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THE ECOLOGICAL LIFE ZONES OF PUERTO RICO AND THE U. S. VIRGIN ISLANDS

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RESUMEN

La mayoría de los países neotropicales, excepto México y Brasil, han sido delineados en mapas por el sistema Holdridge de zonas de vida natural. Para poder comparar con estas áreas, se hizo un mapa de Puerto Rico y las Islas Vírgenes, el que incluye una descripción de cada una de sus zonas de vida. El texto en Inglés contiene balances hídricos, una descripción de la teoría Holdridge sobre biotemperatura, y muchos más detalles en general. La corta versión en Español se ofrece como manual de campo para ser usada con el mapa.

En estas islas hay seis zonas de vida, las cuales existen también en Centro y Sur América, representando allí áreas extensas. Con este mapa será posible aplicar directamente en estas áreas investigaciones hechas en Puerto Rico y las Islas Vírgenes y, a la inversa, prácticas satisfactorias llevadas a cabo en dichas áreas serán aplicables en las zonas de vida correspondientes en Puerto Rico y las Islas Vírgenes.

SUMMARY

Most of the neotropical nations except Mexico and Brazil are mapped according to the Holdridge system of ecological life zones. In order to have comparability with these areas, Puerto Rico and the U.S. Virgin Islands were mapped and a discussion and a description of each life zone were written. The manuscript in English offers water balances, a description of the Holdridge theory of biotemperature, and greater detail in general. The shortened version in Spanish is intended as a field manual to be used with the map.

Six life zones are present on these islands and are present also in South and Central America, representing large areas there. Research done on the islands will be directly applicable to those areas and conversely, successful practices done there will be applicable in corresponding life zones on the islands.

THE ECOLOGICAL LIFE ZONES OF PUERTO RICO AND THE U. S. VIRGIN ISLANDS[1]

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INTRODUCTION

The ecosystems of the Commonwealth of Puerto Rico and the U. S. Virgin Islands are extremely important for two reasons. First, they form a substantial component of the life-support system for nearly three million people. Second, environmental changes due to man's impact show up quickly on densely populated islands; this region can, therefore, indicate to other tropical and subtropical countries the kinds of changes that they might expect in the near future.

During the past 100 years Puerto Rico and the U. S. Virgin Islands have gone through a cycle consisting of massive degradation of their natural ecosystems (see, for example, Wadsworth, 1950) followed by an increasing general awareness, within the past five years, of the importance and unique and fragile nature of the plant-animal communities of this region. Ecosystem modification in the past was primarily due to agricultural activities, while today the issues are highways, transmission lines, ports, refineries, mines, power plants, and urbanization. Although ecological considerations now constitute an integral part of most land use planning, much remains to be done.

This life zone map, tied to a world-wide system, was prepared to facilitate comparisons and the flow of related ecological information into Puerto Rico and the U. S. Virgin Islands from countries which encompass similar environments. Likewise, these countries, most of which have not yet undergone the degree of ecological modification that Puerto Rico and the U. S. Virgin Islands have, may benefit from the experiences of these islands.

In Puerto Rico and the Virgin Islands the ecosystems have been better studied than in most tropical regions. Ecological studies of the area prior to 1900, most of which were qualitative observations, have been summarized by Wadsworth (1950). Murphy (1916) was one of the first to provide detailed descriptions of Puerto Rico's forests after the turn of the century. His work was followed by the classical study (involving less than four months of field work!) by Gleason and Cook (1926) (see also, Cook and Gleason, 1928), which is still a standard reference for descriptions of Puerto Rican plant communities. About 20 years after the Gleason and Cook study, J. S. Beard began a series of investigations throughout the Caribbean, summarized in his monograph on the vegetation of the Windward and Leeward Islands (Beard, 1949). Dansereau (1966) published physiognomic and floristic descriptions of more than 100 vegetation types in Puerto Rico, but did not include a detailed map of his units. A companion article by Buell and Dansereau (1966) did, however, contain maps of the vegetation of the Roosevelt Roads military base. Williams (1967) described several vegetation types in Puerto Rico from a physiognomic and

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floristic viewpoint and compared them to forests in Southeast Asia and Texas. He used the map of forest types and forest regions prepared by Little and Wadsworth (1966). Several in-depth studies of specific forests have recently been carried out in Puerto Rico, most notably the studies by Odum and co-workers (Odum, 1970a) and by Howard and co-workers (Howard, 1968, plus sequential articles in same journal) in two vegetation types within the Luquillo Experimental Forest.

The basis of classification used for this map was the life zone system devised by Holdridge (1947, 1967). Its desirable features include: 1.) it is simple enough to permit classification based on data likely to be available or easily obtained; 2.) it encompasses the variation inherent over the earth's surface, yet without creating a huge number of units which differ only slightly among themselves; 3.) it is reproducible, such that individuals working independently classify similar landscape units in the same way; 4.) it is hierarchical, permitting the subdivision of primary units into locally important sub-units; and 5.) its units seem to bear a close relationship to natural and biologically meaningful landscapes, *i.e.* the units produced a recognizable order from the apparent chaos of nature.

The life zones mapped are broad bioclimatic units, each of which may encompass a variety of soils, vegetation, microclimates, and land use patterns. The Holdridge system of life zone classification has now been applied to enough areas (Table 1) so that it has become a useful tool for comparing widely separated locations. Some of the maps (*e.g.* Perú, Colombia, Venezuela, Ecuador, Dominican Republic, Panamá) have been accompanied by monographs containing descriptions of many of the life zones, their vegetation, and the prevalent land use patterns.

THE HOLDRIDGE MODEL

Holdridge first published his classification of world plant formations (now more correctly termed "life zones") in 1947. In the ensuing 26 years various minor refinements and modifications were made in that original scheme—primarily changes in nomenclature—and these have been incorporated into the presently used diagram, Figure 1.

Life Zones

Each life zone lies within: 1.) a Latitudinal Region (left side of Figure 1); 2.) an Altitudinal Belt (right side of Figure 1); and 3.) a Humidity Province (bottom of Figure 1). The variables used to delineate any given life zone are mean annual precipitation and mean annual biotemperature.

Mean biotemperature is mean air temperature modified by substituting zero for values outside the range of 0 to 30 C, as discussed in Appendix A. The mean biotemperature scale appears along the sides of Figure 1. The values decrease geometrically from 30 at the bottom to 1.5 C at the top. The Latitudinal Region at any given location is determined by increasing the mean biotemperature to the value it would have at sea level. For making this conversion a lapse rate of 6 C per 1000 m is commonly used; most areas of the world fall in the range of 5.5 to 6.5 C per 1000 m. The mean biotemperature *not* corrected for elevation at any place determines the Altitudinal Belt. In naming life zones the name of the Altitudinal Belt is dropped from the lowest Altitudinal Belt within a given Latitudinal Region. Thus, we refer to Subtropical Wet Forest, rather than Subtropical Premontane Wet Forest.

Table 1. Countries which have been mapped according to Holdridge's life zone system.

COUNTRY	MAP SCALE	REFERENCE*
Colombia	1:1,000,000	Espinal *et al.* (1963)
Costa Rica	1:750,000	Tosi (1969)
Dominican Republic	1:250,000	Tasaico (1967)
Ecuador	1:1,000,000	Vivanco de la Torre, *et al.* (no date)
El Salvador	1:1,000,000	Holdridge (1959a)
Guatemala	1:1,000,000	Holdridge (1959b)
Haiti	1:500,000	OAS (1972)
Honduras	1:1,000,000	Holdridge (1962b)
Jamaica**	1:500,000	Gray and Symes (1969)
Nicaragua	1:1,000,000	Holdridge (1962c)
Nigeria**	1:3,000,000	Tosi (1968)
Panamá	1:500,000	FAO (1971)
Perú	1:1,000,000	Tosi (1960)
Thailand (seven sites)	1:500,000	Holdridge *et al.* (1971)
United States, East of the Rockies**	1:26,800,000	Sawyer and Lindsey (1964)
Venezuela	1:2,000,000	Ewel *et al.* (1968)

* For countries which have been mapped more than once only the most recent work is cited.
** From climatological and topographic data.

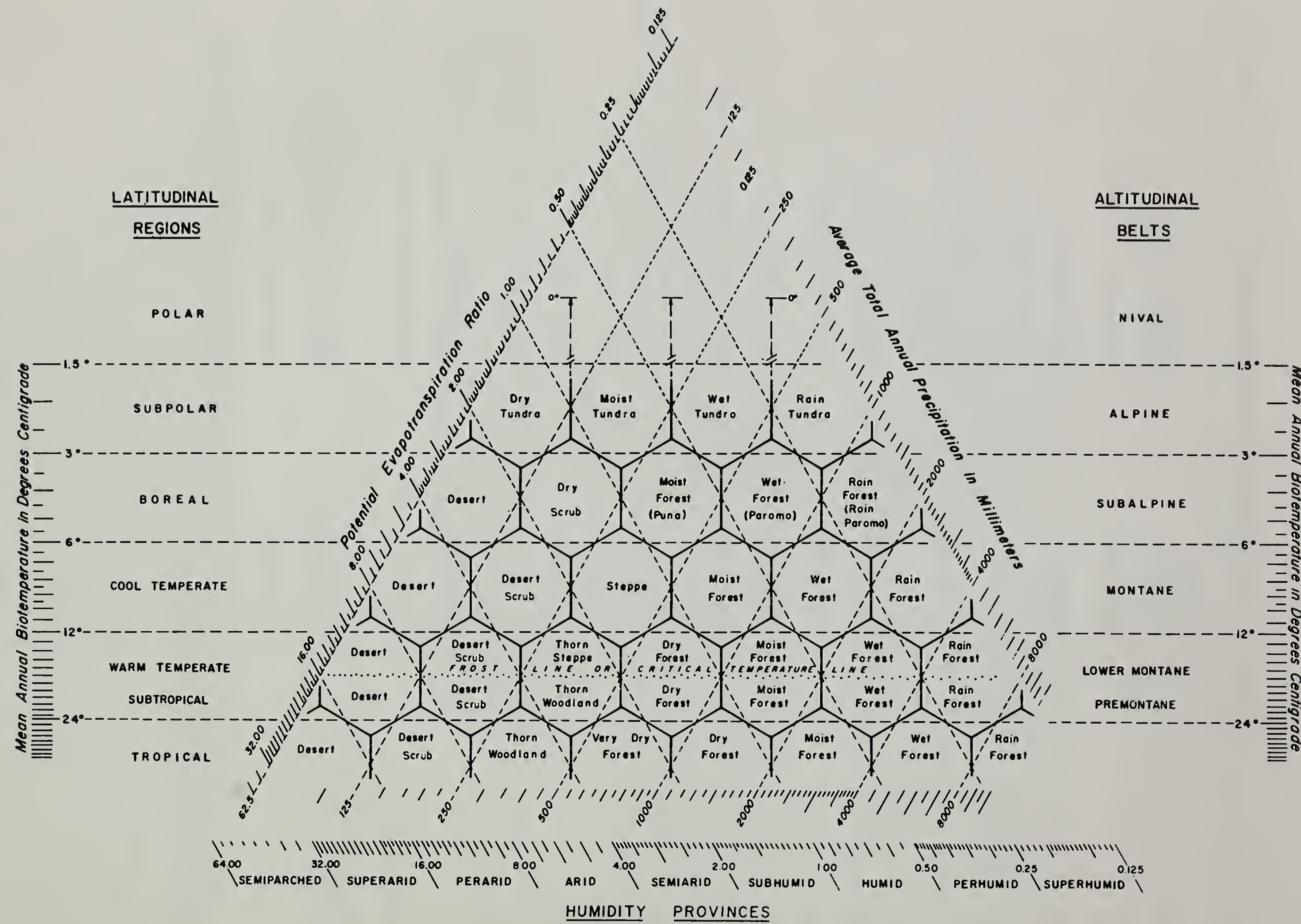

Figure 1 Diagram for the classification of world life zones according to the Holdridge system. (Diagram courtesy of Tropical Science Center, San José, Costa Rica).

Mean annual precipitation is the second variable used to define life zones. Precipitation lines traverse Figure 1 from the bottom upward and to the right at a 60° angle. The values shown increase from a low of 62.5 mm per year at the left-hand side of Figure 1 to values in excess of 8000 mm per year at the lower right-hand corner of the chart. As with biotemperature, the scale of mean annual precipitation is geometric.

Mean annual biotemperature and mean annual precipitation bound in two directions the hexagons which circumscribe life zones on the chart. The final boundaries are formed by the potential evapotranspiration ratio, which is the ratio between mean annual potential evapotranspiration and mean annual precipitation. It is, therefore, a general statement of wetness or dryness of the environment as indicated by the names of the humidity provinces at the base of Figure 1. The potential evapotranspiration ratio line of 1.00, where mean annual precipitation equals mean annual potential evapotranspiration, is drawn diagonally across the chart. Life zones to the left of this line tend to have an annual water deficit, while life zones located to the right of this unity line tend to have an annual water surplus.

The hexagonal boundaries which delineate the life zones connect the midpoints of the series of triangles resulting from the intersection of the precipitation, biotemperature, and potential evapotranspiration lines. The corners of each hexagon constitute transitional portions of the life zone and may contain many features common to adjacent life zones. These transitional areas are sometimes distinguished as separate mapping units.

Subunits

The life zones are broad, first-order units of classification, each of which may contain any number of subunits defined by such factors as soils, rainfall distribution, or drainage. Holdridge (1967) calls the second-order units defined by such factors *associations*, but describes them in terms of the physiognomy of mature vegetation, rather than floristics. The use of physiognomy rather than taxonomy as a basis for distinguishing associations permits the identification of similar or identical associations in biogeographically distinct regions. Within one region, however, there are often floristically derived names which are helpful in describing associations, as for example the cativo (*Prioria copaifera* Gris.) forests of lower Middle America and northern Colombia, or the tabonuco (*Dacryodes excelsa* Vahl) forests on Puerto Rico and some of the Lesser Antilles.

Definition of a site as corresponding to a particular association characterizes only the mature vegetation to be expected there. However, the site might well have been modified and consequently now occupied by successional vegetation: perhaps crops, pasture, secondary forest, or a fire-arrested subclimax. Life zones and the associations of which they are composed then, define only the potential vegetation, or range of vegetation types which might be found in an area, but do not define what might actually be there at any given time. It may well be, however, that successional processes are well correlated with life zones and associations. Through knowledge of the larger units it might be possible to predict the physiognomy, floristics, rate of change, and net primary productivity of seral vegetation. Such information will surely be of value in the near future as we become more and more concerned with man's impact on his environment.

Most applications of the Holdridge system so far have been concerned as is this work, with classification at the life zone level. More detailed maps have been prepared for some areas, however, and the recent book by Holdridge *et al.* (1971) includes detailed descriptions of the soils, climate, and vegetation of 46 associations. A logical next step in Puerto Rico and the Virgin Islands would be classification, at the association level, of areas of particular interest: perhaps the National and Commonwealth Forests, areas undergoing agricultural or urban development, or critical watersheds. Soils maps are available for both Puerto Rico (Roberts, 1942) and the U. S. Virgin Islands (Rivera *et al.,* 1970); superposition of these upon the life zone map would delineate, at the soil series level, many of the second-order units, or associations. Another work which should be very useful in the subdivision of life zones is the hydrogeologic map prepared by Briggs and Akers (1965). The life zone map is intended to be a first step, providing a baseline for more detailed studies in the future.

MAPPING PROCEDURES

Previous Efforts

Holdridge's system was first applied to Puerto Rico by Tosi (1959), but his work covered only the western part of the island and was done prior to the elimination of high temperatures in the calculation of biotemperature. Kumme and Briscoe (1963) mapped the island using climatic data, but they modified the climatic limits of the life zone boundaries, so their work is of limited value for comparing Puerto Rico with regions where the usual boundaries have been applied.

Climatic Data

Puerto Rico and the Virgin Islands have typical insular climates, with the influence of the surrounding ocean much in evidence. The northeast trades, plus land-sea breeze systems, ameliorate coastal temperatures particularly on the north side. Most precipitation is orographic and there is a definite rainshadow effect evident in southern Puerto Rico and, to a lesser extent, in some interior valleys. The rainfall distribution pattern on islands surrounding the Caribbean is much more even than on most land areas within the tropics. An informative and very readable description of local climate has been prepared by Calvesbert (1970).

Prior to starting the field work the literature was searched for precipitation and temperature data. Sources consulted for long-term means were the U. S. Weather Bureau supplements for 1931 through 1952 and 1951 through 1960 (U. S. Weather Bureau, 1959? ; U. S. Weather Bureau, 1965), and the 1969 annual summary for Puerto Rico and the Virgin Islands (ESSA, 1970). For stations which had been discontinued prior to 1960, the paper by Kumme and Briscoe (1963) was used, as it includes data summarized back to 1900. The result was a list of 143 stations for Puerto Rico alone (plus 40 for the Virgin Islands), each with one or more years of precipitation data. Of those in Puerto Rico, 122 had at least five years, 104 had at least ten years, and 88 had at least fifteen years of data recorded. The unusually high density of one pluviometer per 56 km^2 provided excellent ground control for the mapping. Also, 119 of the stations had at least one year of temperature data recorded. Most of the mean temperature data were based on daily averages of the maximum and minimum.

Base Maps

Excellent base maps, both with and without topography, are available for Puerto Rico and the U. S. Virgin Islands. Those relied on most heavily were:

U. S. Dept. of Interior, Geological Survey. 1952. Puerto Rico e Islas Limítrofres. 1:240,000.

Estado Libre Asociado de Puerto Rico, Autoridad de Carreteras. 1969. Mapa de Carreteras Estatales de Puerto Rico. 1:222,222.

Rand McNally and Co. 1968. Road Map of Puerto Rico. 1:300,000.

U. S. Dept. of Interior, Geological Survey. 1954-1958. Virgin Islands of the United States. (8 sheets). 1:24,000.

The final life zone boundaries were drawn on the U. S. G. S. Virgin Islands sheets at 1:24,000 cited above, and on the 1:120,000 version (1951) of Puerto Rico e Islas Limítrofes, U. S. G. S. All information was then transferred to the following two sheets, which served as the principal base for preparation of the final published life zone map:

Dept. of Defense, Aeronautical Chart and Information Center, U. S. Air Force. 1969. San Juan. 1:250,000, and: 1967. Fajardo, Puerto Rico; British Virgin Islands; Virgin Islands of the United States. 1:250,000.

Field Reconnaissance

The mapping procedure consisted of driving over roads where changes in topography or the available climatic data indicated that two or more life zones would be encountered. Puerto Rico has about 11,000 km of paved roads, and these, plus many secondary roads, made almost every area on the island readily accessible. Life zone boundary locations were recorded using road maps, vehicle mileage, roadside distance markers, and altimeter-determined elevations. Interpolations between boundary intersections were based on observations in the field and on topography. The life zone boundaries in the Luquillo Forest were based, in part, on the Forest Service type map.

Given a vast number of meteorological stations, plus level terrain, it would be entirely possible to map life zones directly from climatological data. Most areas of the world, however, possess neither of these two characteristics, so considerable field reconnaissance is necessary. The identification of life zones in the field is accomplished by synthesizing and evaluating information flowing into the mapper as he observes a landscape. Some of this information consists of fairly fine detail, such as soil texture and parent material, abundance of epiphytes, leaf sizes and shapes, species composition, and tree heights. Other information, however, is more macroscopic: crown forms, land use practices, vegetation color, layering in forest canopies, and drainage patterns. The mapper integrates this information and tries to separate observations caused by soils, topography, or winds, for example, from observations which reflect long-term average moisture and temperature conditions. Next, this integrated assessment of the landscape is mentally correlated with previous observations made at areas where mean annual precipitation and temperature were known. This process of repeated observation and correlation enables one to place any particular landscape into perspective with regard to numerous other landscapes. Patterns among these emerge, such that the mapper soon has a feel for the amount and kinds of variation which can be expected to be encountered within any life zone in a particular geographic region. The key to life zone mapping is continual, astute observation, coupled as frequently as possible to checkpoints where rainfall and temperature data are available.

In Puerto Rico and the Virgin Islands time did not permit the compilation of species lists or structural measurements of vegetation. In the description of each life zone, however, are listed a few readily recognized species which, when taken together, might be useful locally as life-zone indicators. Any of these species might be found outside the life zone for which it is listed, depending on soil type, drainage and other local environmental factors. When found together and in abundance, however, these species are usually indicative of the gross climatic limits which define the life zone for which they are listed. With few exceptions, botanical nomenclature follows Little and Wadsworth (1964), which was also the source of the common names cited in the text.

The Map

The color scheme employed is the same as that which has been used on most other life zone maps. The yellow-to-green-to-blue-to-purple color sequence indicates increasing moisture, from the subhumid to the superhumid humidity provinces. Solid colors indicate the basal, or sea level, belt, and successively lighter tones indicate increasingly cooler altitudinal belts. Broken black lines separate life zones in the same altitudinal belt, while solid black lines separate life zones in different altitudinal belts. Locations which are transitional among two or more life zones are common in Puerto Rico and the Virgin Islands, but have not been delineated here as they have been on the life zone maps of Colombia, Costa Rica, the Dominican Republic, and Panamá. The lines separating life zones are not contours, isotherms, or isohyets, nor should the map be construed as an attempt to indicate either actual or potential vegetation. The units are ones of broad bioclimatic similarity and each may encompass several forest associations, land uses, and successional stages.

THE LIFE ZONES

In spite of its latitude (approximately 18° N), Puerto Rico, according to Holdridge's system of classification, is in the Subtropical Latitudinal Region. (On life zone maps published prior to 1966 the term "Subtropical" referred to the Premontane Altitudinal Belt in the Tropical Latitudinal Region, as well as to the Subtropical Latitudinal Region.) Sea level mean biotemperatures for Puerto Rico and St. Croix (see Appendix A) are lower than 24°, the lower limit for the Tropical Latitudinal Region. This distinction within the geographic tropics reflects marked differences in the physiognomy and species composition of sea-level forests north or south of about 12 to 15 degrees latitude. The selection of the word Subtropical to refer to these differences in vegetation unfortunately may lead to confusion because of the generally accepted astronomical use of the word tropics to apply to all areas between the Tropics of Cancer and Capricorn (23°27'). Nevertheless, there are major differences in the vegetation within this range of latitude and it is necessary to distinguish them. Holdridge's use of the word Subtropical does refer to latitudinal differences, and not altitudinal differences, as interpreted by Odum (1970b).

Six life zones are found in Puerto Rico and the Virgin Islands, ranging from dry through rain forest in the basal, or sea level, belt, and wet plus rain forest in the Lower Montane Altitudinal Belt. The area occupied by each life zone is shown in Table 2; Subtropical Lower Montane Rain Forest occupies the smallest area, accounting for only 0.1% of the study region, while Subtropical Moist Forest is the dominant life zone, covering more than 58% of the area.

Table 2. Area occupied by each life zone in Puerto Rico and the U. S. Virgin Islands.

Island	Percent Of Total Area	AREA* BY LIFE ZONE (km^2)						
		Subtropical Dry Forest	Subtropical Moist Forest	Subtropical Wet Forest	Subtropical Rain Forest	Subtropical Lower Montane Wet Forest	Subtropical Lower Montane Rain Forest	Total Area* (km^2)
Puerto Rico	93.72	1216.4	5326.1	2124.8	13.2	109.1	12.3	8801.9
St. Croix	2.33	181.8	37.1	0	0	0	0	218.9
Vieques	1.47	93.1	44.8	0	0	0	0	137.9
St. Thomas	0.96	35.1	55.2	0	0	0	0	90.3
Mona	0.60	56.1	0	0	0	0	0	56.1
St. John	0.56	33.5	19.0	0	0	0	0	52.5
Culebra	0.35	32.7	0	0	0	0	0	32.7
Desecheo	0.02	1.6	0	0	0	0	0	1.6
TOTAL	100.00	1650.3	5482.2	2124.8	13.2	109.1	12.3	9391.9
Percent of total area in life zone		17.6	58.4	22.6	0.1	1.2	0.1	

* Areas were determined by planimetering the life zone map. Areas should be within two percent of their true value; differences are due to inclusion or exclusion of associated small islands and estuaries, plus instrument, operator, and map-scale errors.

The following brief descriptions of each of the life zones include bar graphs showing rainfall, soil moisture, and runoff for one or more sites in each life zone. The soil moisture and runoff were calculated using the method devised by Tosi (Ewel *et al.*, 1968; Holdridge *et al.*, 1971; FAO, 1971) which assumes mature vegetation and zonal soils, neither of which predominate at the sites for which water balances were calculated. The bar graphs should, therefore, be used primarily for comparison with water balances calculated for other sites, rather than for the absolute values shown for soil moisture and runoff. The water balance calculations assume an effective soil depth of one meter and available moisture was calculated from the data in Lugo-Lopez (1953), except for the Glynn series, in St. Croix, data for which were provided by L. H. Rivera from the files of the U. S. D. A., Soil Conservation Service. Appendix B includes additional discussion of Tosi's method of water balance calculations, as well as complete water balance tables for the ten sites illustrated in bargraph form.

The Subtropical Dry Forest Zone

This life zone is the driest of the six found in the study region and covers sizable areas in the Virgin Islands, Vieques, southwestern Puerto Rico, plus all of Mona Island, Culebra, and Desecheo. Mean annual rainfall ranges from a minimum of about 600 to a maximum of 1000 or 1100 mm (see Figure 1). Mean monthly rainfall, and calculated soil moisture and runoff are shown for two sites in this life zone: Santa Isabel, Puerto Rico (Figure 2), and Kingshill, St. Croix (Figure 3). The annual patterns at these two sites are very similar and the differences in soil moisture between them are due primarily to soil moisture-holding capacities. At both locations the soil is wettest during the latter four or five months of the year and the small amount of runoff which occurs at these sites (61 mm per year at Santa Isabel and 166 mm per year at Kingshill) is produced in September through November.

The vegetation in this life zone (Figures 4-10) tends to form a complete ground cover, and is almost entirely deciduous on most soils. Palms are usually absent from the canopy, leaves are often small and succulent or coriaceous, and species with thorns and spines are common. Tree heights usually do not exceed 15 m and the crowns are typically broad, spreading, and flattened, with sparse foliage. Fire is common on the better soils, where the successional vegetation includes many grasses, and large amounts of organic debris accumulate on the soil surface during the dry season (Figure 5). On the poorer soils, however, the vegetation is more water-limited and organic debris does not accumulate to the extent that surface fires are possible. Coppicing is a common means of regeneration of many of the woody species found in this life zone and successional forests, therefore, often consist of an almost-impenetrable maze of tangled, close-growing small stems. Plants here are low in moisture content and the wood of most species is hard and durable (Figure 6).

The forests of this life zone, at least on Puerto Rico, are richer in birds than are the wetter life zones. Kepler and Kepler (1970) reported 31 species per 1000 individuals in the Guánica Commonwealth Forest (Subtropical Dry Forest), compared to only 20 species per 1000 individuals in the much wetter Luquillo Experimental Forest. The number of individuals reported by them for the drier forest was higher also: 190 birds per linear kilometer in the Guánica Forest compared with only 57 per kilometer in the Luquillo Forest. In discussing the greater number of insect-eating birds at Guánica, they pointed out that the wetter Luquillo Forest has well-developed lizard and frog populations, which might be performing the same function in the

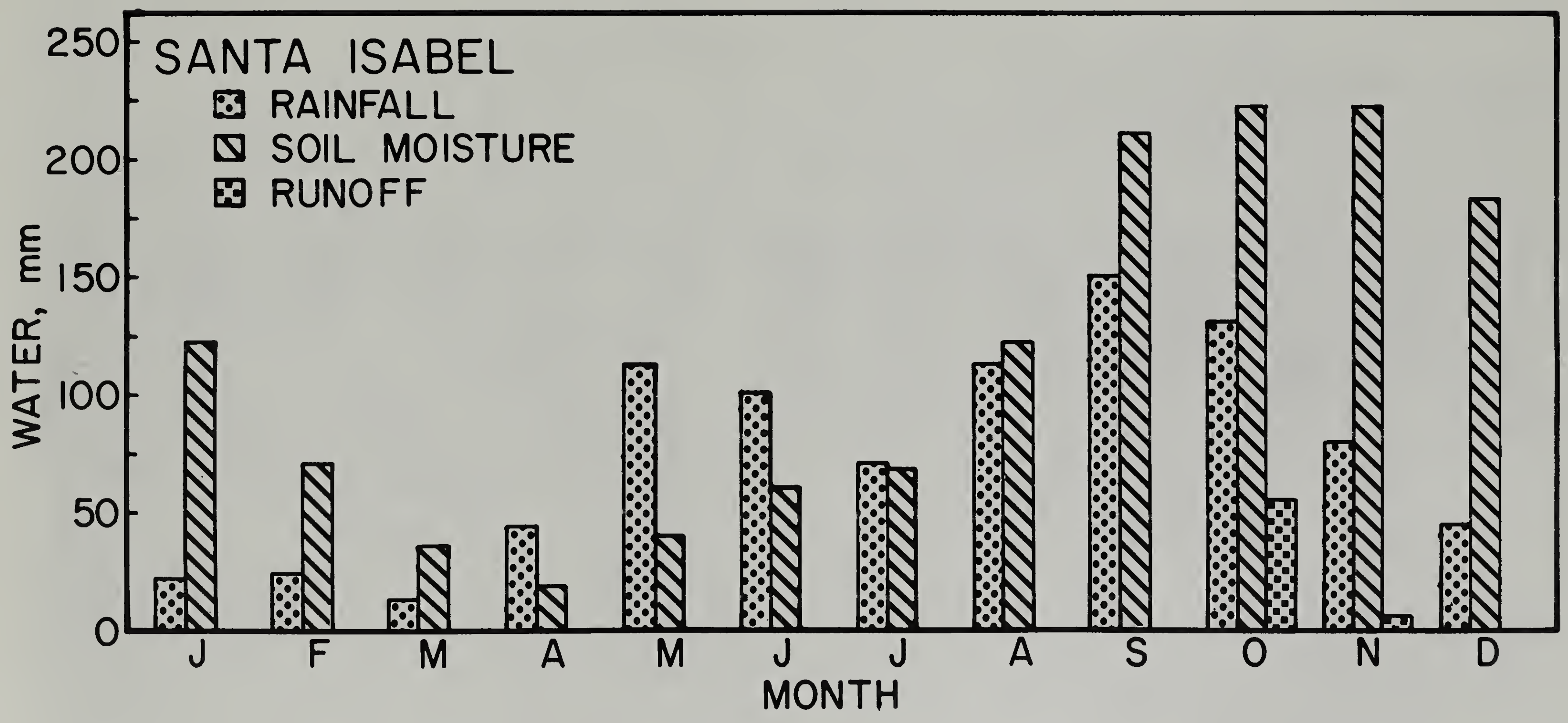

Figure 2 Mean rainfall, soil moisture, and runoff calculated for Santa Isabel, Puerto Rico, in Subtropical Dry Forest. Teresa soil series, with available moisture of 222 mm per meter.

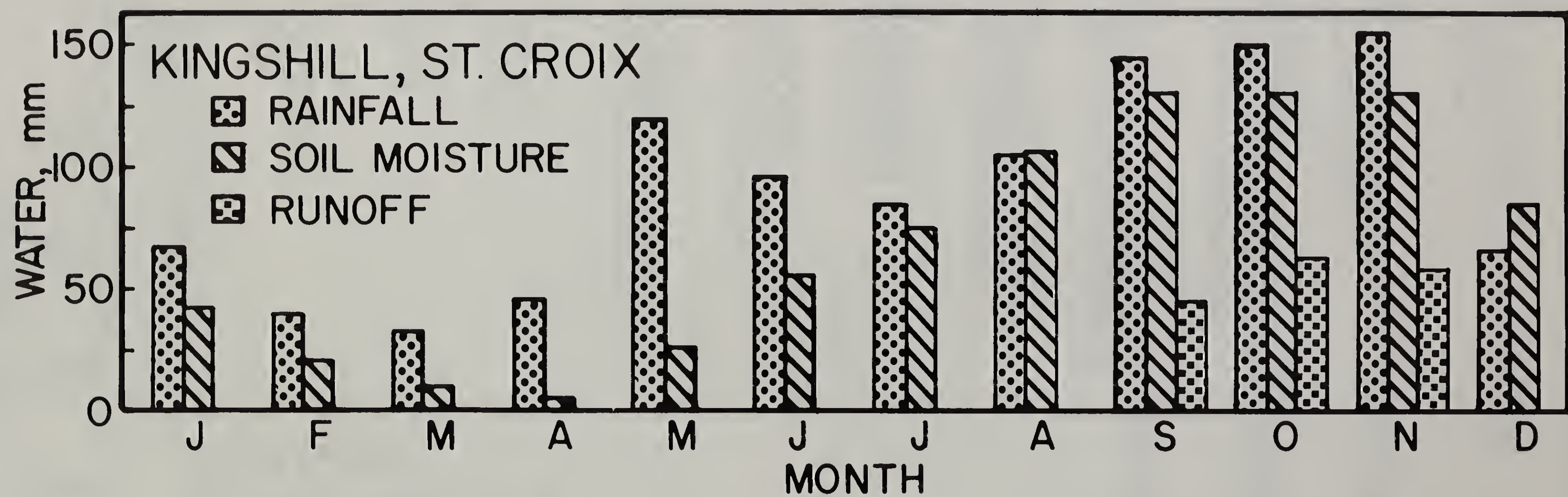

Figure 3 Mean rainfall, soil moisture, and runoff calculated for Kingshill, St. Croix, in Subtropical Dry Forest. Glynn soil series with available moisture of 130 mm per meter.

Figure 4 Subtropical Dry Forest. Xeric hillside with cacti, thorny legumes, and grasses. Southeast coast of St. Croix.

Figure 5 Subtropical Dry Forest. One of the many burned areas seen on St. Croix during the dry months of February through April.

Figure 6 Subtropical Dry Forest. Fence-post quality coppice of the Guánica, Puerto Rico landscape. Coppicing is a common means of regeneration for many dry forest tree species. (Photo by N. Kirby).

Luquillo Forest as insectivorous birds in the drier Guánica Forest. In looking at the broader question of why the structurally simple xeric forest should have more birds, numerically and taxonomically, than the complex wetter forest, they state: "The answer may well lie in the greater relative ability of xeric land birds from potential source areas to colonize oceanic islands, the larger number of xeric, compared to mesic, islands that could serve as stepping stones for dispersion in the Caribbean, and the proximity of the xeric forest to island coasts where potential propagules would first land."

Much of the Subtropical Dry Forest zone in Puerto Rico and the Virgin Islands lies in the warm and wet transitional parts of the life zone, thus has characteristics of the dry part of Subtropical Moist Forest and the cool portion of Tropical Dry Forest. Examples of such areas are the Lajas Valley in Puerto Rico and most of the central part of St. Croix, including Estate Thomas, one of the U. S. Forest Service's experimental areas. These transitional portions of the Subtropical Dry Forest zone support a man-modified vegetation which approaches a savanna-woodland aspect (Figure 7). The grass cover is often complete, evergreen trees are rare, and tall trees with flattened spreading crowns are common. Fire is often a common and important component of this transitional environment.

Extensive areas of the Subtropical Dry Forest zone on the Virgin Islands and in southern Puerto Rico overlie limestone, and the vegetation on these soils (*e.g.* the Aguilita, Ensenada, Fredensborg, and Sion series) is more xerophyllous than that which would be expected on a zonal soil. The soil surface in these associations often lacks any grass or herb cover, and many of the trees and shrubs are evergreen. At East End, St. Croix, a shallow, limestone-derived soil is coupled with a strong, salt-laden sea breeze to produce an extreme edapho-atmospheric association in which the vegetation is open and the trees, with wind-pruned crowns, are less than five meters tall, as seen in Figure 8.

Some of the low alluvial areas on the south coast of Puerto Rico contain saline soils, such as the Santa Isabel series, and the vegetation on these sites is dominated by *Prosopis juliflora* (Sw.) DC. (bayahonda, mesquite), an introduced tree, shown in Figure 9. *Parkinsonia aculeata* L. (palo de rayo, Jerusalem-thorn) is another exotic leguminous tree which often forms nearly pure stands on coastal alluvial soils with imperfect drainage. Mangrove forests, including red (*Rhizophora mangle* L., mangle colorado), black (*Avicennia nitida* Jacq., mangle prieto), and white (*Laguncularia racemosa* (L.) Gaertn. f., mangle blanco) form parts of the coastal associations in this life zone, but the development of tall, luxuriant mangrove forests may, in some locations, be limited by the scarce surface runoff, which can result in higher salinities and lower nutrient inputs than would be the case along coasts with more rainfall. The stand of red mangrove which was used in one of the first metabolic studies of a whole mangrove ecosystem (Golley *et al.*, 1962) was located in the Subtropical Dry Forest zone on the south coast of Puerto Rico.

Species which are easily recognized and which, when taken as a group, are useful indicators of this life zone in Puerto Rico and the U. S. Virgin Islands include *Bursera simaruba* (L.) Sarg. (almácigo, turpentine-tree), *Prosopis juliflora* (Sw.) DC. (bayahonda, mesquite), *Cephalocereus royenii* (L.) Britton and Rose (sebucán, dildo), *Pictetia aculeata* (Vahl) Urban (tachuelo, fustic), *Bucida buceras* L. (ucar, oxhorn bucida), *Guaiacum officinale* L. (guayacan, lignumvitae), *G. sanctum* L. (guayacán blanco, holywood lignumvitae), *Leucaena glauca* (L.) Benth. (zarcilla,

Figure 7 Subtropical Dry Forest. Drought-and fire-resistant *Bursera simaruba* near Salinas, Puerto Rico. The grasses are burned annually.

Figure 8 Subtropical Dry Forest. Eastern-most part of St. Croix. Dry atmpspheric association caused by continual exposure to salt-laden winds.

Figure 9 Subtropical Dry Forest. *Prosopis juliflora* in a pasture near Santa Isabel, Puerto Rico. This species is commonly found on saline soils.

tantan), *Tamarindus indica* L. (tamarindo, tamarind), *Acacia macracantha* Humb. & Bonpl. (tamarindo silvestre, steel acacia), *A. farnesiana* (L.) Willd. (aroma, sweet acacia), *Melicoccus bijugatus* Jacq. (quenepa, Spanish-lime), and five species of *Capparis* (burro, caper).

Agriculture in the Subtropical Dry Forest zone is, at best, a marginal business, except under irrigation. The amounts of water which must be added to maintain crops and pastures are low compared with irrigation demands in many drier parts of the world, however, and the better soils in this life zone are under cultivation. Potential evapotranspiration is greater than rainfall in the Subtropical Dry Forest zone, so the repeated use of irrigation water can sometimes result in salt accumulation in the upper soil horizons. In the Lajas Valley, for example, the use of ground water for irrigation resulted in the loss of agricultural productivity on some soils, until the mid 1950's when water from another area was made available for irrigation (Bogart *et al.*, 1964).

Goats are pastured on the poorer soils but to a much lesser extent than in years past. Charcoal production, a common land use in many high-stress tropical environments, was once common in this life zone in Puerto Rico, but this practice is now almost extinct here. The Guánica Forest, which has been protected from charcoal cutting, goat grazing, and subsistence farming for more than 40 years, is perhaps the best example of natural vegetation in Subtropical Dry Forest anywhere in the world. Forestry has little commercial prospect in this life zone, except in the limited production of exceedingly durable fence posts and a few high-quality specialty woods. *Swietenia mahagoni* Jacq. (caoba dominicana, West Indies mahogany), a prime example (see Figure 10), is native to Subtropical Dry Forest, though not to Puerto Rico and the U. S. Virgin Islands (Little and Wadsworth, 1964). Plantations of this species have been very successful in St. Croix and some, more limited, success has been achieved with this species in the Guánica Forest. *Guaiacum officinale* L. (guayacán, lignumvitae), another species which produces a high-value specialty wood, does occur naturally in the Subtropical Dry Forest zone of these islands. Urbanization of the Subtropical Dry Forest zone is often a water-limited process; water must be supplied by subterranean aquifers, brought in from sources such as reservoirs maintained by runoff from other, wetter life zones, or trapped in artificial catchments, as is common in the Virgin Islands.

The Subtropical Moist Forest Zone

This life zone, which covers more area (almost 5500 km^2, or 58% of the total) in Puerto Rico and the U. S. Virgin Islands than any of the other five life zones found there, is delineated by a mean annual rainfall of 1000 or 1100 mm to about 2000 or 2200 mm and a mean biotemperature between about 18 and 24 C. Monthly rainfall, soil moisture storage, and runoff are shown for three stations in the Subtropical Moist Forest zone in Figures 11, 12, and 13. San Juan (Figure 11), at sea level, has a water regime which is surprisingly similar to those of the higher elevation sites: Barranquitas, at 671 m (Figure 12) and Aibonito, at 640 m (Figure 13). Part of this similarity is due to the fact that the many temperatures at San Juan which exceed 30 C (annual mean of 25.9 C) are substituted by zero when calculating biotemperature (annual mean of 23.0 C); water balance calculations are based on the latter. Another similarity of these three stations is their rainfall distribution patterns. The major differences in Figures 11, 12, and 13 result from the different soil moisture-holding capacities assumed for each of the three sites, which ranged from a low of 119 mm per meter for the Cialitos series at Barranquitas to a high of 245 mm per meter for the Múcara series at Aibonito. At all three sites moisture deficits are a

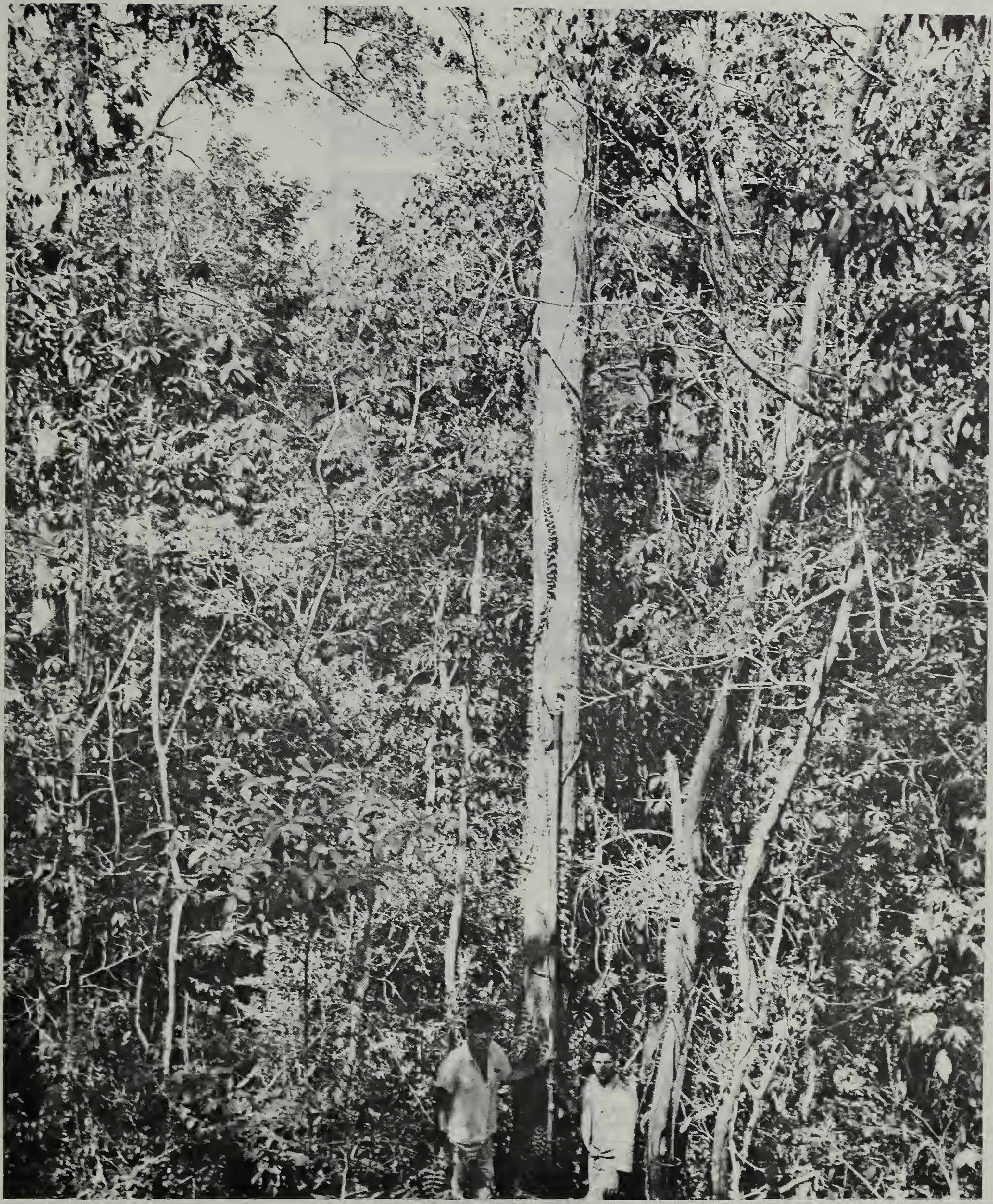

Figure 10 Subtropical Dry Forest. Moist cove, Estate Bellevue, St. Croix with unusually straight small-leaf mahogany, *Swietenia mahagoni*, about 40 years old.

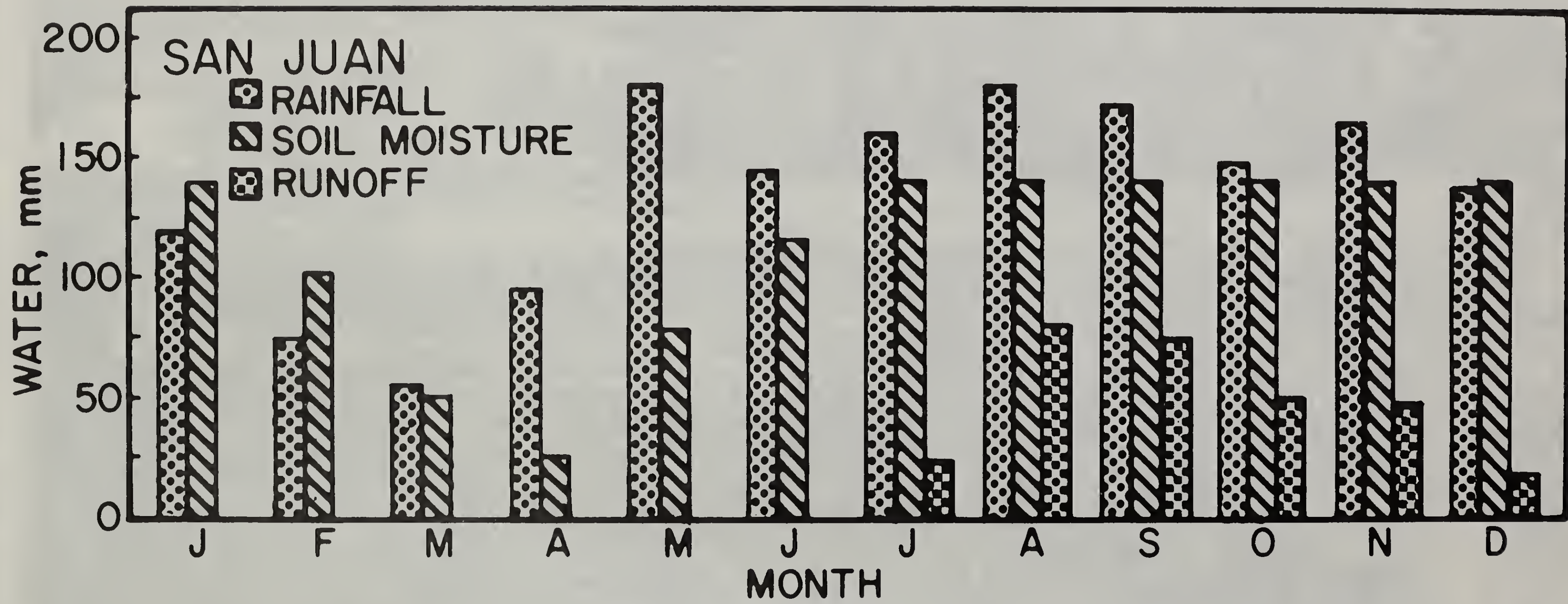

Figure 11 Mean rainfall, soil moisture, and runoff calculated for San Juan, Puerto Rico, in Subtropical Moist Forest. Río Lajas soil series, with available moisture of 141 mm per meter.

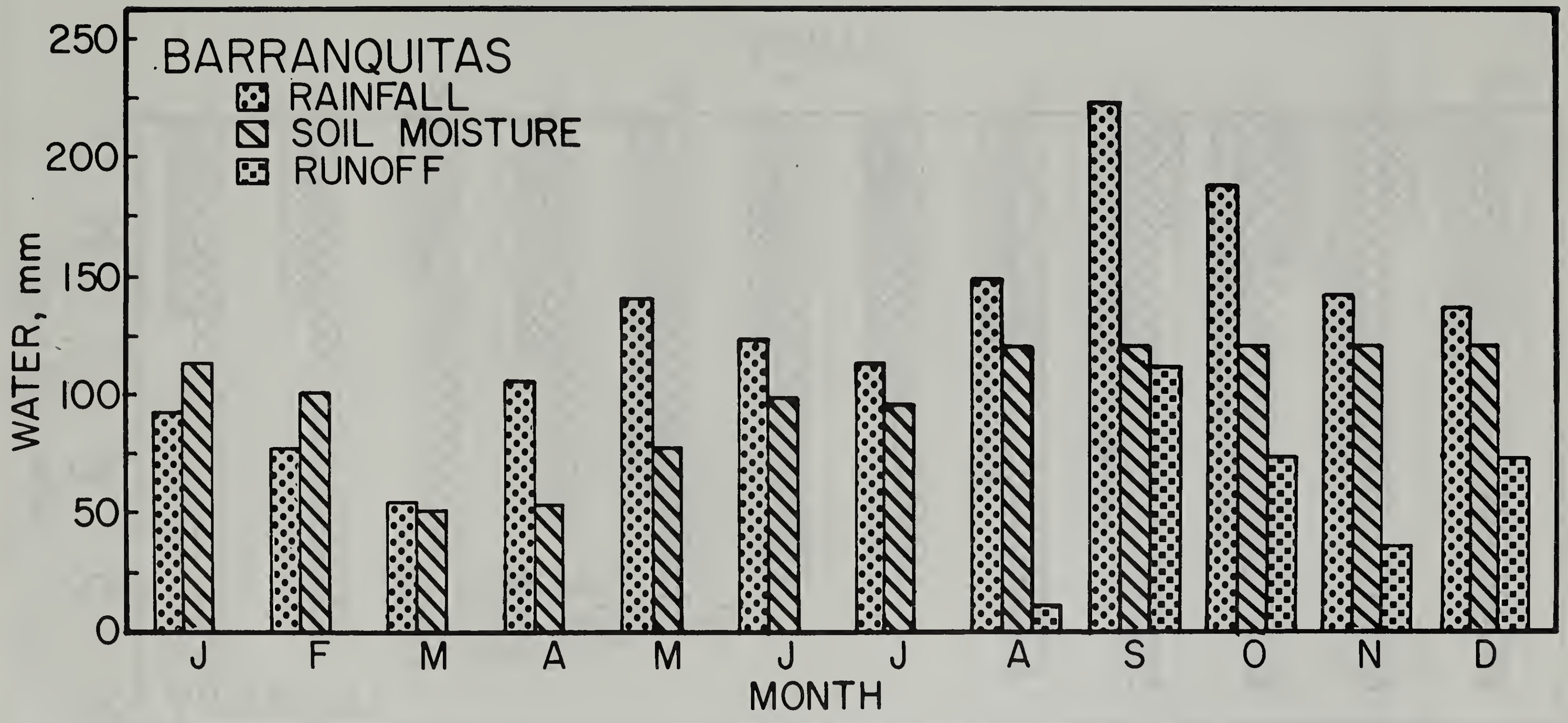

Figure 12 Mean rainfall, soil moisture, and runoff calculated for Barranquitas, Puerto Rico, in Subtropical Moist Forest. Cialitos soil series, with available moisture of 119 mm per meter.

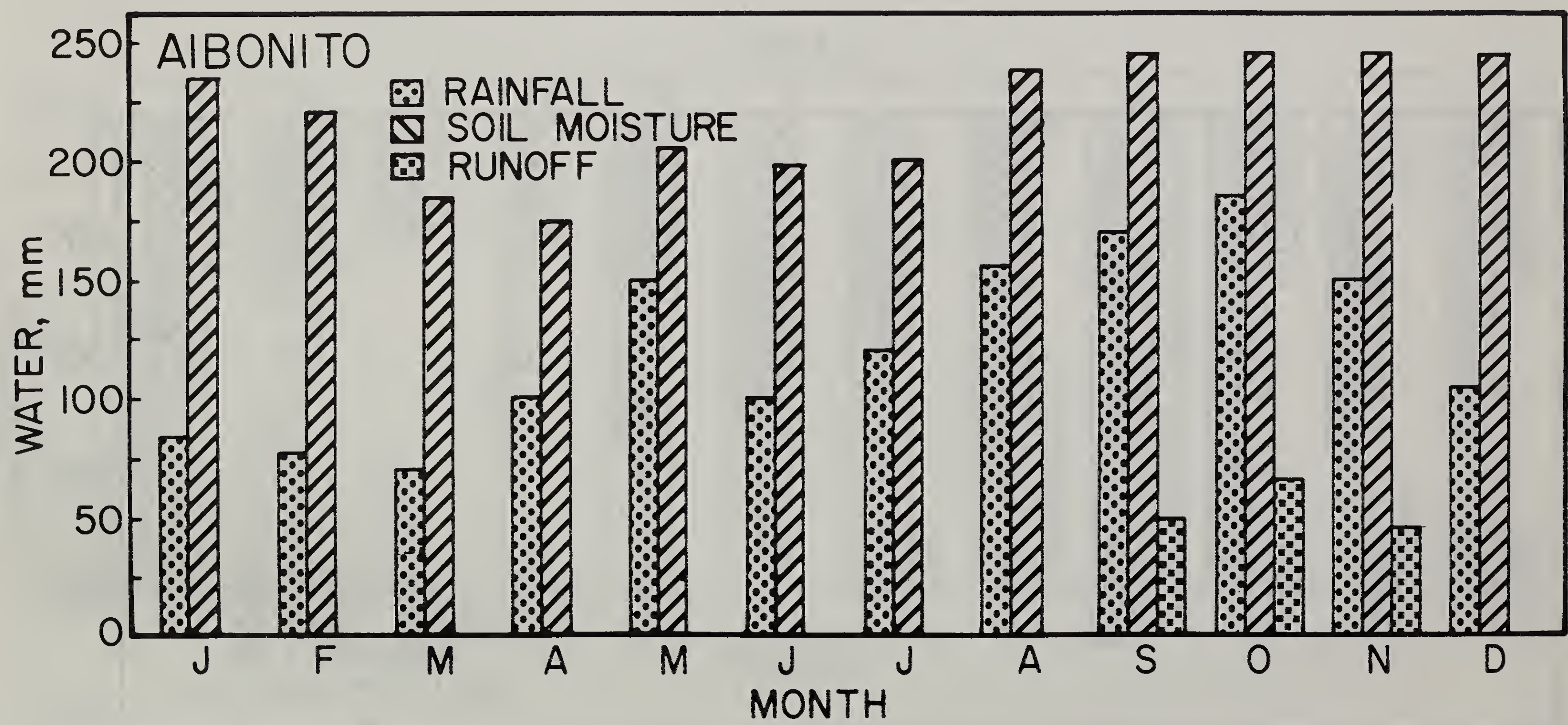

Figure 13 Mean rainfall, soil moisture, and runoff calculated for Aibonito, Puerto Rico, in Subtropical Moist Forest. Múcara soil series, with available moisture of 245 mm per meter.

serious problem only during March and April and considerable runoff occurs during the last three to six months of each year. In general, the moisture regimes in this life zone are nearly ideal on an annual basis, with sufficient water to support agriculture, yet no excessive wetness.

Most of the Subtropical Moist Forest zone in the study region has been deforested at one time or another (as in Figure 14, for example), primarily because the climatic conditions which define its boundaries also encompass good conditions for a wide variety of crops. With the exception of regions of serpentine- or limestone-derived soils, most of the land in this life zone remains in some form of non-forest use. A sizable tract of cutover forest in the zonal association of Subtropical Moist Forest remains in the Luquillo Experimental Forest, occupying the disjunct section located off of the southwest corner of the main forest boundary, southwest of Río Cubuy. This and other scattered remnants of the zonal association vegetation are characterized by trees up to 20 m tall, with rounded crowns, like those of the mango tree. Many of the woody species are deciduous during the dry season and epiphytes are common, but seldom completely cover branches and trunks. Grasses, in both natural and improved pastures, form the dominant landscape in the Subtropical Moist Forest zone in Puerto Rico today (Figure 15). They form a complete ground cover, except on poor soils, and are fire-maintained on the southern slopes of the Cordillera Central, as, for example, on the Múcara soil series around Cayey.

The moist limestone hill region of northern Puerto Rico produces an interesting catena of associations in the Subtropical Moist Forest zone. These hills (Figure 16), which are oriented northeast to southwest, are quite moist on the gentle northern slopes, are even more humid on the extremely steep southwest slopes, and are quite xeric on top. Data from an Institute of Tropical Forestry Annual Report (U. S. Forest Service, 1950) show that diameter growth rates of trees on the west-facing (leeward) slopes averaged almost twice as great as those on the east-facing (windward) slopes; further, growth rates at the tops of the slopes were significantly slower than those reported for the bottoms. These differences in vegetation and tree growth are apparently due to differences in microclimate and soils resulting from aspect and slope. *Guassia attenuata* (O. F. Cook) Beccari (palma de lluvia) is a palm endemic to Puerto Rico and a conspicuous component of the limestone hill forests in Subtropical Moist Forest. It often grows near the summits of the hills and, because it is usually taller than the surrounding trees, is readily identified from a distance. During the mapping this species was not observed on the limestone hills in Subtropical Wet Forest, but it might be found there on some of the more xeric sites. Little and Wadsworth (1964) list 21 tree species as common members of these moist limestone hill forests.

A second edaphic condition which results in an interesting association in the Subtropical Moist Forest zone is the serpentine-derived soil (Nipe and Rosario series) in southwestern Puerto Rico, where good examples can be seen in the Susua Commonwealth Forest. This soil supports a unique vegetation, which contains a number of endemics, but does not support any significant agriculture or forestry. The trees are slender, open-crowned, and usually less than 12 m tall. The forest floor is open, for the excessively drained soil supports little herbaceous growth. Most of the species are sclerophyllous and the vegetation is almost completely evergreen. Tschirley *et al.* (1970) found 105 species of woody plants larger than 2.5 cm dbh on 0.9 ha in this association, compared to only 85 species on 1.4 ha in the wetter, more luxuriant Luquillo Forest. The number of woody stems was the same at both sites: 2.4 per 10 m^2. This surprising richness of the

Figure 14 Subtropical Moist Forest. Steep deforested slopes of the central mountain range, Puerto Rico, where intensive farming and multiple species crops commonly produce high yields (Photo by D. Pool).

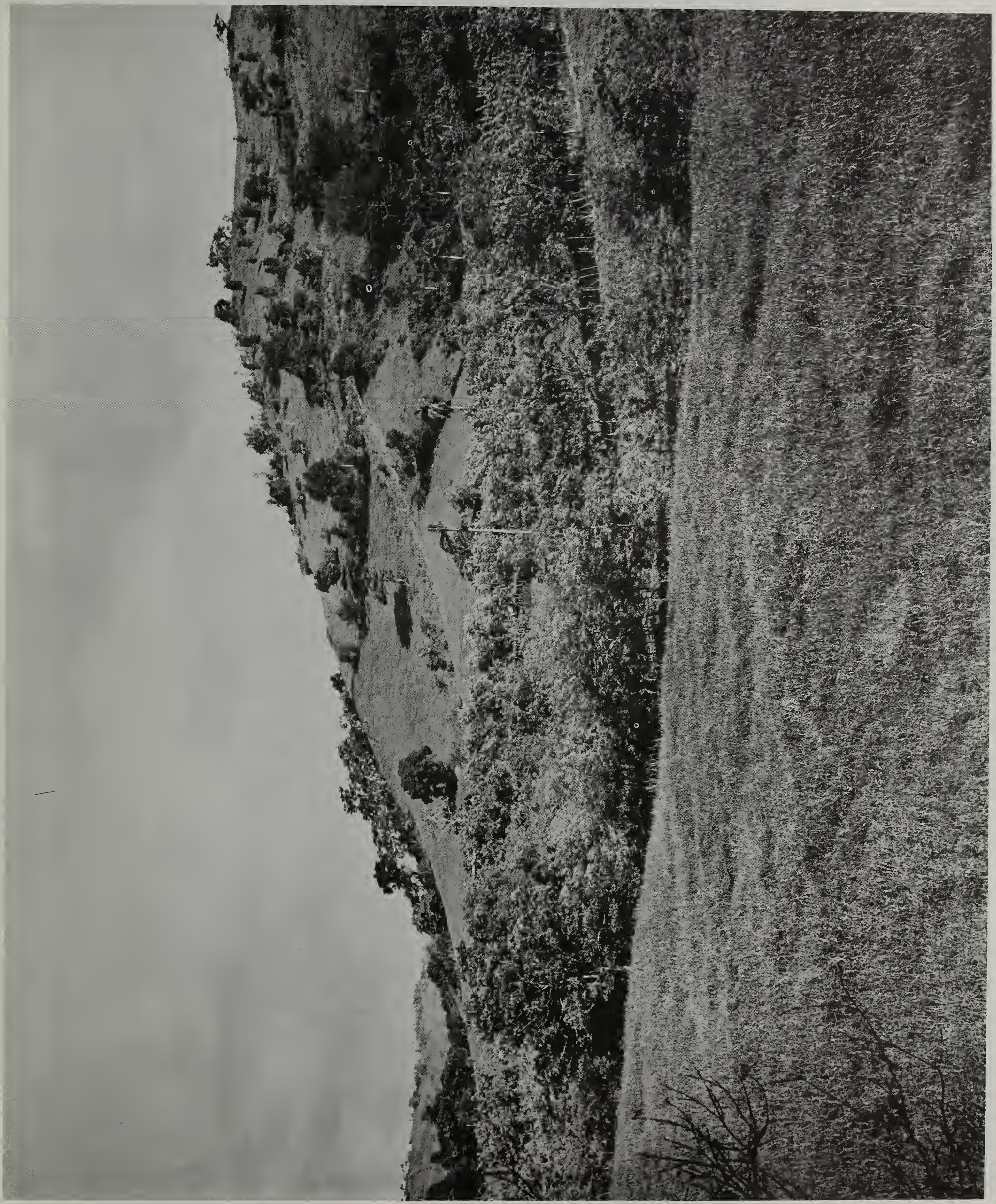

Figure 15 Subtropical Moist Forest. Large areas have been put into pasture grasses. Pastures in this life zone can be highly productive.

Figure 16 Subtropical Moist Forest. Limestone hills association. Described also as haystack hills or "mogotes," this dogtooth pattern of marine origin is typical of nearly 20% of Puerto Rico.

woody flora on the serpentine soil, which contradicts most current ecological dogma, awaits a satisfactory explanation.

Mangroves are found along the coast in the Subtropical Moist Forest zone where they appear to grow taller than in the Subtropical Dry Forest zone, the only other sea-level life zone found in Puerto Rico and the Virgin Islands. Just inland from the mangrove forests are alluvial soils where the ground water may be slightly brackish. Most of these soils were cleared long ago for agriculture, but they probably supported impressive forests at one time. Gleason and Cook (1926) (also in Cook and Gleason, 1928) described a stand of *Pterocarpus officinalis* Jacq. (palo de pollo, swamp bloodwood), with their impressive ribbon buttresses (Figure 17), located near Humacao in southeastern Puerto Rico. Other remnants of alluvial swamp forest in the Subtropical Moist Forest zone remain near Dorado, on the north coast of Puerto Rico, and at La Boquilla, north of Mayaguez.

Roystonea borinquena O. F. Cook (palma real, Puerto Rico royalpalm), endemic to Puerto Rico, Vieques, and St. Croix (Little and Wadsworth, 1964) and shown in the center of Figure 18, is a common and readily identified species found in many areas within the Subtropical Moist Forest zone. *Tabebuia heterophylla* (DC.) Britton (roble blanco, "white cedar") sometimes forms nearly pure stands in abandoned fields, particularly in those portions of the life zone where the mean annual precipitation exceeds 1600 mm. Species of *Nectandra* and *Ocotea*, commonly called "laureles," are prominent in many of the older secondary forests. *Spathodea campanulata* Beauv. (tulipán africano, African tulip tree) plus the common coffee shade trees, *Erythrina poeppigiana* (Walp.) O. F. Cook (bucayo gigante, mountain immortelle), *Inga vera* Willd. (guaba), and *I. laurina* (Sw.) Willd. (guamá, "sweetpea"), are also common and readily recognized from a distance. *Cedrela odorata* L. (cedro hembra, Spanish-cedar), *Hymenaea courbaril* L. (algarrobo, West-Indian-locust), *Delonix regia* (Bojer) Raf. (flamboyán, flamboyant-tree), and *Ficus laevigata* Vahl (jaguey blanco, shortleaf fig) are common roadside trees. Members of the Melastomaceae, Piperaceae, and Rubiaceae are common shrubs. *Cecropia peltata* L. (yagrumo hembra, trumpet-tree) and *Didymopanax morototoni* (Aubl.) Decne. and Planche. (yagrumo macho, matchwood) are found in successional forests in all moist, wet, and rain life zones of Puerto Rico and the Virgin Islands, but rarely extend into dry forest areas.

Throughout the world, Subtropical Moist Forest (and its Premontane counterpart in the Tropical Latitudinal Region) is among the most intensively used life zones. Pasture seems to be the predominant land use in this zone in Puerto Rico today, but sugarcane, which requires little or no irrigation water in this life zone, and coffee still occupy large areas. Pineapples are planted in the drier portions of the Subtropical Moist Forest zone along Puerto Rico's north-central and northwest coast, while tobacco is still grown extensively in certain areas, notably in the Comerio-Cidra-Barranquitas region.

The Subtropical Moist Forest zone, with its intermediate moisture conditions—neither excessive rainfall nor high irrigation requirements—is the life zone in Puerto Rico and the Virgin Islands which is best adapted for a wide variety of land use systems, many of which offer potentially high yields. Intensive food production on the flats, forage production on the moderate slopes, and managed tree crops on the steep slopes are all possible here. In addition, this life zone provides a much-needed supply of water on some of the drier islands, such as the Virgin Islands and Vieques.

Figure 17 Subtropical Moist Forest. There are few remnants of the alluvial swamp forest left in Puerto Rico, all under heavy development pressures. This wet-season scene includes buttresses of *Pterocarpus officinalis*, with ferns of the genus *Acrostichum* in the background.

Figure 18 Subtropical Moist Forest. *Roystonea borinquena* (center), tobacco shed (right side) and dwellings on slope (left) in the central mountain range, Puerto Rico (Photo by D. Pool).

The Subtropical Wet Forest Zone

Subtropical Wet Forest occupies much of the higher parts of Puerto Rico's mountains and, like the wet- and rain-forest life zones yet to be described, is not found in any other island in the study region. This is a high rainfall life zone, encompassing areas with mean annual precipitation within the approximate range of 2000 to 4000 mm per year. Rainfall, soil moisture, and runoff graphs are included for three locations (Figure 19, 20, and 21) which range in mean annual rainfall from 2150 mm (Carite Dam, Figure 19) to 2900 mm (Río Blanco, Figure 21). Soil moisture drops below field capacity at these three stations only for three months, at most, and the water deficit is very small. Significant amounts of runoff occur at each of these sites during at least seven months and, in some cases, all year. The annual runoff at these three sites (827 mm to more than 1600 mm) is greater than the rainfall input in most areas of the Subtropical Dry Forest zone.

The abundant moisture of this life zone is evident in the character of the vegetation. Epiphytic ferns, bromeliads, and orchids are common, the forests are relatively rich in species, and the growth rates of successional trees are rapid. A mat-forming fern, *Gleichenia bifida* Spreng. and the common tree-fern, *Cyathea arborea* (L.) J. E. Smith (helecho gigante) form a common roadside combination here, as shown in Figure 22. Mature forest remnants in this life zone exist in the Carite and Toro Negro Commonwealth Forests and the Luquillo Experimental Forest. The zonal association of Subtropical Wet Forest in Puerto Rico corresponds to what is locally referred to as the tabonuco type, named for the dominant tree, *Dacryodes excelsa* Vahl (Figure 23). Two other very prominent species are *Sloanea berteriana* Choisy (motillo) and *Manilkara bidentata* (A.DC.) Chev. (ausubo, bulletwood). This is an impressive forest, containing more than 150 species of trees, and forming a dark, complete canopy at about 20 m. One of the best brief descriptions, both physiognomic and dendrological, of this association can be found in the article by Wadsworth (1951). A multitude of studies on tropical forestry and ecology have been carried out in this association over the last 40 years, primarily in the Luquillo Experimental Forest. By far the most complete and broad-based of these was the series of investigations reported on in the massive volume edited by Odum (1970a), which makes this one of the most intensively studied forest types in the world.

Serpentine areas, described for the Subtropical Moist Forest zone, are also found in the Subtropical Wet Forest zone. The vegetation on serpentine is similar in the two life zones, except that it is greener, denser, more lush, and, most strikingly, contains more epiphytes in the Subtropical Wet Forest. The species are almost all evergreen and sclerophyllous, giving the impression of an anomalous wet desert or dry rain forest. Excellent examples of this association are available in the Maricao Commonwealth Forest.

As in the case in the Subtropical Moist Forest zone of Puerto Rico, described previously, limestone is the parent material for many of the soils in the Subtropical Wet Forest zone as well. These limestone-derived soils characterize several important azonal associations in this life zone and include most of the Río Abajo Commonwealth Forest. Both *Swietenia macrophylla* King (caoba hondureña, Honduras mahogany) and *Tectona grandis* L. f. (teca, teak), introduced to Puerto Rico from climates much drier than that of Subtropical Wet Forest (*e.g.* Subtropical Dry Forest, Tropical Dry Forest, Tropical Moist Forest), have done well in plantations on the limestone-derived soils in the Río Abajo Forest. The natural vegetation on these soils is much

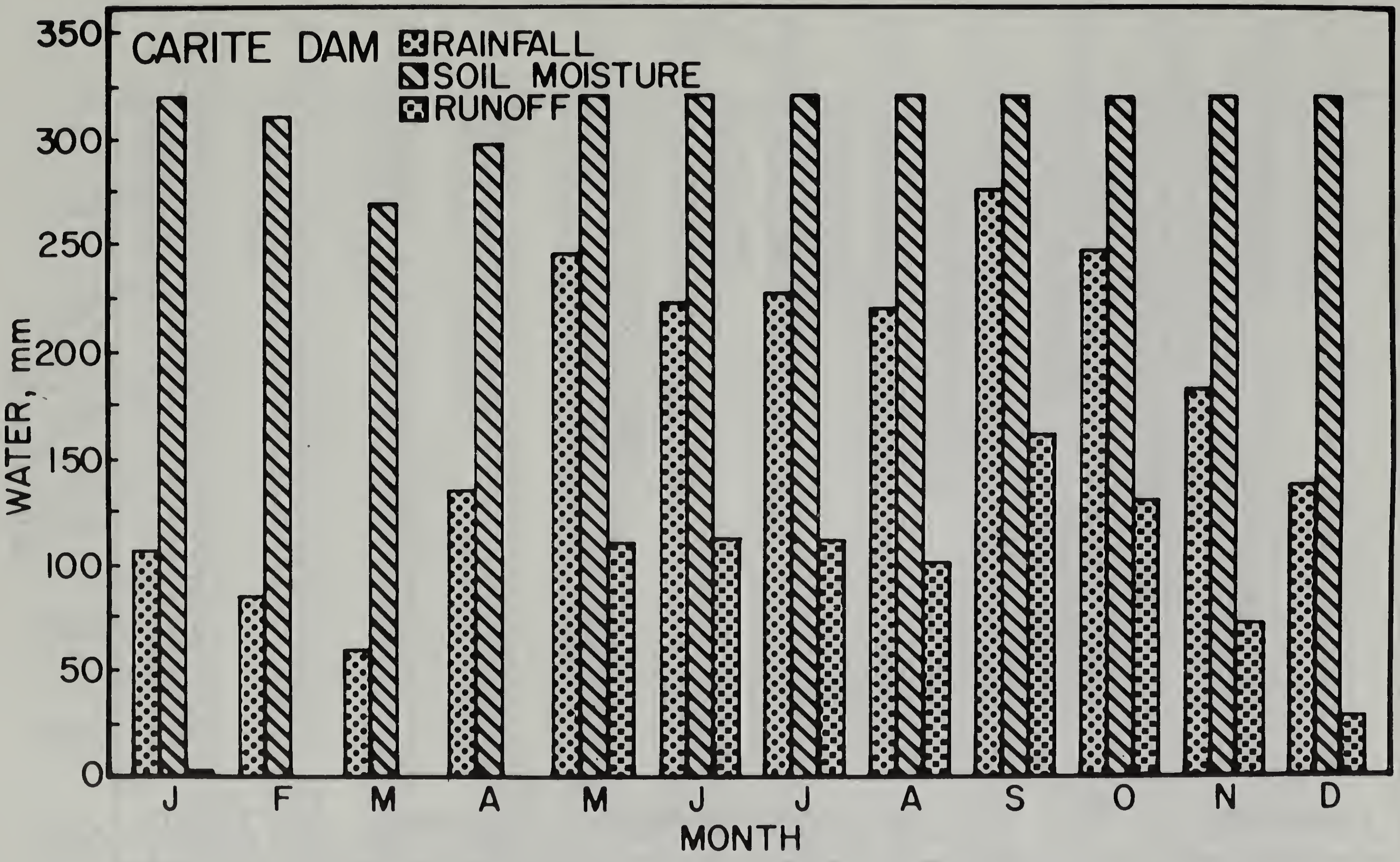

Figure 19 Mean rainfall, soil moisture, and runoff calculated for Carite Dam, Puerto Rico, in Subtropical Wet Forest. Los Guineos soil series, with available moisture of 320 mm per meter.

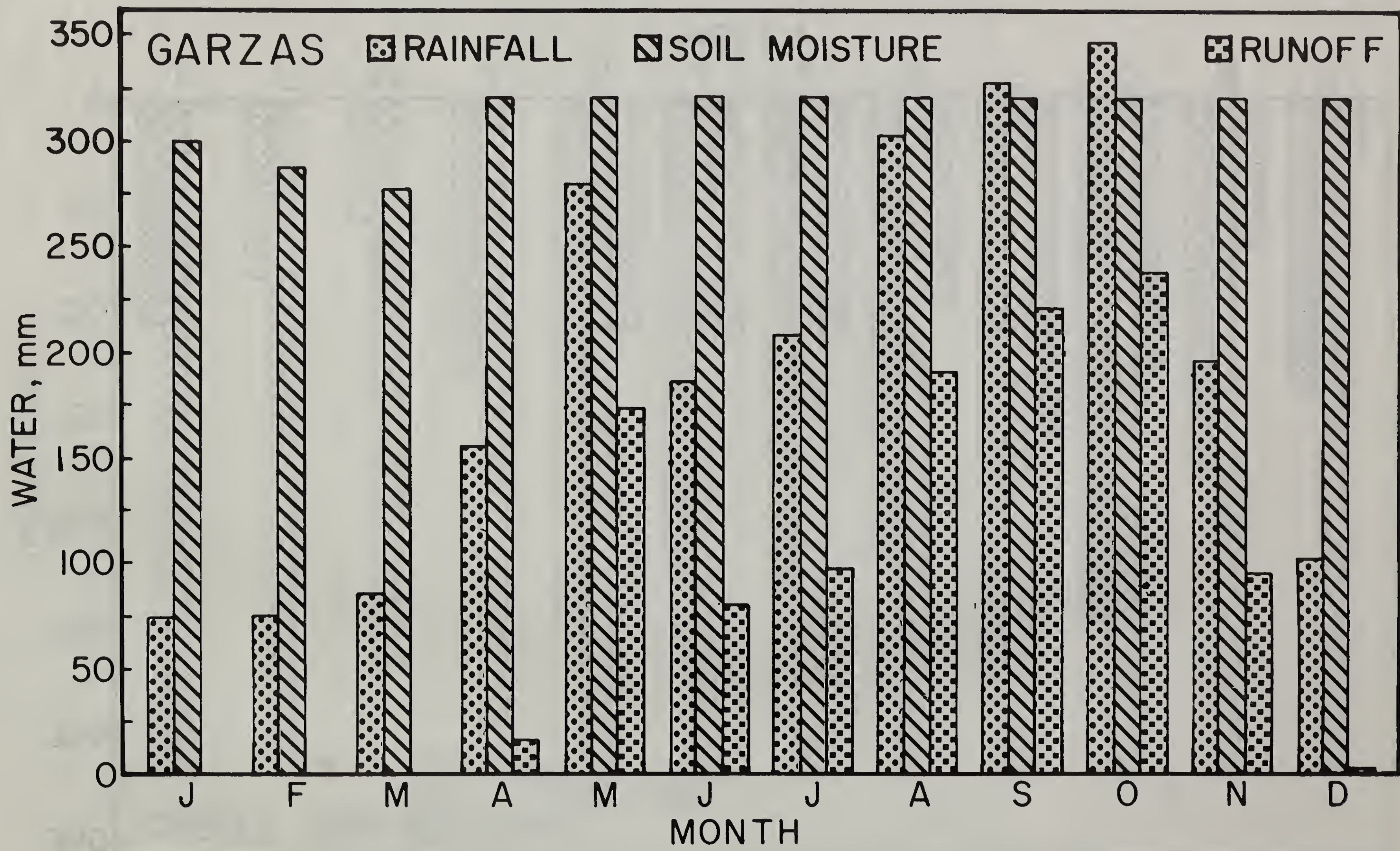

Figure 20 Mean rainfall, soil moisture, and runoff calculated for Garzas, Puerto Rico, in Subtropical Wet Forest. Los Guineos soil series, with available moisture of 320 mm per meter.

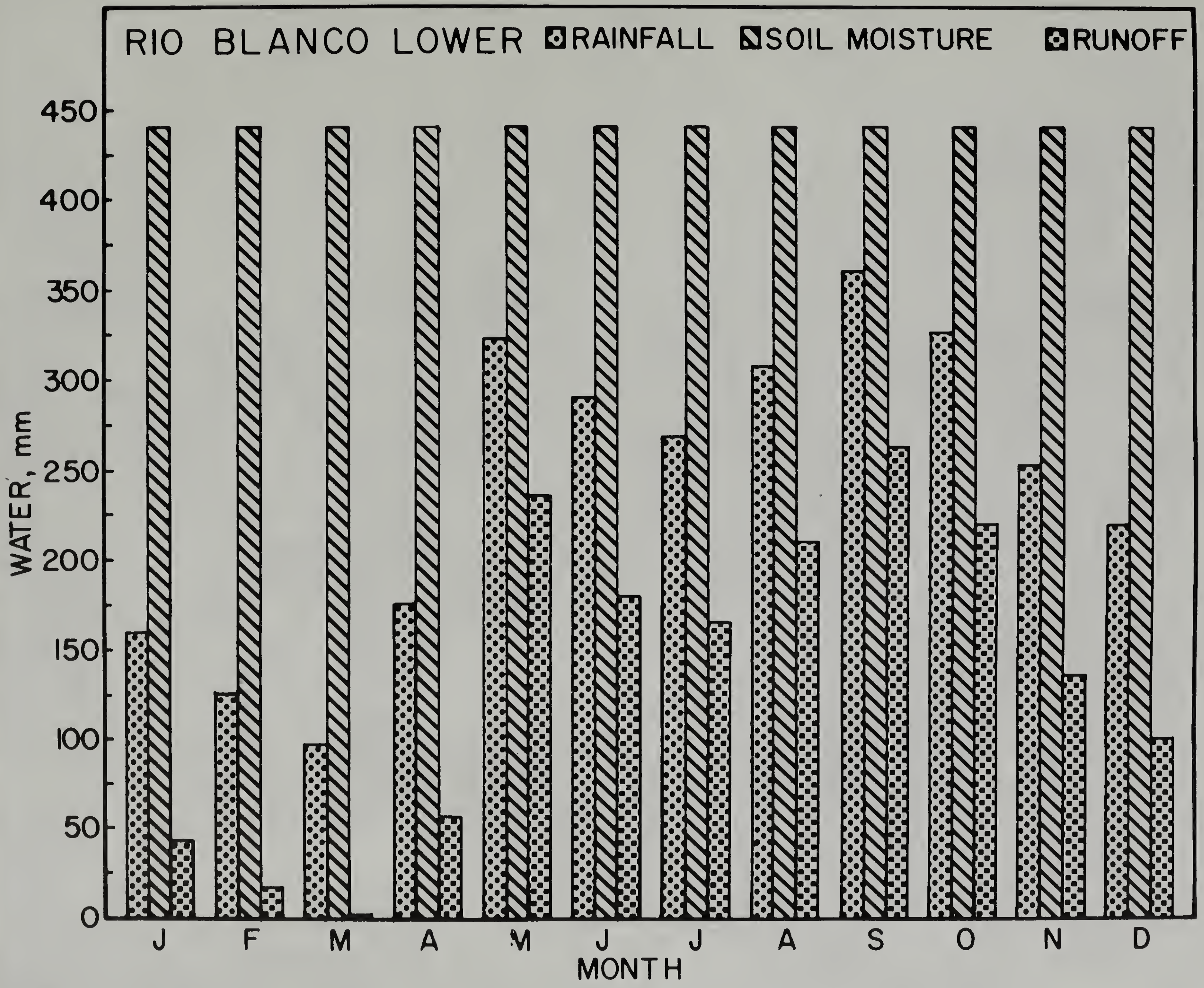

Figure 21 Mean rainfall, soil moisture, and runoff calculated for Río Blanco, Puerto Rico, in Subtropical Wet Forest. Pandura soil series, with available moisture of 441 mm per meter.

Figure 22 Subtropical Wet Forest. *Cyathea arborea* spreading over mat of *Gleichenia bifida* in the higher central mountains of Puerto Rico. These two plants commonly invade roadsides in this life zone.

Figure 23 Subtropical Wet Forest. Two examples of *Dacryodes excelsa* in the climatic association of the Luquillo Mountains. Both trees are about a meter in diameter.

more xerophytic than would be expected under the high rainfall of Subtropical Wet Forest, as is true of most limestone-derived soils. The dry edaphic condition, therefore, has an effect similar to that of reduced rainfall, a consideration which must be taken into account in land use planning.

Much of this life zone in Puerto Rico is covered by successional vegetation as a result of the emigration of much of the former rural population, due in part at least, to the inappropriateness of most of the Subtropical Wet Forest zone for agriculture, as described by Tosi (1959). On these unoccupied lands *Piper aduncum* L. (higuillo) often forms nearly pure stands. *Cecropia peltata* L. (yagrumo hembra, trumpet-tree), *Didymopanax morototoni* (Aubl.) Decne. and Planch. (yagrumo macho, matchwood), and *Ochroma lagopus* Sw. (guano, balsa) are abundant in many successional forests (see Figure 24). *Prestoea montana* (R. Grah.) Nichols (=*Euterpe globosa* Gaertn. in Little and Wadsworth, 1964) (palma de sierra, sierra palm) is very common in the wetter portions of the Subtropical Wet Forest zone. The species listed by Little and Wadsworth (1964) as components of their Lower Luquillo Province pertain chiefly to Subtropical Wet Forest, as do the species enumerated by Smith (1970 a & b).

Much of this life zone, particularly in the western portion of the island, is covered by coffee plantations, but to a lesser extent than formerly. A coffee plantation, consisting of an overstory of trees, a middle layer of coffee bushes, and a ground cover, is an agricultural ecosystem which physiognomically resembles the forest it replaced. Shade-grown coffee has historically been a stable and successful land use in many wet, mountainous tropical areas. Some sugarcane is grown in this life zone also, as no irrigation water is required here, though it is possible that insolation may sometimes be limiting. The dominant trend in land use however, as on the rest of Puerto Rico, seems to be an increase in grazing, but pasture management in the Subtropical Wet Forest can be difficult due to both the vigorous growth of weeds and problems of soil compaction. Perhaps the greatest value of the Subtropical Wet Forest zone in Puerto Rico is as a source of runoff which supplies water to the drier coastal areas where the population is concentrated. Future land use planning of areas within the Subtropical Wet Forest life zone should certainly recognize the fact that any manipulations here may have very important downstream effects.

The Subtropical Rain Forest Zone

This, the wettest of the sea-level belt of Subtropical life zones (lower rainfall limit about 3800 mm), occupies very little area in Puerto Rico, occurring only in a single crescent-shaped band on the windward faces of the Luquillo Mountains. It lies wholly within the Luquillo Experimental Forest and encompasses, appropriately enough, much of the area traversed by visitors going to the recreation area in "the rain forest." This life zone is characterized by a superabundance of precipitation, as shown in Figure 25. The water regime at La Mina (Figure 25, based on only eight years of rainfall data) indicates that the soil is at field capacity all year, and abundant runoff is produced every month, with six months each year yielding more than 300 mm. The annual total of 3400 mm of runoff is more than twice as much as most areas of the world receive as annual rainfall input! The constantly wet soil eliminates water as a potentially limiting growth factor in this environment, but oxygen stress, which can inhibit root respiration, may exert an important influence on plant growth.

The species found here are the same, for the most part, as those found in the surrounding Subtropical Wet Forest. This may be due, in part, to the fact that water is not a limiting factor in

a) Cecropia peltata

b) Didymopanax morototoni

c) Ochroma lagopus

Figure 24 Subtropical Wet Forest. Three common, fast-growing, large-leaved, successional tree species with similar physiognomies: a) *Cecropia peltata,* b) *Didymopanax morototoni,* and c) *Ochroma lagopus.*

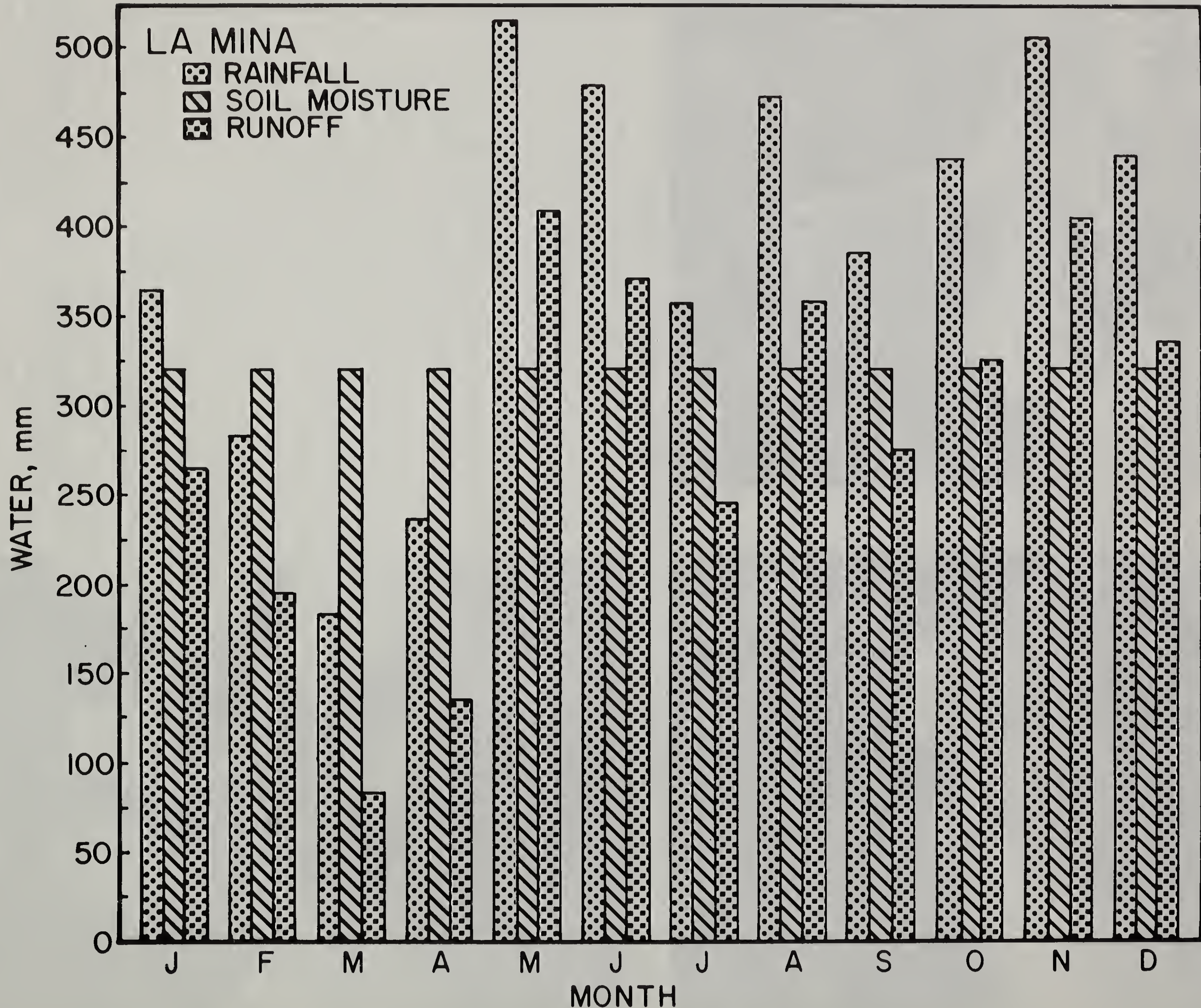

Figure 25 Mean rainfall, soil moisture, and runoff calculated for La Mina, Puerto Rico, in Subtropical Rain Forest. Los Guineos soil series, with available moisture of 320 mm per meter.

either of these two life zones, or, in part, to the fact that in Puerto Rico, as is often the case on islands, a few species perform many functions and spread over a wide variety of environments, much more so than would be the case on a continent. If the life zone occupied a large area or were adjacent to a source of potential colonizers from the same life zone, one might well expect the flora to be distinct from that of Subtropical Wet Forest, but that is not the case on Puerto Rico. The main features of the Subtropical Rain Forest are the high frequency of palms, *Prestoea montana* (R. Grah.) Nichols (palma de sierra, sierra palm) in this case (Figures 26 and 27), and a superabundance of epiphytes; no stem, building, highway marker, or fence post escapes colonization and most leaves, even those in the upper canopy, are covered with epiphyllae. The spiny tree-fern, *Nephelea portoricensis* (Kuhn) Tryon, is more abundant here than in the Subtropical Wet Forest.

Because of the small area it occupies, the Subtropical Rain Forest in Puerto Rico is primarily of academic interest and recreational value. Last year nearly a million people visited the recreation area at La Mina. The Baño de Oro Natural Area, much of which lies in this life zone, may be the only place in the world where an example of the mature vegetation of Subtropical Rain Forest is likely to receive long-term protection, while still being readily accessible.

The Subtropical Lower Montane Wet Forest Zone

There are two Lower Montane life zones in Puerto Rico, of which this is by far the most extensive, occurring in both the eastern and central parts of the island up to the summits of most mountains above 1000 meters and occasionally extending down to almost 700 meters. No peaks in Puerto Rico are high enough to encounter the low temperatures necessary for the occurrence of the next highest, or Montane, Altitudinal Belt. Rainfall, soil moisture, and runoff are shown in Figure 28 for Guineo Reservoir, located in the Lower Montane Wet Forest life zone. Like the Subtropical Rain Forest station (La Mina, Figure 25), the soil at Guineo Reservoir is at field capacity all year and runoff occurs each month, but the total (1700 mm annually) is only about half of that at La Mina.

The colorado forest type, named for the common *Cyrilla racemiflora* L. (palo colorado, swamp cyrilla) corresponds to the mature vegetation of the zonal association in Subtropical Lower Montane Wet Forest. The *Cyrilla* is the same species which grows as a shrub or small tree in the titi swamps in the southeastern U. S., but in the mountains of Puerto Rico it is a large, reddish-barked canopy tree. The hollow trunks of the older individuals are the main nesting sites for the nearly extinct Puerto Rican parrot, *Amazona vittata vittata* (Boddaert). This forest is characterized by open-crowned trees, many of which have their leaves grouped toward the ends of the branches, and whose crowns, when seen in profile, resemble somewhat-flattened bouquets. The leaves tend to be coriaceous and dark, giving the canopy a brownish or even reddish cast. This forest is poorer in species than the adjacent Subtropical Wet Forest; Wadsworth (1951) reported that only 53 tree species have been found in this type, compared to more than 150 species in the adjacent tabonuco type in Subtropical Wet Forest. In addition to the *Cyrilla*, he lists *Ocotea spathulata* Mez. (nemocá), *Micropholis chrysophylloides* Pierre (caimitillo), and *M. garciniaefolia* Pierre (caimitillo verde) as abundant components of this association, at least in eastern Puerto Rico.

Two additional associations are commonly found in Lower Montane Wet Forest in Puerto Rico. The first of these is a cloud-forest type, variously referred to as elfin woodland, mossy

Figure 26 Subtropical Rain Forest. *Prestoea montana*, dominant species on cove sites, scattered individuals on other sites. Epiphytes are extremely abundant (Photo by N. Kirby).

Figure 27 Subtropical Rain Forest. *Prestoea montana* roots, apparently an adaptation to saturated soil.

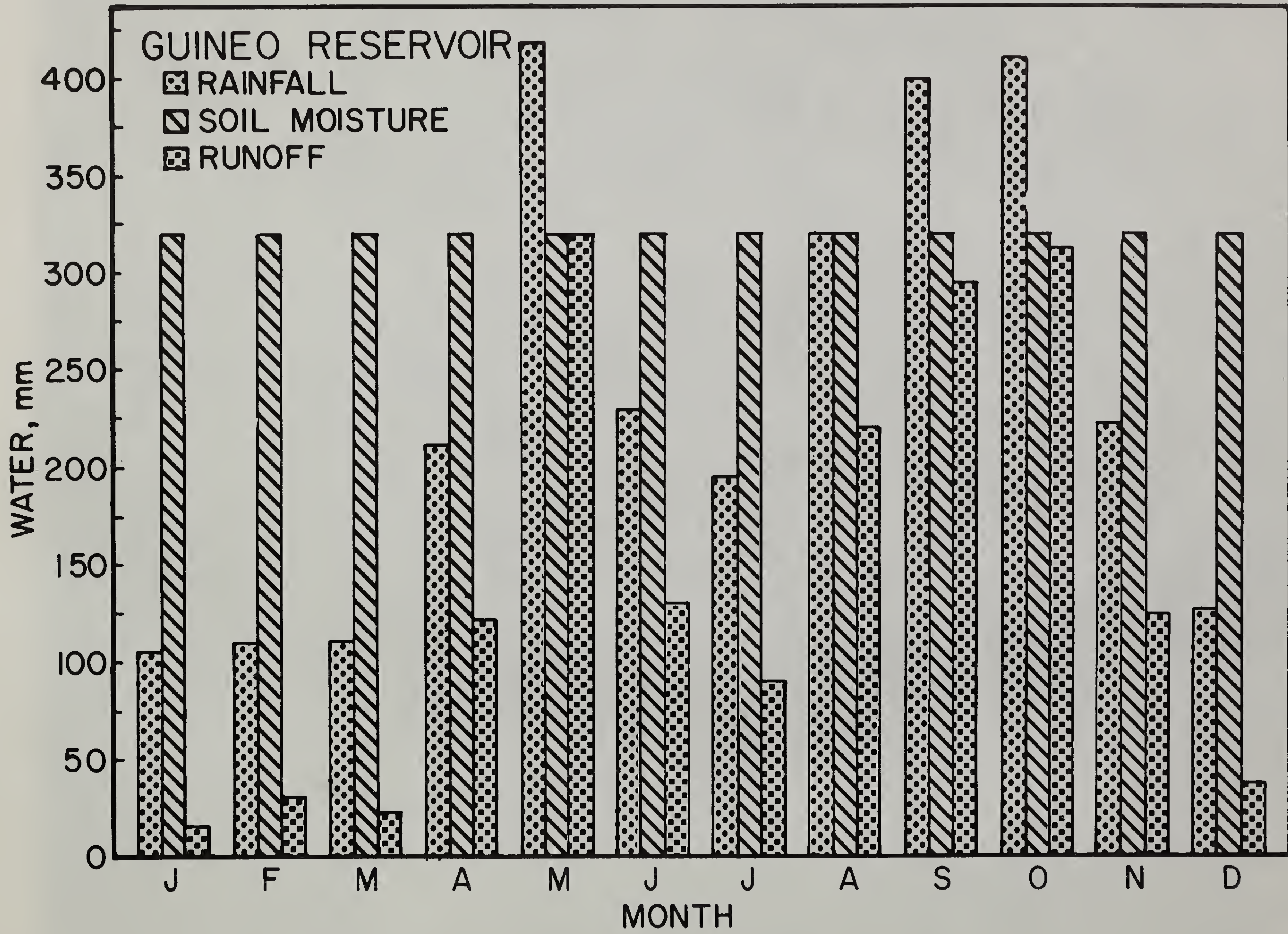

Figure 28 Mean rainfall, soil moisture, and runoff calculated for Guineo Reservoir, Puerto Rico, in Subtropical Lower Montane Wet Forest. Los Guineos soil series, with available moisture of 320 mm per meter.

forest, montane thicket, or dwarf forest. A detailed study of this association, in a site which straddles both the Lower Montane Wet Forest and Lower Montane Rain Forest life zones, was recently carried out by Howard and coworkers in the Pico del Oeste area of the Luquillo Mountains. Their results were reported in a series of papers (16 published through 1971) in the *Journal of the Arnold Arboretum.* The introductory article in the series (Howard, 1968) included physiognomic and floristic descriptions of the association, as well as an excellent review of previous work. The vegetation is characterized by gnarled trees less than seven meters tall, high basal area, small diameters, a large number of stems per unit area, and extremely slow growth rates. All trees are evergreen and sclerophyllous here, and the leaves tend to be grouped near the ends of the branches. Common trees include *Ocotea spathulata* Mez (nemocá), *Eugenia borinquensis* Britton (guayabota), *Tabebuia rigida* Urban (roble de sierra), *Weinmannia pinnata* L. (oreganillo), and *Calycogonium squamulosum* Cogn. (jusillo), all of which (except *W. pinnata*) are also found in the zonal association, or colorado type. Interestingly enough, the palo colorado (*Cyrilla racemiflora* L.), which is so common in the zonal association, is not found in this atmospheric association.

Decomposition is apparently slow in this association, and the upper soil seems to be almost pure organic matter, while the subsurface soils are clayey and oxygen-deficient. Tree roots form a tight, complete mat on the surface and do not appear to penetrate the soil very deeply. Another impressive feature of this association is the epiphyte load, which covers almost all stems, even those which are perfectly vertical and smooth-barked (see Figures 29 and 30).

In an event entirely unexpected for an area as well known biologically as Puerto Rico, Kepler and Parkes (1972) recently discovered a new bird species, *Dendroica angelae* Kepler and Parkes (elfin woods warbler), which is apparently endemic to this association in Puerto Rico.

Several theories have been proposed to explain the dwarf stature of the trees in this association. Murphy (1916) felt that exposure to strong winds affected the physiognomy of this vegetation, which he referred to as the "hurricane hardwood" type. Gleason and Cook (1926) and Beard (1942) also attributed it to the high winds which continually buffet these peaks, which, when coupled with the wet soils, might produce physiological drought. Wadsworth and Bonnet (1951) discussed water-saturated soils, with their impeded drainage, as factors influencing tree growth in the adjacent colorado type. Odum (1967) considered the dwarf cloud forest to be transpiration-limited, in that the continual cloud cover and saturated air impede transpiration, resulting in limited flow of essential mineral nutrients from the soil into the leaves. This theory was recently bolstered by the findings of Weaver *et al.* (1973), who measured extremely low transpiration rates for several tree species in the dwarf cloud forest association.

A second azonal association in the Lower Montane Wet Forest zone is the palm brake, consisting of nearly pure strands of *Prestoea montana* (R. Grah.) Nichols; examples of this association are readily accessible in both the Luquillo and Toro Negro Forests. The palm brake, seen in Figure 31, has several characteristics of a successional ecosystem: it is dominated by a single species, the borders between it and adjacent associations are very sharp, and it extends across life zone boundaries, reaching down into Subtropical Wet Forest and Subtropical Rain Forest. Beard (cited in Wadsworth, 1951) felt that the occurrence of palm brake was related to

Figure 29 Lower Montane Wet Forest. Liverworts account for most of the epiphyte biomass in this dwarf cloud forest atmospheric association (Photo by D. Pool).

Figure 30 Lower Montane Wet Forest. Dwarf cloud forest liverworts capture horizontally moving water while bromeliads such as this one collect throughfall and rainfall (Photo by D. Pool).

Figure 31 Lower Montane Wet Forest. Palm brake association. Cause of these communities, dominated by *Prestoea montana*, is still in doubt (Photo by D. Pool).

rates of erosion and that some of the areas where the palm formed pure stands were probably former landslides. Destruction of all trees by hurricanes, except the sierra palm which sheds its fronds in high winds and therefore does not uproot (Murphy, 1916), might be another factor which may account for the pure stands in Puerto Rico. In addition to forming nearly pure, possibly successional, stands on steep soils, *Prestoea* is also an important component of the mature, mixed forest. The details of its life cycle there were worked out by Bannister (1970).

Because of the high rainfall here, the Lower Montane Wet Forest zone is too fragile for any commercial forestry or agriculture, although in some areas dairy cattle are pastured, mostly on molasses grass (*Melinus minutiflora* Beauv.). Here again, as in other life zones with exceedingly high rainfall, the primary value lies in watershed yield, and managers of lands within this life zone should probably hold that as their foremost goal.

The Subtropical Lower Montane Rain Forest Zone

This life zone occupies less area than any other in Puerto Rico and the U. S. Virgin Islands, and is found only in a narrow band on the windward slopes of the Luquillo Mountains, immediately above the Subtropical Rain Forest. No weather stations have operated in this life zone long enough to justify the calculation of a complete water balance, but Baynton (1968) measured several standard weather variables for one year, from March 1966 through February 1967. He reported a mean annual temperature (based on the mean of average daily maximum and average daily minimum) of 18.6 C, an annual rainfall of 4533 mm, and a mean realtive humidity of 98.5 percent! If these conditions can be considered representative of the long-term mean values for this site, they would indicate an average, year-round runoff of almost 300 mm per month, and some months could yield almost twice that amount.

The vegetation of this life zone in Puerto Rico is very similar to that of Lower Montane Wet Forest; the characteristic which distinguishes the two is the greater abundance of epiphytes, epiphyllae, palms, and tree ferns in the Lower Montane Rain Forest. Most of this life zone in Puerto Rico is in the dwarf cloud forest association, where much of the vegetation on the exposed ridges has a windswept appearance (see Figure 32). Howard (1969) described the morphology and structure of many of the species found in this environment, while Gill (1969) documented the formation of aerial roots, which are extremely abundant on many species in this association. The water-saturated soil is covered with a soil-free root mat, and the root-soil-earthworm relationships here were investigated by Lyford (1969). Epiphytes, most of which are leafy hepatics, cover everything (Figure 33); this component of the flora was described by Fulford *et al.* (1970). In a recent study, Weaver (1972) removed all of the epiphytes from three plots and compared these to plots with the epiphytes left intact. He found that although the total amount of water reaching the ground was little affected, the distribution pattern of throughfall and stemflow was significantly altered.

Lower Montane Rain Forest in Puerto Rico is primarily a biological curiosity, but an invaluable one since it represents an environmental extreme and, as such, is an excellent tool for investigating the response of natural ecosystems to environmental stress. It is indeed fortunate that the limited amount of this life zone in Puerto Rico is located in a publicly-controlled forest, including the upper parts of the Baño de Oro Natural Area, where long-term protection is the goal.

Figure 32 Lower Montane Rain Forest. Dwarf cloud forest association, East Peak Road, Luquillo Mountains. The windward slope vegetation is affected by constant breezes and cloud cover (Photo by D. Pool).

Figure 33 Lower Montane Rain Forest. Dwarf cloud forest association. An eerie habitat dominated by perpetual wetness and semi-darkness. The fern is *Cyathea pubescens*, common on the higher peaks and ridges of Puerto Rico (Photo by D. Pool).

APPENDIX A: BIOTEMPERATURE

Many factors, including light quality, temperature range, seasonality, and prevalence of hurricanes, vary with latitude and thus might influence the changes in vegetation one observes as one moves north or south of the equator. Holdridge (1967) hypothesized that one factor which might be closely related to these changes is biotemperature, since the presence of high temperatures, with their effects on increased respiration and water stress, might reduce the net assimilation of vegetation in these areas. He therefore suggested that biotemperature calculations exclude not only temperatures below 0 C, but also temperatures above some upper limit, beyond which photosynthesis might be exceeded by respiration. He proposed 30 C as a tentative value to be used as an upper cutoff. The best that can be expected at the level of whole ecosystems, however, is that there may be some good, albeit empirical, correlation between high temperatures, as recorded in standard weather stations, and the observed changes in vegetation. Holdridge (1967) suggested that one method of calculating a biotemperature value which might correlate well with these vegetation changes would be to substitute zero for all air temperatures greater than 30 C. Such calculations were made for ten weather stations in Puerto Rico and the U. S. Virgin Islands.

The temperature data came from four sources: data for two of the stations, San Juan Airport and Santa Isabel, were obtained from the 1966 hourly data summaries published by ESSA (U. S. Weather Bureau); the data from Kingshill, St. Croix were obtained from the U. S. D. A. Agricultural Research Service; the data for the El Verde Experiment Station were supplied by the Puerto Rico Nuclear Center; the data from the remaining six stations came from Briscoe (1966).

The ten stations, their elevations, and the percent of temperatures which were greater than 30 C for each month are shown in Table A.1. On an annual basis, these percentages ranged from 0 at El Verde (510 m above sea level) and El Yunque (1060 m) to a high of 14.8 at Kingshill, St. Croix (67 m). Several stations–Santa Isabel, Río Blanco, Cape San Juan, Gurabo, Kingshill–had individual months where more than 20% of the recorded temperatures exceeded 30 C.

Calculating biotemperatures by substitution of zero for temperatures greater than 30 C has the effect of depressing the mean temperature over any period which includes such high temperatures. The results of the biotemperature calculations are plotted, by months, in Figure A.1. The shaded portion of each plot represents the amount by which the biotemperature is decreased below the mean air temperature. All stations are plotted in Figure A.1 except El Verde and El Yunque, where there was no difference between air temperature and biotemperature. Three of the stations–Santa Isabel, San Juan Airport, and Kingshill–show a greater difference between air temperature and biotemperature during the latter part of the year, about June through November. Three other stations–Cape San Juan, Fajardo, and Catalina–show greater differences during the early part of the year, February through May. The other stations show no apparent seasonal patterns. The difference between biotemperature and air temperature decreases with increasing altitude. Catalina, at 150 m above sea level, has an annual biotemperature regime only slightly lower than its air temperature (Figure A.1). At the El Verde Experiment Station, located at 510 m, air temperatures above 30 C occurred for only five hours during a one-year period.

Table A.1. Frequency of temperatures greater than 30 C. Values shown are percent of hours when temperatures exceeded 30 C; number in parenthesis under each percent is the number of days record upon which the percent is based. Only days with complete 24-hour records were used. Value of "0" indicates that no temperatures exceeded 30 C, while "0.0" indicates that some hourly temperatures exceeded 30 C but that these accounted for less than 0.1 percent of the record examined.

STATION	ELEV. (meters)	J	F	M	A	M	J	J	A	S	O	N	D	YEAR
		MONTH												
Santa Isabel	11	0 (31)	0 (28)	0 (31)	0.0 (30)	1.7 (31)	7.2 (30)	19.3 (31)	21.5 (31)	17.7 (30)	16.5 (31)	8.8 (30)	2.6 (31)	8.0 (365)
San Juan Airport (Weather Bureau)	19	0 (31)	0 (28)	0.4 (31)	0.7 (30)	0 (31)	10.7 (30)	10.2 (31)	14.9 (31)	13.9 (30)	14.6 (31)	2.6 (30)	4.0 (31)	6.0 (365)
Río Blanco	31	0.3 (30)	0.3 (29)	14.2 (31)	1.9 (30)	21.8 (29)	7.9 (30)	13.2 (30)	14.6 (30)	14.3 (26)	9.7 (30)	2.4 (29)	0 (30)	8.3 (354)
Cape San Juan	39	1.9 (30)	9.3 (29)	24.4 (27)	20.0 (30)	28.5 (26)	11.2 (29)	5.1 (31)	7.2 (22)	3.7 (27)	12.5 (13)	7.6 (29)	0 (30)	10.7 (323)
Gurabo	50	5.2 (31)	9.0 (27)	14.3 (30)	8.2 (29)	27.4 (29)	9.3 (30)	14.5 (31)	19.4 (31)	11.3 (25)	14.4 (30)	10.5 (27)	0 (19)	12.4 (339)
Kingshill, St. Croix	67	3.5 (31)	2.8 (6)	5.2 (16)	13.9 (30)	13.4 (31)	14.7 (30)	30.6 (14)	26.5 (25)	23.1 (28)	19.4 (29)	12.5 (27)	4.9 (18)	14.8 (285)
Fajardo*	71	0 (25)	0.6 (29)	11.4 (30)	4.9 (30)	9.8 (31)	1.9 (30)	1.2 (30)	2.7 (31)	1.1 (30)	0 (31)	3.9 (30)	0.6 (28)	3.3 (355)
Catalina	150	0.1 (31)	0.9 (28)	7.1 (31)	4.2 (30)	3.1 (31)	0 (28)	0 (27)	0 (31)	0.1 (29)	0.2 (26)	0.9 (29)	0 (31)	1.4 (352)
El Verde (Experiment Station)	510	0 (31)	0 (29)	0 (31)	0 (30)	0.0 (31)	0.0 (30)	0 (31)	0.0 (31)	0 (30)	0 (31)	0 (30)	0 (31)	0.0 (366)
El Yunque	1060	0 (18)	0 (26)	0 (18)	0 (29)	0 (25)	0 (29)	0 (30)	0 (29)	0 (30)	0 (28)	0 (28)	0 (29)	0 (319)

* This station is located at the Fajardo water filtration plant; not at the city of Fajardo (see Briscoe, 1966).

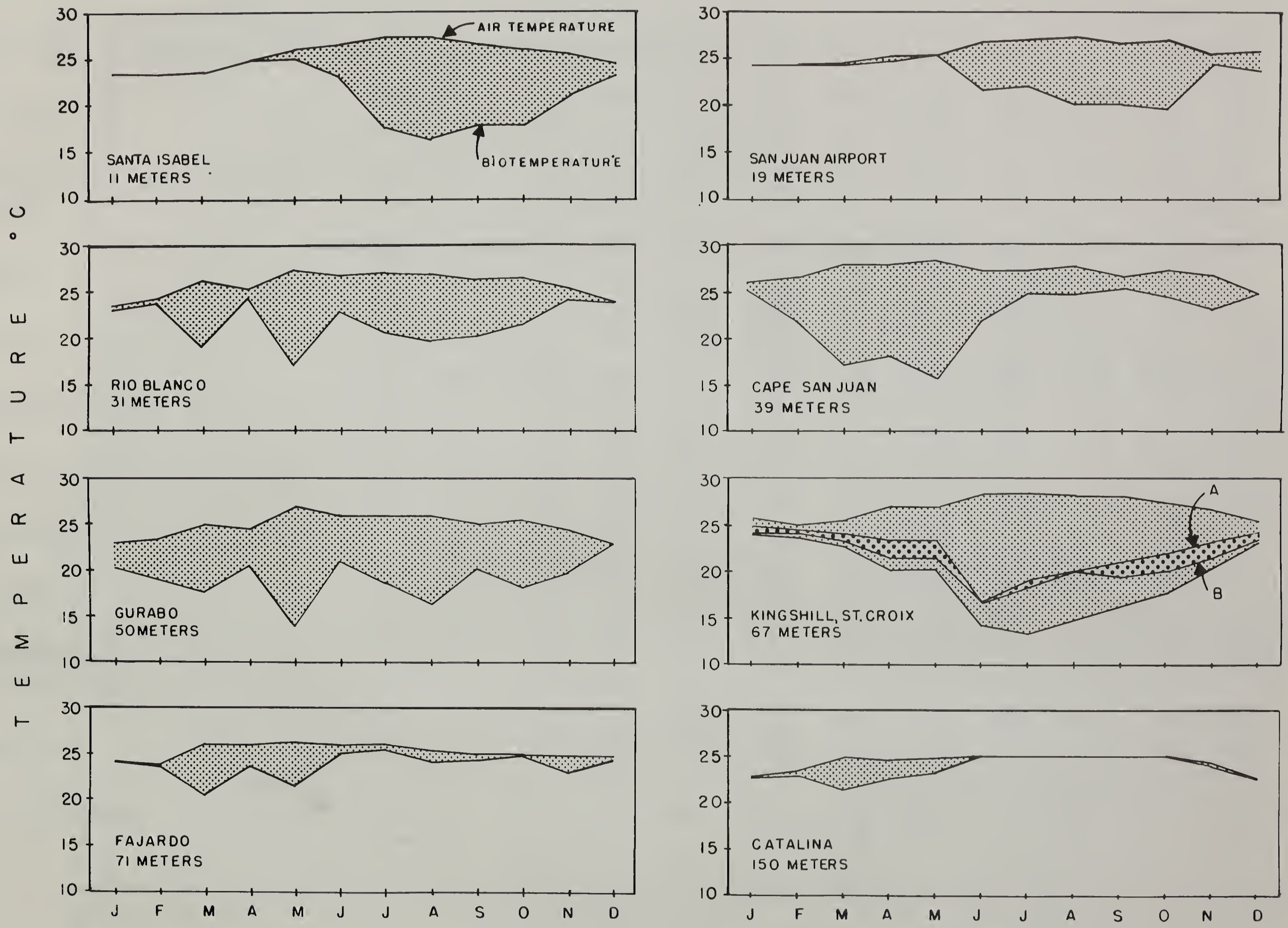

Figure A.1 Monthly mean air temperatures and biotemperatures at eight stations in Puerto Rico and the U. S. Virgin Islands. For Kingshill, line A is temperature calculated by substitution of 30 for all temperatures greater than 30 C; line B resulted from the exclusion of all temperatures greater than 30 C from the calculations.

Table A.2 shows the mean annual air temperature compared with the mean annual biotemperature at each of the ten stations. The greatest difference was at Gurabo, where mean annual air temperature was 5.7 C higher than the mean annual biotemperature, while at Catalina the mean annual biotemperature was only 0.7 C lower than the mean annual air temperature.

The biotemperature calculations clearly suggest that, assuming there is some biological validity to the upper limit of 30 C, Puerto Rico and the U. S. Virgin Islands should be classified as belonging to the Subtropical Latitudinal Region, according to Holdridge's nomenclature. All of the ten mean annual biotemperatures are less than 24 C, Holdridge's lower limit for the Tropical Latitudinal Region.

In Costa Rica, Holdridge *et al.* (1971) estimated biotemperatures from limited hourly data coupled with mean maximum and mean minimum temperatures. They estimated the differences between mean annual air temperature and mean annual biotemperature to be, in most cases, less than 2 C. The stations they dealt with ranged from about 8° 30' N to about 11° 00' N latitude; all of their study region was classified as belonging to the Tropical Latitudinal Region. Shibata (1970), who also worked with data from Costa Rica, found that, even at 1500 meters above sea level, there was a slight (less than 0.5 C) depression of the biotemperature. She used data from only four hours per day, however, rather than the full 24 hour record. At Managua, Nicaragua (12° 8' N) Shibata (1970), again using four data points per day, found that the mean annual air temperature of 27.4 C reduced to a biotemperature of 19.0 C; a drop of 8.4 C, or 30.7 percent. She classified Managua as part of the Subtropical Latitudinal Region. She concluded, on the basis of published vegetation maps and temperature calculations, that 31 C might be a better upper cutoff for biotemperature calculations than 30 C.

Using data provided by S. C. Snedaker (School of Forest Resources and Conservation, University of Florida) for Finca Murcielagos (15 meters above sea level, located on Lake Izabal, Guatemala, at 15° 30' N), the mean annual biotemperature was calculated to be 17.6 C, compared to a mean annual air temperature of 25.1 C. Slightly more than 15 percent of the total record (1962-1967) of almost 30,000 hourly temperatures were greater than 30 C. Finca Murcielagos, located about three degrees lower in latitude than Puerto Rico, has a biotemperature which is depressed even more below air temperature than are the biotemperatures of sea-level stations in Puerto Rico.

There are, of course, many ways to manipulate temperature data in hopes of obtaining some sort of empirical correlation with natural vegetation. Figure A.1, for example, shows the results of calculating biotemperature at Kingshill, St. Croix three different ways: 1.) by excluding all hours with temperatures greater than 30 C from the calculations; 2.) by substituting 30 C for all hourly temperatures greater than 30 C; and 3.) by substituting zero for all hourly temperatures greater than 30 C. The result is three very different temperature regimes; which of these, if any, however, is functionally related to the structure of natural ecosystems remains to be tested in the field.

A second example utilizes the extensive weather data published by Briscoe (1966). Using his tables, which provided mean hourly temperatures by months, the data were scanned for values greater than 30 C. Zero was substituted for these high temperatures, and biotemperatures were

Table A.2. Mean annual values of air temperature and biotemperature for ten stations in Puerto Rico and the U. S. Virgin Islands. These calculations were based on hourly values.

Station	Elevation (meters)	Mean Annual Air Temperature* (°C)	Mean Annual Biotemperature (°C)	Difference (°C)	Decrease (%)
Santa Isabel	11	25.2	21.3	3.9	15.5
San Juan Airport (Weather Bureau)	19	25.9	23.0	2.9	11.2
Río Blanco	31	25.6	21.6	4.0	15.6
Cape San Juan	39	27.0	22.2	4.8	17.8
Gurabo	50	24.7	19.0	5.7	23.1
Kingshill, St. Croix	67	26.8	22.1	4.7	17.5
Fajardo**	71	25.4	23.8	1.6	6.3
Catalina	150	24.1	23.4	0.7	2.9
El Verde (Experiment Station)	510	22.1	22.1	0.0	0
El Yunque	1050	18.7	18.7	0.0	0

* May differ from value shown in Table A.3 because the two means are based on different periods of record.

** This station is located at the Fajardo water filtration plant; not at the city of Fajardo (see Briscoe, 1966).

calculated in the usual way. The result of this method of biotemperature calculation is shown in Table A.3 for those seven stations for which mean hourly temperatures by months were available. Since the data were expressed as hourly means, by months, rather than individual hourly values, the biotemperature is much closer to the air temperature when calculated this way. That is, a mean of 30 or 31 hourly values is much less likely to be greater than 30 C than is any of the individual hourly values which go into making up that mean.

A major research need is a series of studies at two levels: 1.) to determine what quantitative aspects of natural ecosystems are well correlated with various weather-station temperature data, and 2.) to determine which environmental factors that are well correlated with air temperatures directly affect the structure and function of whole ecosystems. Only such studies can properly test the various hypotheses concerning the relationships between weather station data and natural vegetation.

Table A.3. Mean annual values for air temperature and biotemperature for seven stations in Puerto Rico. These calculations were based on the mean monthly values, by hours, of Briscoe (1966).

Station	Elevation (meters)	Mean Annual Air Temperature* (°C)	Mean Annual Biotemperature (°C)	Difference (°C)	Decrease (%)
San Juan Airport (Weather Bureau)	19	25.6	25.4	0.2	0.8
Río Blanco	31	25.5	24.8	0.7	2.7
Cape San Juan	39	26.6	25.9	0.7	2.6
Gurabo	50	24.5	21.5	3.0	12.2
Fajardo**	71	25.0	25.0	0.0	0
Catalina	150	24.3	24.3	0.0	0
El Yunque	1050	18.4	18.4	0.0	0

* May differ from value shown in Table A.2 because the two means are based on different periods of record.

** This station is located at the Fajardo water filtration plant; not at the city of Fajardo (see Briscoe, 1966).

APPENDIX B: WATER BALANCES

The following tables (B.1 through B.10) are the complete water balance for ten stations in Puerto Rico and the U. S. Virgin Islands. The method used was that of Tosi (Ewel *et al.*, 1968; Holdridge *et al.*, 1971; FAO, 1971), which combines features of Holdridge's life zone system and its relation to water budgets (see, for example, Holdridge, 1962a) with the tabular accounting developed by Thornthwaite (1948; Thornthwaite and Mather, 1957). One of Tosi's innovative features is the correction applied to potential evapotranspiration in climates where the potential evapotranspiration is greater than the annual precipitation (i.e. where P. ET/R>1). Tosi proposed that special adaptations of the vegetation in dry areas result in a decrease of potential evapotranspiration; this corrected potential evapotranspiration is shown for the two driest stations, Tables B.1 and B.2.

The calculated water balances, in keeping with Tosi's criteria, assume the presence of mature, natural vegetation. This is not the case at most of the sites included, so the water-use rates shown in the tables should be taken as maximum probable values; actual evapotranspiration is usually greater from mature terrestrial ecosystems than from those which are successional.

Holdridge assumes that mean annual potential evapotranspiration is a linear function of mean annual biotemperature, with the intercept at 0 and a slope of 58.93 mm $°C^{-1}$. Smith (1967) compared potential evapotranspiration calculated according to Holdridge's assumption with values obtained during an eleven-year period from four Thornthwaite-type potential evapotranspirometers in Jamaica and found that the annual values differed by only about four percent, but monthly deviations were often greater.

Moisture relations of the soils shown in the tables are from data in Lugo-López (1953), except for the Glynn series, data for which were provided by L. H. Rivera from the files of the U. S. D. A., Soil Conservation Service. An effective rooting depth of one meter was assumed for all soils; soil moisture changes in millimeters therefore refer to millimeters per meter of soil depth.

One further caveat with regard to the water balances: the calculations are based on long-term means, so the actual values shown might be combinations which never occur in nature. The water balance calculations should, therefore, be used primarily for the trends they indicate, rather than for the prediction of actual conditions at a specific point at a particular time.

Water balances such as these are perhaps most useful when used in conjunction with additional empirical data from specific sites. For example, streamflow data are available for a number of drainages in Puerto Rico and this information, coupled with the water balances, can result in useful guides to land utilization planning in various kinds of environments. Antonini *et al.* (1973) recently applied water balance calculations such as these to a watershed encompassing four life zones in the Dominican Republic. The water budgets were coupled to a model of land use changes to predict the effects of various land use policies on siltation in a downstream reservoir.

Bogart *et al.* (1964) compiled much of the watershed data available for Puerto Rico and calculated water budgets, including rainfall inputs, evapotranspiration, runoff, ground-water discharge, and storage, for the whole island. Similar calculations, using rainfall and streamflow data combined with Thornthwaite's water balances have been reported for Puerto Rico by Giusti and López (1967) and for the U. S. Virgin Islands by Bowden (1968) and Bowden *et al.* (1970). The life zone map, together with the Tosi water balances, might be one useful way to look at important subdivisions of the area's water budget.

Another useful application might be the simulation of water budgets assuming that rainfall can vary considerably with respect to its longferm mean; such calculations might be useful if combined with predictive variables, such as Palmer's drought index, which Calvesbert (1967) has applied to Puerto Rico.

Long-term mean		Month												Year (mean or total)
		Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	
Air temperature	°C	23.1	23.1	23.5	24.7	25.8	26.3	27.1	26.9	26.4	25.8	25.4	24.5	25.2
Biotemperature	°C	23.1	23.1	23.5	24.7	24.9	22.9	17.6	16.4	17.7	17.8	21.1	23.2	21.3
Potential evapotranspiration	mm	116	105	118	120	125	111	88	82	86	89	102	116	1258
P. ET. adjusted for dry climate	mm	83	75	84	86	90	79	63	59	62	64	73	83	901
Precipitation	mm	22	24	13	43	112	100	70	113	150	131	79	44	901
Actual evapotranspiration	mm	83	75	48	61	90	79	63	59	62	64	73	83	840
Water surplus	mm	0	0	0	0	22	21	7	54	88	67	6	0	
Soil moisture change	mm	-61	-51	-35	-18	+22	+21	+7	+54	+88	+12	0	-39	
Moisture available in soil at end of the month	mm	122	71	36	18	40	61	68	122	210	222	222	183	
All runoff	mm	0	0	0	0	0	0	0	0	0	55	6	0	61
Soil moisture deficit	mm	100	151	186	204	182	161	154	100	12	0	0	39	
Precipitation deficit	mm	61	51	71	43	0	0	0	0	0	0	0	39	
Total moisture deficit	mm	161	202	257	247	182	161	154	100	12	0	0	78	

Table B.1 Water balance for Santa Isabel, Subtropical Dry Forest, assuming mature vegetation on Teresa soil series (available moisture = 222 mm). Elevation = 8 m, P. ET./R = 1.40.

Long-term mean		Month												Year (mean or total)
		Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	
Air temperature	°C	25.7	24.9	25.4	26.9	26.9	28.3	28.4	28.1	28.0	27.3	26.6	25.3	26.8
Biotemperature	°C	23.9	23.7	22.8	20.1	20.2	14.3	13.3	14.8	16.2	17.7	20.3	23.0	19.2
Potential evapotranspiration	mm	120	108	114	97	101	69	67	74	78	89	98	115	1130
P. ET. adjusted for dry climate	mm	117	105	111	95	98	67	65	72	76	87	96	112	1102
Precipitation	mm	67	39	32	46	119	96	84	104	145	150	154	66	1102
Actual evapotranspiration	mm	109	60	43	51	98	67	65	72	76	87	96	112	936
Water surplus	mm	0	0	0	0	21	29	19	32	69	63	58	0	
Soil moisture change	mm	-42	-21	-11	-5	+21	+29	+19	+32	+24	0	0	-46	
Moisture available in soil at end of the month	mm	42	21	10	5	26	55	74	106	130	130	130	84	
All runoff	mm	0	0	0	0	0	0	0	0	45	63	58	0	166
Soil moisture deficit	mm	88	109	120	125	104	75	56	24	0	0	0	46	
Precipitation deficit	mm	50	69	79	49	0	0	0	0	0	0	0	46	
Total moisture deficit	mm	138	178	199	174	104	75	56	24	0	0	0	92	

Table B.2 Water balance for Kingshill, St. Croix, Subtropical Dry Forest, assuming mature vegetation on Glynn soil series (available moisture = 130 mm). Elevation = 61 m; P. ET./R = 1.03

Long-term mean	Month												Year (mean or total)
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	
Air temperature °C	24.2	24.3	25.4	25.1	25.5	26.9	27.2	27.5	26.9	27.1	25.7	25.9	25.9
Biotemperature °C	24.2	24.3	24.3	24.8	25.5	21.8	22.2	20.2	20.2	19.8	24.4	23.9	23.0
Potential evapotranspiration mm	121	111	122	120	128	106	111	101	98	99	118	120	1356
Precipitation mm	119	74	56	95	181	144	159	181	172	148	165	138	1632
Actual evapotranspiration mm	121	111	107	120	128	106	111	101	98	99	118	120	1341
Water surplus mm	0	0	0	0	51	38	48	80	74	49	47	18	
Soil moisture change mm	-2	-37	-51	-25	+51	+38	+24	0	0	0	0	0	
Moisture available in soil at end of the month mm	139	102	51	26	79	117	141	141	141	141	141	141	
All runoff mm	0	0	0	0	0	0	24	80	74	49	47	18	291
Soil moisture deficit mm	2	39	90	115	64	24	0	0	0	0	0	0	
Precipitation deficit mm	2	37	66	25	0	0	0	0	0	0	0	0	
Total moisture deficit mm	4	76	156	140	64	24	0	0	0	0	0	0	

Table B.3 Water balance for San Juan (Airport, Weather Bureau), Subtropical Moist Forest, assuming mature vegetation on Río Lajas soil series (available moisture = 141 mm). Elevation = 4 m; P. ET./R = 0.83.

Long-term mean	Month												Year (mean or total)
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	
Air temperature (=Biotemperature) °C	19.6	19.9	21.4	22.9	23.3	23.9	23.7	23.4	23.4	23.6	21.7	21.0	22.3
Potential evapotranspiration mm	98	91	107	111	117	116	119	117	113	118	105	105	1317
Precipitation mm	89	77	70	101	149	108	121	155	169	184	150	104	1478
Actual evapotranspiration mm	98	91	107	111	117	116	119	117	113	118	105	105	1317
Water surplus mm	0	0	0	0	32	0	2	38	56	66	45	0	
Soil moisture change mm	-9	-14	-37	-10	+32	-8	+2	+38	+7	0	0	-1	
Moisture available in soil at end of the month mm	235	221	184	174	206	198	200	238	245	245	245	244	
All runoff mm	0	0	0	0	0	0	0	0	49	66	45	0	160
Soil moisture deficit mm	10	24	61	71	39	47	45	7	0	0	0	1	
Precipitation deficit mm	9	14	37	10	0	8	0	0	0	0	0	1	
Total moisture deficit mm	19	38	98	81	39	55	45	7	0	0	0	2	

Table B.4 Water balance for Aibonito, Subtropical Moist Forest, assuming mature vegetation on Múcara soil series (available moisture = 245 mm). Elevation = 640 m; P. ET./R = 0.89.

Long-term mean		Month												Year (mean or total)
		Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	
Air temperature (=Biotemperature)	℃	19.7	19.7	20.5	21.3	22.1	22.8	22.7	23.1	22.9	22.7	21.8	20.3	21.7
Potential evapotranspiration	mm	99	90	103	103	111	110	114	116	111	114	106	102	1279
Precipitation	mm	93	77	54	105	140	123	112	148	222	187	142	136	1539
Actual evapotranspiration	mm	99	90	103	103	111	110	114	116	111	114	106	102	1279
Water surplus	mm	0	0	0	2	29	13	0	32	111	73	36	34	
Soil moisture change	mm	–6	–13	–49	+2	+29	+13	–2	+23	0	0	0	0	
Moisture available in soil at end of the month	mm	113	100	51	53	82	98	96	119	119	119	119	119	
All runoff	mm	0	0	0	0	0	0	0	9	111	73	36	34	263
Soil moisture deficit	mm	6	19	68	66	37	21	23	0	0	0	0	0	
Precipitation deficit	mm	6	13	49	0	0	0	2	0	0	0	0	0	
Total moisture deficit	mm	12	32	117	66	37	21	25	0	0	0	0	0	

Table B.5 Water balance for Barranquitas, Subtropical Moist Forest, assuming mature vegetation on Cialitos soil series (available moisture = 119 mm). Elevation = 671 m; P. ET./R = 0.83.

Long-term mean		Month												Year (mean or total)
		Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	
Air temperature (=Biotemperature)	℃	20.9	20.8	21.3	21.8	22.3	22.9	23.2	23.7	23.7	23.4	22.8	21.8	22.4
Potential evapotranspiration	mm	105	95	107	106	112	111	116	119	115	117	110	109	1322
Precipitation	mm	107	86	65	134	245	223	227	220	276	247	182	137	2149
Actual evapotranspiration	mm	105	95	107	106	112	111	116	119	115	117	110	109	1322
Water surplus	mm	2	0	0	28	133	112	111	101	161	130	72	28	
Soil moisture change	mm	0	–9	–42	+28	+23	0	0	0	0	0	0	0	
Moisture available in soil at end of the month	mm	320	311	269	297	320	320	320	320	320	320	320	320	
All runoff	mm	2	0	0	0	110	112	111	101	161	130	72	28	827
Soil moisture deficit	mm	0	9	51	23	0	0	0	0	0	0	0	0	
Precipitation deficit	mm	0	9	42	0	0	0	0	0	0	0	0	0	
Total moisture deficit	mm	0	18	93	23	0	0	0	0	0	0	0	0	

Table B.6 Water balance for Carite Dam, Subtropical Wet Forest, assuming mature vegetation on Los Guineos soil series (available moisture = 320 mm). Elevation = 610 m; P. ET./R = 0.62.

Long-term mean		Month												Year (mean or total)
		Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	
Air temperature (=Biotemperature)	°C	18.9	19.1	19.1	20.0	21.1	22.1	22.2	22.3	22.1	21.7	20.8	20.0	20.8
Potential evapotranspiration	mm	95	87	96	97	106	107	111	112	107	109	101	100	1228
Precipitation	mm	74	75	86	156	279	186	208	302	327	346	195	101	2335
Actual evapotranspiration	mm	95	87	96	97	106	107	111	112	107	109	101	100	1228
Water surplus	mm	0	0	0	59	173	79	97	190	220	237	94	1	
Soil moisture change	mm	-21	-12	-10	+43	0	0	0	0	0	0	0	0	
Moisture available in soil at end of the month	mm	229	287	277	320	320	320	320	320	320	320	320	320	
All runoff	mm	0	0	0	16	173	79	97	190	220	237	94	1	1107
Soil moisture deficit	mm	21	33	43	0	0	0	0	0	0	0	0	0	
Precipitation deficit	mm	21	12	10	0	0	0	0	0	0	0	0	0	
Total moisture deficit	mm	42	45	53	0	0	0	0	0	0	0	0	0	

Table B.7 Water balance for Garzas, Subtropical Wet Forest, assuming mature vegetation on Los Guineos soil series (available moisture = 320 mm). Elevation = 829 m; P. ET./R = 0.53.

Long-term mean		Month												Year (mean or total)
		Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	
Air temperature	°C	23.4	24.1	26.1	25.3	27.3	26.6	26.9	26.7	26.2	26.3	25.2	23.6	25.6
Biotemperature	°C	23.3	23.9	19.2	24.3	17.1	22.8	20.5	19.6	20.0	21.2	24.0	23.6	21.6
Potential evapotranspiration	mm	116	109	96	118	86	110	103	98	97	106	116	118	1273
Precipitation	mm	159	126	97	175	322	289	268	307	359	325	251	218	2896
Actual evapotranspiration	mm	116	109	96	118	86	110	103	98	97	106	116	118	1273
Water surplus	mm	43	17	1	57	236	179	165	209	262	219	135	100	
Soil moisture change	mm	0	0	0	0	0	0	0	0	0	0	0	0	
Moisture available in soil at end of the month	mm	441	441	441	441	441	441	441	441	441	441	441	441	
All runoff	mm	43	17	1	57	236	179	165	209	262	219	135	100	1623
Soil moisture deficit	mm	0	0	0	0	0	0	0	0	0	0	0	0	
Precipitation deficit	mm	0	0	0	0	0	0	0	0	0	0	0	0	
Total moisture deficit	mm	0	0	0	0	0	0	0	0	0	0	0	0	

Table B.8 Water balance for Río Blanco Lower, Subtropical Wet Forest, assuming mature vegetation on Pandura soil series (available soil moisture = 441 mm). Elevation = 40 m, P. ET./R = 0.44.

Long-term mean		Month												Year (mean or total)
		Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	
Air temperature (=Biotemperature)	°C	19.8	19.3	19.9	20.8	21.3	22.1	22.3	22.7	22.7	22.3	21.6	20.5	21.3
Potential evapotranspiration	mm	99	88	100	101	107	107	112	114	110	112	106	103	1259
Precipitation	mm	364	283	183	236	515	478	357	472	385	437	511	439	4660
Actual evapotranspiration	mm	99	88	100	101	107	107	112	114	110	112	106	103	1259
Water surplus	mm	265	195	83	135	408	371	245	358	275	325	405	336	
Soil moisture change	mm	0	0	0	0	0	0	0	0	0	0	0	0	
Moisture available in soil at end of the month	mm	320	320	320	320	320	320	320	320	320	320	320	320	
All runoff	mm	265	195	83	135	408	371	245	358	275	325	405	336	3401
Soil moisture deficit	mm	0	0	0	0	0	0	0	0	0	0	0	0	
Precipitation deficit	mm	0	0	0	0	0	0	0	0	0	0	0	0	
Total moisture deficit	mm	0	0	0	0	0	0	0	0	0	0	0	0	

Table B.9 Water balance for La Mina, Subtropical Rain Forest, assuming mature vegetation on Los Guineos soil series (available moisture = 320 mm). Elevation = 625 m; P. ET./R = 0.27.

Long-term mean		Month												Year (mean or total)
		Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	
Air temperature (=Biotemperature)	°C	17.6	17.4	17.8	18.6	19.7	20.7	21.1	21.1	20.7	20.3	19.6	18.4	19.4
Potential evapotranspiration	mm	88	79	89	90	99	100	106	100	104	98	98	89	1140
Precipitation	mm	104	109	111	212	418	231	196	321	400	411	223	127	2863
Actual evapotranspiration	mm	88	79	89	90	99	100	106	100	104	98	98	89	1140
Water surplus	mm	16	30	22	122	319	131	90	221	296	313	125	38	
Soil moisture change	mm	0	0	0	0	0	0	0	0	0	0	0	0	
Moisture available in soil at end of the month	mm	320	320	320	320	320	320	320	320	320	320	320	320	
All runoff	mm	16	30	22	122	319	131	90	221	296	313	125	38	1723
Soil moisture deficit	mm	0	0	0	0	0	0	0	0	0	0	0	0	
Precipitation deficit	mm	0	0	0	0	0	0	0	0	0	0	0	0	
Total moisture deficit	mm	0	0	0	0	0	0	0	0	0	0	0	0	

Table B.10 Water balance for Guineo Reservoir, Subtropical Lower Montane Wet Forest, assuming mature vegetation on Los Guineos soil series (available moisture = 320 mm). Elevation = 914 m; P. ET./R = 0.40.

Literature Cited

Antonini, G. A., K. C. Ewel, and J. J. Ewel. 1973. Ecological modelling of a tropical watershed: a guide to regional planning. Chapt. 5 *In*: B. S. Hoyle, ed. Spatial aspects of development. John Wiley and Sons, Chichester, England. (in press).

Bannister, B. A. 1970. Ecological life cycle of *Euterpe globosa* Gaertn. Chapt. B-18:299-314 *In*: H. T. Odum, ed. A tropical rain forest. USAEC, Oak Ridge, Tennessee.

Baynton, H. W. 1968. The ecology of an elfin forest in Puerto Rico, 2. The microclimate of Pico del Oeste. Jour. Arnold Arb. 49:419-430.

Beard, J. S. 1942. Montane vegetation in the Antilles. Carib. Forest 3:61-74.

Beard, J. S. 1949. The natural vegetation of the Windward and Leeward Islands. Oxford Forestry Memoirs 21. 192 p.

Bogart, D. B., T. Arnow, and J. W. Crooks. 1964. Water Resources of Puerto Rico, a Progress Report. Water Resources Bulletin No. 4. U. S. G. S. in cooperation with the Commonwealth of Puerto Rico. 102 p.

Bowden, M. J. 1968. Water balances of a dry island: the hydroclimatology of St. Croix, Virgin Islands and potential for agriculture and urban growth. Geography publications at Dartmouth, No. 6. Hanover, N. H. 89 p.

Bowden, M. J., N. Fischman, P. Cook, J. Wood, and E. Omasta. 1970. Climate, water balance, and climatic change in the north-west Virgin Islands. Caribbean Research Institute, College of the Virgin Islands. St. Thomas, V. I. 127 p.

Briggs, J. P. and J. P. Akers. 1965. Hydrogeologic Map of Puerto Rico and Adjacent Islands. Fig. 22 *In*: D. B. Bogart, T. Arnow, and J. W. Crooks. 1964. Water Resources Bulletin No. 4. U. S. G. S. in cooperation with the Commonwealth of Puerto Rico.

Briscoe, C. B. 1966. Weather in the Luquillo Mountains of Puerto Rico. U. S. D. A. Forest Service Res. Paper ITF-3. Institute of Tropical Forestry, Río Piedras, P. R. 250 p.

Buell, P. F. and P. Dansereau. 1966. Studies on the vegetation of Puerto Rico. 2. Analysis and mapping of the Roosevelt Roads area. Special Pub. No. 1., Univ. of Puerto Rico, Institute of Caribbean Science, Mayaguez. 287 + maps.

Calvesbert, R. J. 1967. Climatology of meteorological drought in Puerto Rico. pp. 42-56. *In*: B. Floyd, ed., Proceedings of a conference on climatology and related fields in the Caribbean. University of the West Indies, Mona, Jamaica.

Calvesbert, R. J. 1970. Climate of Puerto Rico and U. S. Virgin Islands. Climatography of the U. S. No. 60-52. Climates of the States, U. S. Department of Commerce, Washington, D. C. 29 p.

Cook, M. T. and H. A. Gleason. 1928. Ecological survey of the flora of Porto Rico. Jour. Dept. Agric. Porto Rico. 12:3-137.

Dansereau, P. 1966. Studies on the vegetation of Puerto Rico. 1. Description and integration of the plant-communities. Special Pub. No. 1, University of Puerto Rico, Institute of Caribbean Science, Mayaguez. 287 p.

Espinal, L. S. and E. Montenegro (with J. A. Tosi, Jr. and L. R. Holdridge). 1963. Formaciones vegetales de Colombia; y mapa ecológico de Colombia. Instituto Geográfico "Augustín Codazzi." Bogotá. 201 p. + map.

ESSA. 1970. Climatological data. Puerto Rico and Virgin Islands. Annual Summary 1969. 15:135-142.

Ewel, J., A. Madríz, and J. A. Tosi, Jr. 1968. Zonas de vida de Venezuela; y mapa ecológico de Venezuela. Ministerio de Agricultura y Cría, Dirección de Investigación. Caracas. 265 p. + map.

FAO. 1971. Inventariación y demostraciones forestales, Panamá. Zonas de Vida, basado en la labor de Joseph A. Tosi. FO:SF/PAN 6. Informe técnico 2. Rome, Italy. 89 p. + map.

Fulford, M., B. Crandall, and R. Stotler. 1970. The ecology of an elfin forest in Puerto Rico, 11. The leafy hepaticae of Pico del Oeste. Jour. Arnold Arb. 51:56-69.

Gill, A. M. 1969. The ecology of an elfin forest in Puerto Rico, 6. Aërial roots. Jour. Arnold Arb. 50:197-209.

Giusti, E. V. and M. A. López. 1967. Climate and stream flow of Puerto Rico. Carib. Jour. of Sci. 7:87-93.

Gleason, H. A. and M. T. Cook. 1926. Plant ecology of Porto Rico. Vol. 7, Parts 1 and 2 + plates. pp. 1-173. *In*: Scientific Survey of Porto Rico and the Virgin Islands. N. Y Acad. of Sciences, New York.

Golley, F. B., H. T. Odum, and R. F. Wilson. 1962. The structure and metabolism of a Puerto Rican red mangrove forest in May. Ecology. 43:9-19.

Gray, K. M. and G. A. Symes. 1969. Forest Inventory Map No. 3, Life Zones, 1:500,000. U. N. D. P. Forestry/Watershed Management Project - Kingston, Jamaica.

Holdridge, L. R. 1947. Determination of world plant formations from simple climatic data. Science 105:367-368.

Holdridge, L. R. 1959a. Mapa ecológico de El Salvador. Interamerican Institute of Agricultural Science, Turrialba, Costa Rica.

Holdridge, L. R. 1959b. Mapa ecológico de Guatemala, A. C. Interamerican Institute of Agricultural Science, Turrialba, Costa Rica.

Holdridge, L. R. 1962a. The determination of atmospheric water movements. Ecology 43:1-9.

Holdridge, L. R. 1962b. Mapa ecológico de Honduras. Organization of American States, Washington, D. C.

Holdridge, L. R. 1962c. Mapa ecológico de Nicaragua, A. C. United States Agency for International Development, Managua, Nicaragua.

Holdridge, L. R. 1967. Life zone ecology. Tropical Science Center, San Jose, Costa Rica. 206 p.

Holdridge, L. R., W. C. Grenke, W. H. Hatheway, T. Liang, and J. A. Tosi, Jr. 1971. Forest environments in tropical life zones, a pilot study. Pergamon Press, Oxford. 747 p.

Howard, R. A. 1968. The ecology of an elfin forest in Puerto Rico, 1. Introduction and composition studies. Jour. Arnold Arb. 49:381-418.

Howard, R. A. 1969. The ecology of an elfin forest in Puerto Rico, 8. Studies of stem growth and form and of leaf structure. Jour. Arnold Arb. 50:225-267.

Kepler, C. B. and A. K. Kepler. 1970. Preliminary comparison of bird species diversity and density in Luquillo and Guánica Forests. Chapt. E-14; 183-191. *In*: H. T. Odum, ed. A tropical rain forest. USAEC, Oak Ridge, Tennessee.

Kepler, C. B. and K. C. Parkes. 1972. A new species of warbler (Parulidae) from Puerto Rico. Auk. 89:1-18.

Kumme, K. W. O. and C. B. Briscoe. 1963. Forest formations of Puerto Rico. Carib. Forest. 24:57-65 + map.

Little, E. L., Jr. and F. H. Wadsworth. 1964. Common trees of Puerto Rico and the Virgin Islands. Agriculture Handbook No. 249. U. S. D. A., Forest Service. Washington, D. C. 548 p.

Lugo-López, M. A. 1953. Moisture relationships of Puerto Rican soils. Tech. Paper 9. University of Puerto Rico, Agricultural Experiment Station, Río Piedras, P. R. 97 p.

Lyford, W. H. 1969. The ecology of an elfin forest in Puerto Rico, 7. Soil, root, and earthworm relationships. Jour. Arnold Arb. 50:210-224.

Murphy, L. S. 1916. Forests of Porto Rico, past, present, and future, and their environment. U. S. D. A. Bull. 354. Washington, D. C. 99 p.

OAS. (Organization of American States). 1972. Ecologie, República D'Haiti. Washington, D. C.

Odum, H. T. 1967. Work circuits and systems stress. p. 81-138 *In*: Symposium on primary productivity and mineral cycling in natural ecosystems. University of Maine Press, Orono.

Odum, H. T., ed. 1970a. A tropical rain forest. Division of Technical Information, USAEC, Oak Ridge, Tennessee.

Odum, H. T. 1970b. The El Verde study area and the rain forest systems of Puerto Rico. Chapt. B-1:3-32 *In*: H. T. Odum, ed. A tropical rain forest, USAEC, Oak Ridge, Tennessee.

Rivera, L. H., W. D. Frederick, C. Farris, E. H. Jensen, L. Davis, C. D. Palmer, L. F. Jackson, and W. E. McKinzie. 1970. Soil Survey, Virgin Islands of the United States. U. S. D. A., Soil Conservation Service. Washington, D. C. 78 p. + maps.

Roberts, R. C. 1942. Soil Survey, Puerto Rico. U. S. D. A., Bureau of Plant Industry and University of Puerto Rico Agricultural Experiment Sta., Series 1936, No. 8. Washington, D. C. 503 p. + maps.

Sawyer, J. O., Jr. and A. A. Lindsey. 1964. The Holdridge bioclimatic formations of the eastern and central United States. Proc. Indiana Acad. Sci. 73:105-112.

Shibata, S. 1970. Algumas considerações sobre o critério de biotemperatura de Holdridge. unpub. thesis. Instituto Interamericano de Ciencias Agrícolas de la OEA. Turrialba, Costa Rica. 89 p.

Smith, G. W. 1967. A nomogram for estimating soil moisture deficits. pp. 28-41. *In*: B. Floyd, ed. Proceedings of a conference on climatology and related fields in the Caribbean. University of the West Indies, Mona, Jamaica.

Smith, R. F. 1970a. List of common plant species at El Verde. Chapt. B-4:59-61. *In*: H. T. Odum, ed. A tropical rain forest. USAEC, Oak Ridge, Tennessee.

Smith, R. F. 1970b. The vegetation structure of a Puerto Rican rain forest before and after short-term gamma irradiation. Chapt. D-3:103-140 *In*: H. T. Odum, ed. A tropical rain forest. USAEC, Oak Ridge, Tennessee.

Tasaico, H. 1967. Reconocimiento y evaluación de los recursos naturales de la República Dominicana: estudio para su desarrollo y planificación (con Mapa Ecológico de la República Dominicana, 1:250,000). Pan American Union, Washington, D. C.

Thornthwaite, C. W. 1948. An approach to a rational classification of climate. Geog. Rev. 38:55-94.

Thornthwaite, C. W. and J. R. Mather. 1957. Instructions and tables for computing potential evapotranspiration and the water balance. Publications in Climatology 10:185-311. Drexel Institute of Technology, Philadelphia, Pa.

Tosi, J. A., Jr. 1959. Forest land utilization in western Puerto Rico. Ph.D. Dissertation, Clark University, University Microfilms, Inc. Ann Arbor, Michigan. 511 p.

Tosi, J. A., Jr. 1960. Zonas de vida natural en el Perú: memoria explicativa sobre el mapa ecológico del Perú. Boletín Técnico, No. 5. Instituto Interamericano de Ciencias Agrícolas de la O. E. A., Zona Andina, Lima. 271 p.

Tosi, J. A., Jr. 1968. Provisional ecological map of Nigeria. Tropical Science Center, San Jose, Costa Rica.

Tosi, J. A., Jr. 1969. República de Costa Rica, Mapa Ecológico. Tropical Science Center, San Jose, Costa Rica.

Tschirley, F. H., C. C. Dowler, and J. A. Duke. 1970. Species diversity in two plant communities of Puerto Rico. Chapt. B-7:91-96 *In*: H. T. Odum, ed. A tropical rain forest. USAEC, Oak Ridge, Tennessee.

U. S. Forest Service. 1950. Micro-environment significant to tree growth in limestone region. Institute of Tropical Forestry, Annual Report. Río Piedras, Puerto Rico.

U. S. Weather Bureau (1959?) Climatography of the United States No. 11-45. Climatic Summary of the United States–supplement for 1931 through 1952. Puerto Rico and United States Virgin Islands. Supt. Doc., U. S. Govt. Printing Office, Washington, D. C.

U. S. Weather Bureau. 1965. Climatography of the United States No. 86-45. Climatic Summary of the United States–supplement for 1951 through 1960. Puerto Rico and the United States Virgin Islands. Supt. Doc., U. S. Govt. Printing Office, Washington, D. C.

Vivanco de la Torre, O., M. Cárdenas Cruz, G. Cortaire Iturraide, and J. A. Tosi, Jr. (no date). Croquis ecológico parcial del Ecuador. IERAC. Quito, Ecuador.

Wadsworth, F. H. 1950. Notes on the climax forests of Puerto Rico and their destruction and conservation prior to 1900. Carib. Forest. 11:38-47.

Wadsworth, F. H. 1951. Forest management in the Luquillo Mountains, I. The setting. Carib. Forest. 12:93-114.

Wadsworth, F. H. and J. A. Bonnet. 1951. Soil as a factor in the occurrence of two types of montane forest in Puerto Rico. Carib. Forest. 12:67-70.

Weaver, P. L. 1972. Cloud moisture interception in the Luquillo Mountains of Puerto Rico. Carib. Jour. of Sci. 12:129-144.

Weaver, P. L., M. D. Byer, and D. L. Bruck. 1973. Transpiration rates in the Luquillo Mountains of Puerto Rico. Biotropica 5:123-133.

Williams, L. 1967. Forests of Southeast Asia, Puerto Rico, and Texas. CR 12-67. U. S. D. A., Agricultural Research Service, Washington, D. C. 410 p.

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ECOLOGICAL LIFE ZONES OF PUERTO RICO
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J.J. EWEL and J.L. WHITMORE
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Limite Forestal
International Boundary
Limite Internacional
CLASSIFICATION OF WORLD LIFE ZONES OR PLANT FORMATIONS
by L.R. Holdridge
df-S SUBTROPICAL DRY FOREST BOSQUE SECO SUBTROPICAL
mf-S SUBTROPICAL MOIST FOREST BOSQUE HUMEDO SUBTROPICAL
wf-S SUBTROPICAL WET FOREST BOSQUE MUY HUMEDO SUBTROPICAL
rf-S SUBTROPICAL RAIN FOREST BOSQUE PLUVIAL SUBTROPICAL
wf-LM LOWER MONTANE WET FOREST BOSQUE MUY HUMEDO MONTANO BAJO
rf-LM LOWER MONTANE RAIN FOREST BOSQUE PLUVIAL MONTANO BAJO
LATITUDINAL REGIONS
ALTITUDINAL BELTS
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ISLA DESECHEO
ISLA MONA
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VIRGIN ISLANDS
SAINT THOMAS
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PONCE
GUAYAMA
RESERVA FORESTAL CAMBALACHE
RESERVA FORESTAL VEGA ALTA
RESERVA FORESTAL GUAJATACA
RESERVA FORESTAL RIO ABAJO
RESERVA FORESTAL PIÑONES
RESERVA FORESTAL CEIBA
LUQUILLO EXPERIMENTAL FOREST
RESERVA FORESTAL TORO NEGRO
RESERVA FORESTAL MARICAO
RESERVA FORESTAL GUILARTE
RESERVA FORESTAL SUSUA
RESERVA FORESTAL CARITE
RESERVA FORESTAL BOQUERON
RESERVA FORESTAL GUANICA
RESERVA FORESTAL AGUIRRE