleabane, and starry cerastium were common on the meadows but individually provided only about 1 to 4% cover. Woody species were so widely scattered on the meadow sites that they did not occur in the sample plots. Total plant cover on montane meadows was about 70%, nearly twice the cover on La Mesa grassland sites. Plant litter was substantially less than on the grassland sites,

Table 3.—Seed mixture applied aeri-ally to the La Mesa Fire grassland area July 12–17, 1977.

Species	Percent (by weight)
Western wheatgrass	70.5
Slender wheatgrass	19.4
Sheep fescue	5.2
Blue grama	3.0
Spike muhly	1.5
Sand dropseed	.4
Total	100.0

occupying only 5% of the soil surface on the meadows. The amount of exposed surface soil was greater in the montane meadows (25.5%) than in the mesa grassland habitat (16.8%). Surface soil exposed in montane meadows was due primarily to pocket gopher activity rather than natural interspaces between plants as on the grassland sites. Exposed surface soil would have been much greater on the grassland sites had the abundant deadfall logs remaining from the La Mesa Fire not been present.

Vegetation on the grazed portion of the Weather Station site appeared very similar to other montane

meadow sites from an initial observation. However, composition of plant cover appeared substantially different where protected from elk grazing for several years (Table 5). Since we had only one site protected from elk grazing, we could not analyze the data statistically. Still, the data may indicate how protection from elk might influence plant cover and species composition. In this one area, total plant cover was about 40% greater where protected from elk grazing. Kentucky bluegrass alone provided over twice the cover where protected from elk compared to where grazed by elk. Western yarrow cover and frequency was also greater where protected from elk grazing. The cover and frequency of white clover and common dandelion decreased dramatically on the area protected from elk use for several years. Plant litter

Table 4.—Percent cover and frequency of plants on Bandelier National Monument montane meadows (Ski Park, Frijoles Canyon, and Weather Station sites), based upon 250, 20 × 50 cm plots.

Lifeform/species Other factors	% Cover	% Frequency (N=250)
GRAMONIDES		
Kentucky bluegrass	23.9	93.2
Fowl grass	3.6	16.4
California brome	1.8	12.8
Slender wheatgrass	1.2	16.0
Sedges	.5	12.8
Pine dropseed	.3	12.0
Reed canarygrass	.1	.8
Blue timothy	T ¹	1.6
Hairy tridens	T	1.2
Parry oatgrass	T	.8
<i>Subtotal</i>	31	4
FORBS		
White clover	15.6	94.0
Common dandelion	14.0	93.2
Western yarrow	3.1	73.2
Itchy fleabane	1.6	35.2
Starry cerastium	1.2	26.8
Wild strawberry	.9	19.2
Annual forbs	.3	12.0
Horse cinquefoil	.5	9.2
Bedstraw	.3	4.4
Black-eyed-susan	.2	8.4
Rocky Mountain iris	.1	1.2
Richardson geranium	T	1.2
Gumweed	T	1.2
Thistle	T	.8
Mountain parsley	T	.8
Blooming Salley	T	.4
Beauty cinquefoil	T	.4
<i>Subtotal</i>	37.8	
TOTAL PLANT	69.2	
Litter	5.0	93.2
Moss	.3	6.0
Rock	T	1.2
TOTAL COVER	74.5	
BARE SOIL	25.5	

¹ T signifies less than 0.05 percent cover.

Table 5.—Percent cover and frequency of grazed and protected plants on Bandelier National Monument Weather Station site, based upon 50, 20 × 50 cm plots.

LIFEFORM/species Other factors	Protected		Grazed by Elk	
	cover	freq (N=50)	cover	freq (N=50)
%				
GRAMINOIDS				
Kentucky bluegrass	42.4	98.0	18.9	100.0
California brome	1.8	32.0	.1	2.0
Slender wheatgrass	1.5	12.0	1.4	26.0
Sedges	1.7	8.0	.8	22.0
Hairy tridens		.2	6.0	
Parry oatgrass		.1	4.0	
Bearded wheatgrass	.1		2.0	
<i>Subtotal</i>	47.5		21.5	
FORBS				
White clover	.8	30.0	16.8	100.0
Western yarrow	11.4	90.0	1.8	72.0
Common dandelion	.8	20.0	2.2	76.0
Sweetclover	.6	22.0	.4	14.0
Itchy fleabane	.1	2.0	.8	20.0
Black-eyed-susan	.1	2.0	.7	26.0
Starry cerastium	.1	4.0	.4	16.0
Annual forbs	.7	28.0		
Parry thistle	.1	2.0	.1	4.0
Beauty cinquefoil	.1	2.0	T	2.0
Horse cinquefoil	.1	4.0		
Gumweed	.1	4.0		
Mountain parsley	.1	4.0		
Bluebell	T ¹	2.0		
<i>Subtotal</i>	14.9		23.4	
TOTAL PLANT	62.4		44.9	
Litter	19.5	100.0	4.0	90.0
Moss	.1	4.0		
TOTAL COVER	82.0		48.9	
BARE SOIL	18.8		51.1	

¹ T signifies less than 0.05 percent cover.

was nearly five times greater on the area protected from elk than on the grazed area and exposed bare soil was nearly three times greater on the area grazed by elk than where protected. It appears the area grazed by elk may be more susceptible to soil erosion than the protected area.

There was a 76% SPCC similarity between grazed and protected areas of the Weather Station site based upon species presence. Quantitative similarity (CZC) between the grazed and protected meadow vegetation was 47%. Protection from grazing did not influence plant species richness, although there were some differences in presence of a few minor species on this site.

Forage Production and Utilization

Total forage production measured on the montane meadows in the fall of 1992 was 712 kg ha⁻¹ (Table 6); however, elk were excluded from the production sample plots only after mid-June 1992 due to delay in construction of the exclosures. Thus, both the production and consumption data for 1992 are probably underestimated, perhaps by 50% or more.

Meadow production on 1 July 1993 was estimated to be 1108 kg ha⁻¹. By that same date, elk had consumed 594 kg ha⁻¹ or 54% of the available meadow forage. Montane meadow herbs continued to grow through the late summer into fall. Under continuous grazing by elk, total production at the end of the 1993 growing season was about 1,600 kg ha⁻¹ on montane meadows and utilization averaged about 45% in late October 1993. Data from 1993 indicate that elk consume roughly about

50% of the meadow forage throughout the growing season.

Nearly 700 kg ha⁻¹ of forage remained on La Mesa Fire grassland sites in late March 1993 (Table 6). Only about 150 kg ha⁻¹ or 20% of the forage was consumed by elk during the 1992–93 winter period, which had fewer elk than usual wintering in this area because of deep, crusty snow conditions (Allen, This volume). These snow conditions also may have reduced forage utilization on study sites during the 1992–93 winter period. In late October 1993, production data indicate that 950 kg ha⁻¹ of forage was measured on these same sites. Elk and other wild herbivores, such as deer, consumed only 250 kg ha⁻¹ or about 25% of the available forage during the summer period; however, most of the elk use is on higher elevation ranges during the summer.

Seasonal Elk Diets

Pellet group density data (Table 7) suggested that elk used montane meadows most heavily in May and June 1993, followed by May through October 1992, with minimal use from fall through early spring. These findings are not unexpected because there is little use of montane meadows by elk during the winter as deep snow typically force them onto lower elevation winter ranges. Conversely, we would expect fairly heavy use of meadows by elk in the spring when the forage plants are most succulent, nutritious, highly palatable, and digestible.

Kentucky bluegrass, beauty cinquefoil, bedstraw, sweetclover, and Louisiana wormwood were the most commonly selected forage plants on montane meadows (Table 7). Beauty cinquefoil and Louisiana wormwood were consumed in abundance throughout the year. However, there were some changes in species selection preference by season. For example, Kentucky bluegrass was the most important herbaceous plant consumed by elk during the summer and substantial proportions of beauty cinquefoil, bedstraw, and sweetclover were consumed during the late fall to early summer period. Other species were not major components of elk diets, although, slender wheatgrass, sage, and gambel oak were common in the July 1993 sample as were Arizona three-awn, sage, and white clover in the March 1993 sample. These and other species were consumed by elk very rarely during other periods of the year.

On montane meadows, the similarity of forage species consumed by elk was greatest during 5 Nov 91 to 10 May 92 and 28 Oct 92 to 23 Mar 93

Table 6. Production and utilization of forage by elk on Bandelier National Monument meadows and grasslands.

Date mo/da/yr	Montane Meadows		Mesa Grasslands	
	total forage	forage consumed	total forage	forage consumed
	kg/ha ⁻¹			
10/28/92 ¹	712±125 ²	192		
03/24/93	677±151	148		
07/01/93	1,108±494	594		
10/26/93	1,590±298	699	953±238	250

¹Total forage and forage consumed is based upon mid-June through October estimates.

²Values are means ± the standard error.

Table 7.—Seasonal composition of elk diets and pellet group density on Bandelier National Monument montane meadows.

Lifeform/species	Sample period			
	2 Sep 91– 10 May 92	10 May 92 28 Oct 92	28 Oct 92– 5 May 93	5 May 93– 1 Jul 93
	----- % of diet -----			
GRAMINOIDS				
Kentucky bluegrass	3.8	25.3	1.7	6.2
Slender wheatgrass	1.7	.0	.0	12.1
Arizona three-awn	2.7	.0	7.9	2.7
Meadow barley	.0	7.4	1.6	.0
California brome	6.8	.0	1.9	.0
Blue grama	.4	.0	4.4	1.8
Sheep fescue	2.0	.0	2.4	.0
Big bluestem	.0	.0	1.1	1.7
Mountain muhly	.0	2.5	.0	.0
Sedge	.0	.5	.6	.5
<i>Subtotal</i>	17.4	35.7	21.6	25.0
FORBS				
Beauty cinquefoil	19.5	6.9	12.9	12.3
Bedstraw	24.5	2.4	11.4	6.8
Sweetclover	16.0	5.5	9.1	1.3
Sage	1.7	.0	9.5	10.3
Rocky Mtn. penstemon 10.4	.0	4.0	.0	.0
White clover	.9	.0	12.8	.5
Common horsetail	.0	5.3	.0	2.8
Mexican silene	.0	5.0	.0	.0
Onion	.0	3.4	.9	.0
Richardson geranium	3.2	.0	.5	.0
Hoary aster	.0	1.7	.0	.2
Globemallow	.5	.0	.0	1.8
Piney golden pea	.0	1.9	.0	.0
Starry cerastium	.0	.0	.0	.8
<i>Subtotal</i>	76.7	32.1	61.1	36.8
BROWSE				
Louisiana wormwood	5.9	22.5	16.9	24.9
Gambel oak	.0	6.8	.0	10.6
Texas desert-rue	.0	.0	.0	2.4
Douglas-fir	.0	2.2	.0	.3
Mexican cliffrose	.0	.7	.4	.0
<i>Subtotal</i>	5.9	32.2	17.3	38.2
TOTAL	100.0	100.0	100.0	100.0
	----- density / 100m ² / month -----			
Pellet groups	1.5	6.3	4.6	10.8

with a SPCC of 79%. The SPCC similarities ranged from 52% to 65% during all other periods except 5 Nov 91 to 10 May 92 and 10 May 92 to 28 Oct 92 periods which had a SPCC of only 32%. Quantitative comparison of diets indicates less similarity between sample periods but again the two periods with greatest similarity were 5 Nov 91 to 10 May 92 and 28 Oct 92 to 23 Mar 93 with a CZC similarity of 55%. Most other periods had CZC similarities of 37 to 50% except for 5 Nov 91 to 10 May 92 and 10 May 92 to 28 Oct 92 periods which had a CZC of only 25%.

Pellet group density on grassland sites was reasonably uniform over all sample periods (Table 8). Pellet group density data suggested that elk use was heavy on grassland sites from fall to early spring during both 1991–92 and 1992–93, but use was also heavy during the spring of 1993. The only period of light use was summer to fall 1992 when most elk are on higher elevation ranges.

Graminoids comprised 43–55% of elk diets on grassland sites throughout the year, although there appears to be substantial variation within species

and lifeform between sample periods (Table 8). Blue grama was the most consistently consumed species throughout the year ranging from 8.7 to 27.3%. Kentucky bluegrass, little bluestem, and slender wheatgrass were also important dietary components during winter-early spring periods some years.

Forbs contributed heavily to year-long diets on the grassland sites providing approximately 36.1 to 44% of the diet. Common horsetail, horse cinquefoil, bedstraw, American vetch, Richardson gera-

nium, and Rocky Mountain penstemon were common elk diet components during at least one season of the year.

Louisiana wormwood, a browse species, was common in elk diets year-long on the grassland sites, comprising approximately 6 to 13% of the forage consumed.

The similarity of elk diets between sample periods was greater on the La Mesa Fire grassland than on montane meadow sites. There was 63–72% SPCC similarity in elk diets among all periods on

Table 8.—Seasonal composition of elk diets and pellet group density on La Mesa Fire grasslands.

LIFEFORM/species	Sample period			
	5 Nov 91– 12 May 92	12 May 92– 10 Nov 92	10 Nov 92– 24 Mar 93	24 Mar 93– 1 Jul 93
	% of diet			
GRAMINOIDS				
Kentucky bluegrass	13.5	1.9	12.5	21.3
Blue grama	8.7	27.3	11.8	14.1
Little bluestem	14.6	.5	.4	2.2
Slender wheatgrass	8.1	1.6	.0	2.6
Sheep fescue	1.5	3.7	8.4	.0
Arizona three-awn	2.3	.0	7.2	.4
Spike muhly	5.6	2.6	3.8	.0
Meadow barley	.0	4.4	.0	.8
Sedge	.4	.0	2.7	2.0
Rush	.0	2.4	.0	.0
California brome	.0	.0	1.2	.0
Letterman needlegrass	.0	.0	1.1	.0
Subtotal	54.7	44.4	49.1	43.4
FORBS				
Common horsetail	10.5	2.5	5.4	9.7
Horse cinquefoil	2.7	9.1	5.8	6.5
Bedstraw	8.9	5.9	.0	7.7
American vetch	.0	4.9	9.1	2.4
White clover	.9	3.6	6.0	3.4
Rocky Mtn. penstemon	2.1	.0	1.6	7.5
Richardson geranium	2.1	3.1	2.7	5.7
Sage	6.4	.6	.0	.0
Hoary aster	.0	2.9	2.1	.0
Bigelow groundsel	.0	3.9	.8	1.1
Mexican silene	.0	.0	2.8	.0
Onion	.5	.0	2.7	.0
Piney golden pea	2.0	.0	.0	.0
Subtotal	36.1	36.5	39.0	44.0
BROWSE				
Louisiana wormwood	6.4	10.3	10.5	12.6
Gambel oak	2.8	8.3	.0	.0
Texas desert-rue	.0	.0	1.4	.0
Slender janusia	.0	.5	.0	.0
Subtotal	9.2	19.1	11.9	12.6
TOTAL	100.0	100.0	100.0	100.0
	density / 100m ² / month			
Pellet groups	4.0	1.3	4.8	4.4

the grassland sites. Quantitative assessment of elk diets on grassland sites indicate a 60% CZC similarity between the periods 5 Nov 91 to 10 May 92 and 28 Oct 92 to 23 May 93 as well as 28 Oct 92 to 23 May 93 and 23 Mar 93 to 1 July 93. Quantitative similarity was less but uniform between other periods. The quantitative assessments suggest there is substantial similarity in forage species and the proportion consumed from year-to-year on a seasonal basis.

DISCUSSION

Blue grama, mountain muhly, mutton grass, and little bluestem are characteristic understory species of the ponderosa pine series (DeVelice et al. 1986). On the La Mesa Fire grassland sites only two of these species, little bluestem and mountain muhly, were common. Blue grama is difficult to establish and this may explain its near absence on the seeded burned sites. Although the present composition of vegetation cover deviates from the native composition, there appears to be adequate plant cover and litter to protect the site from deterioration. There is some evidence of surface erosion (pedestalled plants), but generally the grasslands appear relatively stable.

The montane meadows of Bandelier National Monument contain the typical early to mid-seral stage vegetation described by Elson and Fletcher (1989). Grazing by livestock up to 1977, and by an increasing population of elk since 1977, has slowed or temporarily halted succession. The major response to several years of elk exclusion on the grazed and protected portions of the Weather Station site was: 1) an increase in Kentucky bluegrass, California brome, and western yarrow cover; 2) a decrease in cover of white clover and common dandelion; and 3) the occurrence of several additional forb species.

Herbaceous production estimates from areas grazed by elk were also in agreement with the low to mid-seral stage wet meadows described by Elson and Fletcher (1989). Pond (1961) reported that clipping meadow vegetation to a 3-inch stubble height at two-week intervals did not seriously affect density of native plants but did reduce overall productivity. Clipping to a one-inch stubble height every two weeks, as is more representative of the current conditions on Bandelier National Monument montane meadows, reduced both production and density of native grasses and sedges. Montane meadows appeared stable, but heavy season long use has reduced plant vigor and

meadow vegetation may be susceptible to rapid deterioration following detrimental natural or human-induced events (e.g. drought).

Forbs and browse were consumed by elk in greater proportion than they occurred in study habitat types. A partial explanation of these findings may be either that forbs and browse are preferred by elk or that succulent grasses and forbs are more completely digested than woody browse. Consequently, the importance of species with a higher fiber content, such as browse, tend to be overestimated by the microhistological technique used in this study, while easily digested species are frequently underestimated (Stewart 1967, Croker 1959, and Ward 1990). Microhistological analysis also indicated that elk forage on habitats other than mountain meadows and La Mesa Fire grasslands

A study by Lang (1985) in the Pecos Wilderness indicated 77% of the diet consumed by elk in October consisted of grasses; this proportion is substantially greater than that found in the current study. Lang's data were also based upon stomach content analysis, which may not be directly comparable to fecal analysis data. Another consideration is that elk are mobile and the fecal material collected in one habitat type may not necessarily reflect forage consumed in that type. In fact, forage fragment analysis is probably more indicative of the plant species consumed throughout the home range of elk than that of the species consumed in the habitat type where the fecal material was collected.

Elk diets on grassland sites appear to be more closely correlated to the proportions of grasses, forbs, and browse in the immediate plant community than were found on montane meadows. However, grasses were consumed at a much lower rate than reported by Rowland et al. (1983) from the La Mesa burn site. Also, surprisingly little sheep fescue, the dominant grass locally, is observed in the pellets collected at the mesa sites. Note that the presence of horsetails in mesatop pellets reveals the movement of elk to areas like nearby Frijoles Canyon, where horsetail grows in abundance (C. Allen—personal communication). Collection and analysis of two additional years of data will undoubtedly clarify some of the initial findings.

CONCLUSIONS

Herbaceous vegetation including many native plants dominated the La Mesa Fire grassland sites, which appeared stable. However, two seeded

grasses, sheep fescue and western wheatgrass, cover 23% of the site and provide 55% of the total vegetative cover.

Warm season grasses such as blue grama, little bluestem, spike muhly, and Arizona three-awn were the principal forage species on the grassland sites. Although sheep fescue is the dominant grass here, it is relatively little-used by elk. But common horsetail, horse cinquefoil, bedstraw, and Louisiana wormwood from adjacent habitat types were important forage components throughout the year.

Vegetation cover on montane meadows consisted primarily of low to mid-seral introduced plant species. Heavy use by elk appeared to be the principal factor keeping these meadows in an early successional stage of vegetation. The shift in species cover and litter, after a few years of protection from elk, suggests montane meadows may respond rapidly to reduced elk grazing intensity.

Kentucky bluegrass, beauty cinquefoil, and bedstraw were the most common species consumed by elk on a year-long basis in the montane meadows. Other meadow species were consumed in substantial amounts throughout the year, as were forage species from adjacent habitat types, especially during early spring and summer.

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Heritage Resources and Fire Management: A Resource Management Crossroads

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Abstract.—Until the past few years Forest Service fire management had been characterized by a program of total wildfire suppression coupled with relatively small scale prescribed burning, having fuels reduction as the principle objective. As the organization moves toward “ecosystem management” the fire program is developing multiple, complex objectives employing a combination of wildfire suppression, prescribed natural fire, and both small and large scale prescribed burning. These changes raise some concerns with regard to heritage resource management and protection. However, fire managers and heritage resource specialists have a history of close working relationships in the Southwest, and through continued cooperation we are working to develop implementation strategies appropriate to changing land management objectives.

INTRODUCTION

An important human characteristic is our capacity for retrospection. We may look to the past out of historic, academic or even idle curiosity to gain a better perspective and understanding of some current phenomenon by examining its developmental sequence. Or we may look to the past for specific lessons that it can teach us. We can “revisit” events that occurred or decisions that were made in the past and view them in the light of what has come about over time as a consequence. If the results are largely consistent with our expectations, we may then either take no action or engage in some minor adjustments to a particular course of action. But if the results are not meeting our desires or expectations, we can take whatever steps are deemed appropriate. Lessons from the past will not necessarily tell us what is *the* correct course of action, but they will surely help us avoid repeating obvious mistakes and to alter a course that is not producing desired results.

The discussion that follows is retrospective on several levels. The main objective in the following discussion is to examine the current state of heritage, or cultural, resource management practices and objectives in light of what we have learned from 20 years of experience, but also in relation to developing trends in Forest Service fire manage-

ment practices. What we have learned in the past 20 years can be directly applied in devising management strategies appropriate to changing methods and objectives. To accomplish this it is necessary to set the stage by first discussing the qualities and characteristics of heritage resources which are significant in determining the general parameters of heritage resources management. Then, relying upon historical accounts, fire management policy decisions of the past are examined as a means of providing an understanding of some current day management objectives and related challenges. Finally, a retrospective look at heritage resource management actions and decisions specifically associated with the La Mesa Fire of 1977 is used to suggest that these actions and decisions provided the foundation that has structured the cooperative relationship between fire management and heritage resource management that will take us into the future.

HERITAGE RESOURCE MANAGEMENT REQUIREMENTS

Based upon a proposition that policy and procedures for management of a particular resource

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ought to be determined on the basis of qualities and characteristics inherent in the resource itself, let's first focus upon the specific management requirements of heritage resources apart from other considerations. First and foremost there are two attributes of heritage resources that make requirements of management somewhat unique - heritage resources are fragile and they are non-renewable.

The range of what constitutes heritage resources is very broad, including individual artifacts, such as pottery, arrow points, spear points, knives, manos, metates, ornaments, and the like, but also including a variety of historic and prehistoric sites, such as pueblos, pit houses, cliff dwellings, water diversion structures, soil retention structures, garden plots, caves, rock shelters, log cabins, homesteads, mines, canals, acequias, trails, quarries, rock art panels, and a host of others. On yet another level entire districts of interrelated historic properties can be and have been treated as significant heritage resources, such as the CCC era National Historic District at Bandelier National Monument. But what actually is meant by the notion that heritage resources are fragile?

A central value placed upon heritage resources by archeologists is that they are a source from which we can obtain information important to our understanding of the events and general developments which occurred in both prehistoric and historic times. From our archeological, scientific study of the past we will one day understand how societies came to be as we know them today, why certain societies have failed and disappeared while others have prospered and grown, and perhaps we will be able to formulate general principles of cultural evolution and behavioral change on a par with those of biological evolutionary theory. While there is information to be gained from physical objects and materials, equally if not more important are the spatial relationships between artifacts and features of sites, both on the ground surface and beneath the surface. When an archeological site is excavated according to a preconceived plan, using careful and controlled techniques in conjunction with detailed note taking, mapping, and photography, spatial relationships are preserved through documentation. Objects and their spatial relationships provide the data from which archeologists make inferences and draw conclusions regarding sequences of events at a site and the life style of a site's inhabitants. Operation of a piece of heavy equipment within a site, or any of a number of other surface and subsurface disturbing activities, can crush artifacts and eradicate spatial relation-

ships in an instant. Because it is so easy for human activities to destroy the information potentially obtainable from heritage resource site, heritage resources are regarded as fragile.

It must also be recognized that virtually every site is unique. For example, if we suffer the loss of a 2,500 year old camp site where normally dispersed Archaic peoples occupying a specific territory just south of Grand Canyon once banded together to share food and other resources for the winter season, we will never have the information that this particular site could have provided. We cannot grow another such site, nor can we turn back the clock 2,500 years and ask these Archaic peoples to recreate the events that took place here. Thus heritage sites are regarded as non-renewable.

In addition to the scientific information potential of heritage resource sites, they are valued by others for different reasons. American Indians currently living in the Southwest are the descendants of the peoples who once inhabited many of the heritage resource sites located on federally managed lands here. To this day, Indian peoples often carry out religious observances not only at obvious sites but also at other sacred locations on federal lands generally known only to specific practitioners themselves. Many of these observances are viewed as essential in preserving the tribe or pueblo's traditional way of life while providing a sense of place in the cosmic scheme of things. But not all sites on federal lands pertain to American Indians. Modern day America truly is a diverse nation of peoples from a variety of places and different cultural backgrounds. Many of the ethnic groups who make up our population have been in this country long enough to have established their own "history" here. It is important that we respect these differences in heritage and manage our lands to preserve evidences of everyone's history. Additionally, the overall interest of the American public in the subjects of history and prehistory is phenomenal, as indicated by attendance records at parks and monuments dedicated to preservation and interpretation of history and prehistory.

Other significant attributes of heritage resources that should be considered, at least in the Southwest, are their complexity, their preservation in large numbers, their potential to occur in virtually any physiographic setting (although highly concentrated in woodlands and lower elevation forests), and their occurrence in high to very high densities in particular areas. Given the landforms and vegetative patterns prevalent in the Southwest,

heritage resources located here are also often readily visible and evident even to the untrained eye.

Finally, we must consider the legal aspects of heritage resource management. Congress has demonstrated time and time again, through passage of a series of laws dating back to the 1906 Antiquities Act, a concern for preservation and protection of our nation's heritage resources. These laws have authorized the promulgation of numerous implementing regulations that affect federal land management. The resulting requirements and procedures include various levels of external review and oversight that must be adhered to in the compliance process before implementing land management activities.

In summary, our policies and procedures for managing heritage resources must take into account all of the above attributes: they are fragile, non-renewable, complex, numerous, ubiquitous, valued by a wide range of individuals and ethnic groups for various reasons, and they are specifically protected under a number of federal laws. This is a daunting array of characteristics which need to be taken into account in our basic management strategy, leading some to view heritage resource concerns as one of the more significant constraints upon a program which seeks to use fire to attain a host of resource management objectives. Before we address this concern, let's look first at current day fire management from a historical perspective.

TOTAL FIRE SUPPRESSION POLICY

In retrospect it is now widely recognized and accepted among natural resource managers that a poor management decision was made in American forestry in the early 1900s when a policy was established to rapidly and completely suppress all fire which might occur in our woodlands and forests. With hindsight we now recognize that fire, both natural and man-caused, plays a critical role in perpetuating the structural integrity of ecosystems; periodic fire helps maintain a dynamic equilibrium among the various components of an ecosystem. Fire is essential to the health of many ecosystems.

Based on current day observations of lightning-caused fires, few would argue with the proposition that naturally occurring fire has been a component of terrestrial ecosystems for virtually as long as there have been terrestrial ecosystems. With the eventual arrival on the scene of humankind and ensuing cultural developments over the past few

million years, an additional cause of fire was introduced into ecosystems when, at some unknown time in prehistory, humans appropriated fire from nature. Human-caused fires came to contribute importantly to the presence of fire in the ecosystem (Stewart 1956) and supplemented whatever role natural fire had heretofore played in ecosystem stability as well as change around the world. However, while humans were able to initiate fires which burned over large tracts of grasslands, woodlands, forests, and jungles, they were virtually helpless to control large fires, whatever their origin. But given a milieu of increasing social organizational complexity and technological sophistication in our recent history, man came increasingly to gain control over large fires, eventually arriving at an ability to consistently suppress fire so effectively as to interfere with "natural" processes.

According to one historian, as America moved into the 20th century, natural and man-caused fires had burned, and were continuing to burn, vast expanses of forested lands, while at the same time lumber men were rapidly and wastefully logging away, based on the belief that it was foolhardy to attempt to husband timber since it seemed inevitable to everyone that it would one day be lost to fire (Steen 1976:174). There were some, however, who realized that with rampant, uncontrolled logging and the associated increase in enormous forest fires, the industry would one day, perhaps in the not too distant future, be faced with shortages. Steen (1976: 174) notes that a real "wake up" call came in 1902 when the Yacolt Burn in Washington burned over 400,000 acres of timber and caused great financial losses. Realizing that individual companies were quite vulnerable to similar disastrous loss due to threat of fire, the industry began to band together and lobby for legislation that would lead to creation of a state fire warden's office. After a few spectacular infernos in 1910 in Idaho and Montana on national forest lands, the Forest Service turned its attention toward developing better means of fire-fighting, through actions such as increased patrolling in conjunction with more road and trail construction and improved fire fighting technologies including aerial surveys, smoke-jumpers, the Osborne firefinder, portable pumps, enhanced radio and telephone communications and the like.

While these developments were in progress, there were concurrent complex and somewhat Machiavellian political struggles occurring in the early decades of the 1900s (Steen 1976). What eventually came to be legislated as standard operating proce-

ture for federal forest management, in close cooperation with state and private forestry, was a policy under which all fire was to be rapidly and thoroughly extinguished; the only thorny issue was whether there would be federal or state control and regulation. History thus informs us that the development of the total suppression policy was largely based upon business and financial considerations, rather than, if not contrary to, sound principles of ecology and forestry. Suppression of all fire even became policy in our National Parks, despite their mission to maintain "natural" conditions.

Although it would come back to haunt us, this fire suppression policy was effective for decades. Baker, Dethloff, Maxwell and Treat (1988) note, for example, in the Southwestern Region that the fire situation on the Apache-Sitgreaves National Forest was clearly in control in the year of 1937 and that fire losses over the preceding decade had been extremely minimal, while post-World War II fire prevention on the Kaibab National Forest had been so effective that managers were starting to notice that the absence of fire was having an effect upon the appearance as well as the equilibrium of the forests. The missionary zeal with which the Forest Service implemented the policy is exemplified in events noted by S.J. Pyne (1982:163):

"During 1927 in Lincoln County, New Mexico, the scene of bitter frontier range wars in the nineteenth century, incendiary fires were constantly being set around a certain ranch ... When firefighters were indeed met with rifle shots, the sheriff and local forest supervisor set out after the unrepentant incendiary. In the ensuing shootout an innocent Forest Service clerk, commandeered as a driver, was killed along with the rancher".

THE CONSEQUENCES

Over hundreds of millions of years fire had come to be an essential component of many ecosystems, helping to maintain the dynamic equilibrium that ensured the degree of stability necessary for continuity. Total fire suppression constituted, in effect, removal of one essential component from an ensemble of systemically interconnected phenomena, precipitating accommodative changes in various other components. After a number of years of total fire suppression policy, there began to emerge the recognition that such policy was generating marked physical changes in the character and appearance of wooded and forested areas and was

having very undesirable effects with regard to ecosystem health. For example, consider ponderosa pine forests of the Southwest that experienced low intensity, high frequency fires for millennia. These fire-dependent forests exhibited open stands of large trees, with vigorous grass understories, giving a park-like appearance. Total fire suppression, in conjunction with heavy grazing and logging activities, have changed these forests so that many stands of young trees are crowded together in thickets beneath the few remaining old, large trees, accompanied by heavy accumulations of fuels on forest floors and marked reductions in herbaceous understories (Covington and Moore 1994: 39). Such conditions have led to declines in biodiversity and are conducive to widespread outbreaks of insects and disease problems, with the threat of disastrous, unnaturally intense wildfires ever-present. Indeed, this is the scenario that led to the 1977 La Mesa Fire (Foxy and Potter 1984).

Recognition of the deleterious effects of removing fire from the picture was not an overnight discovery, although as many as 70 years ago some individuals in the Forest Service were well aware of the increased potential for disastrous conflagrations fostered by a build up of fuels (Leopold 1924).

Some foresters, such as Aldo Leopold and C.K. Collins, began to recognize the contribution of fire in the maintenance of grass and pine forest in the Southwest and were aware of the positive results of the burning habits of the Indians, which had contributed to the evolution of the high quality forests that the Anglo-Americans found. (Baker et al. 1988: 115).

Collins and others had discovered that the great achievements in fire suppression since the 1930's had begun to make the national forests a veritable tinderbox. (Baker et al. 1988: 116)

As these changes came to be recognized and their causes came to be understood, Forest Service fire policy began to change in the late 1960s and 1970s. Baker et al. (1988: 116) regard 1967 as a "watershed" in the fire policy of the Southwestern Region when they note that:

Fire suppression began to be replaced by fire control as a major policy objective. The change from the view of fire being only an enemy to fire being both an enemy (wildfire) and a friend (prescribed fire) was slow to take hold within the Forest Service and within the

Southwestern region. The shift took place slowly, perhaps only over the last 20 to 30 years.

STANDING AT THE CROSSROADS

Having recognized various deleterious effects resulting from total fire suppression policy, many are now espousing an urgent need to reintroduce fire into ecosystems through prescribed burning and prescribed natural fire. The use of prescribed fire to reduce accumulating fuel loads has been steadily increasing in the Forest Service since the recognition of its beneficial effects. Over the past 15 to 20 years the prescribed fire program has been characterized by relatively cool burns of sufficiently small scope that any given project was contained within an area having general uniformity of terrain, vegetation type and fuel loading. Individual burn units have typically been small enough that they could be burned during a given work day.

Some managers are understandably eager to return grassland, woodland, and forest ecosystems to healthy conditions immediately and stand poised to rapidly adopt prescribed fire programs designed to accomplish a whole range of resource management objectives including fuels reduction, slash disposal, wildlife habitat improvement, stand replacement, type conversion, and general restoration of ecosystem health. Some of these objectives necessitate very hot fires, while others require large scale burning of project areas containing tens of thousands of acres with a wide range of variability in terrain, vegetation types and fuel loadings. The range of fire behaviors one might anticipate in such extensive projects is likewise relatively wide, which suggests increased complexity of fire control considerations. We are also in the process of instituting prescribed natural fire plans that cover, in some cases, hundreds of thousands of acres.

Thus, we have arrived at a crossroads. Various avenues of management options lie before us, and although we have looked to the past and seen the undesirable consequences of a flawed policy, we cannot simply return to the past. While we are eager to return our environment to a healthy condition, the potential beneficial effects of fire must be weighed against other resource management considerations. The prevailing conditions of today's ecosystems are not the conditions which existed in the days before total suppression - we are operating under a set of changed parameters. We do not

have open, park-like stands of large, mature trees with grass understories. Many forested areas are now characterized by excessively thick growth of small and medium-sized trees underlain with heavy leaf, needle and branch debris. Many woodland areas are now characterized by the virtual absence of ground cover that might act as a carrier for surface fires, forcing us to seek means of burning such areas that are markedly different from the burning of pre-suppression days. Rather than "re-introducing" fire, what we are actually considering is initiating fire into areas and situations that have come to be as they are because of the absence of fire. It also appears that we are moving rather hastily toward fire management projects that fall somewhere between the controlled, prescribed burning of the past, with the primary objective of fuels reduction, and a new range of projects more closely approximating wildfire with a host of resource management objectives. This being the case, there are various resource concerns that will function to constrain and help guide fire management projects, such as heritage resources, soils, air quality, wildlife habitat, and watershed protection.

WILDFIRE IMPACT STUDIES

In the 15-20 years that federal land-managing agencies have been in the business of heritage resource management, we have learned a great deal about potential impacts to the resource from a host of different kinds of undertakings, including fire management. A considerable amount of very useful data have been gathered from several studies conducted following wildfires here in the Southwest. One of the earliest studies, although rather informal, was carried out in connection with the Little Moccasin Canyon Fire in Mesa Verde National Park in 1972. Following a 1,080 acre fire in pinyon, juniper and oak brush, Switzer (1974) documented a number of impacts to heritage resources after a cursory inspection of several burned over sites.

The landmark study which has set the standard for subsequent studies of impacts on heritage resources is *The 1977 La Mesa Fire Study* (Traylor, Hubbell, Wood and Fiedler 1990). The La Mesa Fire burned out of control for seven days over about 15,000 acres on Bandelier National Monument, Santa Fe National Forest and Department of Energy lands. A combination of years of fuel accumulation on the ground, forest structural change, critically low moisture, and high winds created a wildfire situation that necessitated complex, intense,

closely coordinated fire suppression activity involving hand crews, bulldozers, slurry bombers, water tankers, and helicopters. By the time the fire was contained, miles of hand and cat line had been constructed along with clearings for a number of helispots. One of the decisions made in combatting the La Mesa Fire which has since become standard procedure was the deployment of archeologists, about 30 in all, to work along side fire line construction crews and to monitor mop-up activities; this was a "first" in combatting such fires. Following the fire, archeologists conducted surveys and inspections of all construction disturbance areas to assess the impacts to heritage resources. From site surface inspection data, damage was assessed at 58 sites which had been burned over. Three of these sites were excavated, and a fourth tested to determine the extent to which heat had penetrated beneath the surface and to assess whether archeological materials below the surface had been affected.

The La Mesa Fire study is notable for its exceptional documentation of a full range of fire-related impacts to heritage resources through implementation of systematic data gathering and detailed analyses of a host of related cultural and natural phenomena. Although the study was not formally published until 1990, the manuscript had been readily available for a number of years previously and served as the basic body of data in the Southwest, if not the nation, on the effects of fire on heritage resources. The National Park Service deserves much credit for undertaking this pioneering effort. There have been subsequent heritage resource impact studies following wildfires, including the 4,600 acres Radio Fire on the Coconino National Forest in 1977 (Pilles 1984), as yet unpublished work on the Yellowstone fires of 1988, the 3,000 acre Long Mesa Fire in Mesa Verde National Park in 1989 (Einger 1990), and the 800 acre Henry Fire on the Santa Fe National Forest in 1991 (Lent, Gaunt and Willmer: In press). These studies have incorporated a few new considerations, such as complete survey of burn areas, but most have added little to the initial findings from the La Mesa Fire study.

The Henry Fire study did break some new ground in that it attempted to go beyond basic post-fire documentation. Because the fire occurred in an area that had been previously surveyed, some pre-fire baseline data were available for comparison. Most significant, however, was the involvement of fire behavior specialists in the research design, post-fire survey, and analysis. Fire behavior characteristics were estimated for each site, and an attempt was made to correlate those characteristics

with the nature and severity of site damage as determined from field observations and analyses of surface and excavated cultural materials.

What have we learned from these studies? Following past authors (Lissoway and Propper 1990) I find it useful to view fire effects on heritage resources in two broad categories: one includes the impacts resulting from fire itself, and the other involves impacts resulting from fire suppression, mop up and rehabilitation activities. It is useful to further subdivide these categories into direct and indirect effects.

As regards direct effects of fire we know from the La Mesa fire and subsequent studies that the nature and severity of damage depends upon fire intensity, duration of heat (residence time), and heat penetration into the soil. These three conditions, in turn, are directly related to the density and size of fuels on and adjacent to a site. Depending upon the exact nature of the above conditions, wooden objects, bone, plant remains, plant pollen - any combustible material - can be consumed partially or completely by fire. Stones used in building and food grinding/processing can become discolored, cracked, spalled or even disintegrated. Cracking, spalling, and discoloration can also occur to chert and obsidian lithic materials used for tool making, while obsidian, a volcanic glass, can be melted. Pottery sherds, the source for a wealth of archeological information, can become spalled, split into pieces and/or discolored, sometimes having surface designs burned completely away or clay paste characteristics altered. Rock faces containing pictographs and petroglyphs can be scorched and spalled. The potential to derive dates from pottery, obsidian, tree-rings, charcoal and/or fire hearths can be destroyed if such materials are on or near the ground surface.

For a number of years, fire effects studies described the points at which damage starts to occur in terms of temperature, a measure not very usable in fire behavior analysis. The results of the Henry Fire study were encouraging because they indicate that thresholds where damage begins might be identifiable for particular classes of cultural materials for fairly specific fire behavior characteristics, such as fire line intensities. Indirect effects of fire on heritage resources include erosion and eventual uprooting of fire-killed trees that can damage site features and displace artifacts.

Studies have also documented that the most severe impacts to heritage resources result not from fire itself but from fire suppression, mop up and

rehabilitation activity. These activities have a direct potential to damage or destroy artifacts, architecture, and other site features, and to obliterate information-rich spatial relationships among materials both above and below the surface. Such suppression-related activities include hand line construction, cat line construction, road and helispot construction, general vehicular traffic in a burn area, laying out and moving hoses, retardant dropping, digging of burning roots and stumps, snag felling, water bar construction, berm leveling, use of heavy equipment for seeding or site prep prior to planting, salvage logging, and fuelwood collecting. Indirectly, heritage resources are put at risk because their locations become known to large numbers of people working in an area where site visibility is greatly enhanced due to the absence of vegetation. The more widely known the location of a site, the greater the chances that surface collecting and illegal excavation will occur.

Fortunately, a number of factors have helped reduce the impact of suppression and related activities on heritage resources. Archaeologists are now routinely included on most suppression and rehab teams when heritage resources are present. Modules on the effects of fire on heritage resources have been added to agency fire management training programs. And discussions of heritage resource values are frequently included in fire management conferences and publications, all contributing to increased awareness and sensitivity. A recent bibliography on fire effects on cultural resources, published by the Bureau of Land Management (Knight 1994), attests to the amount of attention this topic has received, particularly over the past ten years. On the Henry Fire, for example, heritage sites were a major consideration in the suppression effort, and damage due to fire suppression and mop up activities was minimal. However, because this is not uniformly the case, continued emphasis in this area is essential.

IMPLICATIONS FOR PRESCRIBED FIRE

The above findings are based on conclusions drawn from wildfire studies, and one might well ask how the findings pertain to prescribed fire. It should be apparent that any of the listed ground-disturbing activities, many of which also occur in the conduct of prescribed burn projects, have the same potential to affect heritage resources. We also know from wildfire-related studies that the nature and extent of damage to archeological materials is directly related to fire intensity, duration, and heat

penetration into the soil. But in prescribed burning we can exercise a certain degree of control over these parameters of fire behavior. This improved control, in conjunction with reductions in ground-disturbing activity, present prescribed fire managers with at least the potential for reducing risks to heritage resources, with corresponding reductions in the amount of pre-burn survey and site protection or mitigation measures. This is reflected in some of the management strategies currently followed in the Forest Service.

Not all kinds of sites are equally at risk from fire at lower intensities nor do all areas of the forest have equal potential for the presence of sites. There are certain steps short of complete survey that can be taken to assess the likelihood of historic sites in an area, such as checking results of previous surveys in the area, consulting historical maps and records, examining aerial photographs, and directing personnel who are involved in fuels inventories and other pre-burn activities to be especially watchful for historic sites with combustible materials. In some cases where the presence of sites with combustible materials can be reasonably ruled out, we have burned certain high elevation areas and steep slope areas with low intensity fires with minimal or no survey in concurrence with State Historic Preservation Office review. Prescribed burning has also proceeded with reduced survey in project areas located at lower elevations or on gentler slopes if fire line intensities are going to be kept low and less fragile sites are the only kinds of sites known or expected to be in the area. However, in certain instances, such as when fire intensities are likely to be high and fire-sensitive sites are likely to be present, burn areas receive complete survey and most sites are recommended for protection or mitigation. This certainly does not mean the project cannot proceed; it does mean that extra caution and care are required. In such cases sites can be protected through various means, such as briefing all burn personnel on identification and required protection for sites, eliminating a portion of the area from burning, wet lining or black lining around sites to exclude fire, and removal or reduction of fuels from in and around sites. Using these and other practices, prescribed burning projects can proceed while heritage resource sites receive appropriate protection.

CURRENT RESEARCH

In developing the appropriate strategy for heritage resource management in particular prescribed

fire projects, we generally opt for a conservative or cautious approach. Although we know from wild-fire studies that low fire intensities are not a threat to certain kinds of heritage resource sites, we do not currently know the thresholds at which fire damage starts to occur to various archeological materials. Building from the Henry Fire study (Lent et al.: In press), the Forest Service's Rocky Mountain Forest and Range Experiment Station, in partnership with the Santa Fe National Forest, New Mexico BLM, and the NPS Southwest Region, established a cooperative agreement with the Museum of New Mexico to conduct research aimed at determining these thresholds. Much of the field work is taking place on the Santa Fe National Forest. The basic approach to research consists of experimental burning across both actual and artificial sites under different fuel loadings within different fuel models to try to establish these thresholds. Although fire managers can potentially burn under any one of 12 fuel models, the research is focused upon the six most commonly burned in the Southwest. Burning is initially conducted under conditions of both light and moderate fuel loading, with an option to also test under heavy fuel loadings if appropriate. At both actual and artificially created sites a variety of specific provenience locations (e.g., on top of the duff layer, on the ground surface but beneath the duff layer, five centimeters below the ground surface, etc.) are "salted" with artifacts. The physical condition of these artifacts is thoroughly analyzed and documented prior to placement. Archeologists work closely with fire personnel in determining which sites are to be burned, which fuel models are represented, what fuel loadings are present, and when the burn should occur. The actual controlled burning is carried out completely by fire personnel, preferably in conjunction with an already planned prescribed fire project. Following the burn, archeologists recover all materials and once more analyze them to determine fire effects and assess whether or not effects are significant in terms of loss of integrity, research potential, or other factors. The results of this research will provide some badly needed data to help us devise management strategies appropriate to the various circumstances and conditions under which we conduct prescribed burning today and in the future.

CONCLUSIONS

Although the research outlined above is still in progress, preliminary indications are that fire dam-

age to heritage resource sites and materials occurs where slash from logging and thinning has accumulated on the surface beyond what might occur naturally, leading to a very hot fire with relatively long residence time. Many areas of the forests and some woodland areas contain these unnatural accumulations of slash. Such areas are commonly the location of prescribed burning projects in the Forest Service. This underscores the need to proceed with caution as we move to undertake vastly larger burn projects with complex objectives. Variability in terrain, vegetation types and fuel loading over large areas makes it more difficult to accurately predict fire behavior at any specific locality. If fire behaves in a manner significantly different from pre-burn predictions, we may be faced with conditions that approximate those of wildfire in certain portions of large burns. Experience has shown that we simply must be able to first predict then control fire intensity and duration on or adjacent to heritage resource sites if we are to prevent damage or loss. For example, in a recent large prescribed fire on the Santa Fe National Forest, fire entered six sites having combustible materials present where we had taken what we felt were adequate precautions to see that fire was excluded. The sites were damaged to various degrees. This indicates that it may be necessary to exclude certain portions of large projects and burn them under more tightly controlled conditions. Additionally, in large complex burns the chances of fire getting out of control are multiplied. If controlled fire escapes and becomes wildfire, the likelihood of damage to not just heritage resources but to a host of resources including timber, fuelwood, range, soils, wildlife and wildlife habitat, as well as water quality, are greatly increased. Thus burning of large areas with complex patterns of terrain, vegetation, and fuel loadings should be approached with considerably more caution than burning of small areas where conditions are generally much more uniform.

However, I believe that as we move toward management of multiple resources from an ecosystems perspective, we need to direct management efforts in our fire program, as well as in other functional areas, to those projects which will result in the greatest benefit to the greatest number of resources considered together. When we become too narrowly focused upon a single management objective, then any of the various other resource objectives tend to be viewed as constraints or limitations upon our focal objective. Working closely with fire managers, beginning essentially with the La Mesa Fire, archeologists have learned a great deal about

the potential for fire and fire management activities to effect heritage resources. Prior to the La Mesa Fire many would likely have scoffed at the notion of archeologists accompanying fire fighting crews. In retrospect this was an excellent management decision and the practice has now become standard operating procedure in many places. Archeologists are now routinely "red-carded" and frequently participate in various aspects of fire management. Working closely with fire managers, as in the research project cited above, has given archeologists the necessary understanding to devise strategies for protection of heritage resources that call for greater care and vigilance in our burn projects, but ultimately do not unduly restrain attainment of fire management objectives.

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Management Lessons of the La Mesa Fire

Milford R. Fletcher¹

When I was asked to summarize the management lessons learned from the La Mesa fire, I thought to myself that this would be a short discussion. Staff and management changes often leave Parks and National Forests with little historical or institutional knowledge of past events such as floods or fire. As a result, historical and institutional memory are lost. Additionally, many managers are not completely aware of the powerful influences that fire has on ecosystems, and the consequences of a "hands off" philosophy in fire management.

For example, in the mid-1970's the Southwest regional office of the National Park Service gathered fire managers and superintendents together with noted fire researchers to learn new techniques and research regarding fire management. E.V. Komarek of the Tall Timbers Research Institute was one of the speakers, and, in his dynamic way, he pointed out the benefits of fire management and the consequences of immediately extinguishing all fires. When the conference was over, Deputy Director (NPS) Ted Thompson came to me and expressed his concern. He had spent his entire career "protecting" park resources from fire, only to find out later that his efforts were not only misguided, but actually harmful to the very resources he was dedicated to protect.

The contrast between then and now is striking. National Park Service Deputy Regional Director Mary Bradford opened this conference, and welcomed the knowledge that this symposium will bring to public land managers. She charged land managers to use that knowledge in the planning of strategies to include fire as a natural component of ecosystem management. Today, I believe that most of our land managers are aware of the basic need to include fire considerations in many aspects of land management, from improving winter range for livestock and wildlife to managing cultural resources in the backcountry.

Unlike the 1970's, when much of the opposition to prescribed fire management came from within, the opposition now comes from outside the fire and management community - specifically from a

public which is largely ignorant of the role fire plays in the ecosystems of the Southwest. With the passage of the Clean Air Act smoke management has become a public issue, and blackened areas in parks or public forests always cause public comment.

I submit that the education process now needs to be broadened, from resources managers to the public in general. In New Mexico we have more than 25% of the population concentrated in one metropolitan area. We need to take every advantage to inform the public as to what we are doing and the rationale behind the decisions. At one time the Southwest Fire Council in cooperation with various fire management agencies had a booth at the State Fair, with a uniformed representative of an agency on duty to answer questions, hand out information, and generally meet and greet the public. This was a good idea, and still is. In 14 days we can meet over 300,000 citizens.

We *can* inform the public and change the way they perceive us and our management of fire. We taught the public to "pack it in, pack it out", and to recycle plastic, aluminum and so forth, and even educated them on very controversial subjects, like removing feral burros from Bandelier, Death Valley, and Grand Canyon to preserve the native ecosystems. This challenge is no greater than those we have faced in the past. Let's all go out and do what we can to tell our story, and make people understand why an occasional blackened forest or smoke cloud is not necessarily detrimental to the resources we manage and they enjoy.

In conclusion, I am extremely impressed by the volume and depth of the information which has resulted from the research on the La Mesa fire. It has exceeded our hopes when we started this project some 17 years ago. The data presented at this symposium provide a substantial basis for future interpretation and fire management activities in the Southwest. Now we need to interpret cryptogams and nitrogen cycles in terms of Bambi and

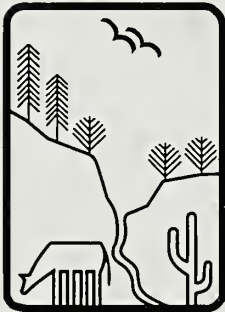
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bluebirds - subjects more familiar and dear to the public. In our interpretation of research data from the La Mesa Fire, we need to find common denominators with which the public can identify and associate, and proceed with the task of explaining the rationale behind fire management on public lands.

We have learned a great deal about the ecology of fire since the 1977 La Mesa Fire. I hope that we can all get together in 17 more years, in 2011, and share our continuing discoveries on the long-term effects of fire in the Southwest.



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Mountains



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Rocky Mountain Forest and Range Experiment Station

The Rocky Mountain Station is one of seven regional experiment stations, plus the Forest Products Laboratory and the Washington Office Staff, that make up the Forest Service research organization.

RESEARCH FOCUS

Research programs at the Rocky Mountain Station are coordinated with area universities and with other institutions. Many studies are conducted on a cooperative basis to accelerate solutions to problems involving range, water, wildlife and fish habitat, human and community development, timber, recreation, protection, and multiresource evaluation.

RESEARCH LOCATIONS

Research Work Units of the Rocky Mountain Station are operated in cooperation with universities in the following cities:

Albuquerque, New Mexico
Flagstaff, Arizona
Fort Collins, Colorado*
Laramie, Wyoming
Lincoln, Nebraska
Rapid City, South Dakota

*Station Headquarters: 240 W. Prospect Rd., Fort Collins, CO 80526

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