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# Baño de Oro Natural Area Luquillo Mountains, Puerto Rico

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## SUMMARY

The 745-ha Baño de Oro Natural Area, established by the U.S. Department of Agriculture, Forest Service, in 1949, was made part of the Luquillo Experimental Forest Biosphere Reserve in 1976. The Natural Area, situated at elevations between 245 and 1,025 m in the wettest part of Puerto Rico, encompasses four major forest types that are free of human disturbance. Past and current research in the Baño de Oro Natural Area is summarized in this document to serve as a basis for further investigation. The current state of knowledge regarding the environment (i.e., geology, physiography, soils, climate, hydrology, flora, and fauna) is outlined.

## ACKNOWLEDGMENTS

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Cover:

*Overview of Baño de Oro Natural Area from the Yokahu Tower.*

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# Baño de Oro Natural Area Luquillo Mountains, Puerto Rico

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## BACKGROUND INFORMATION

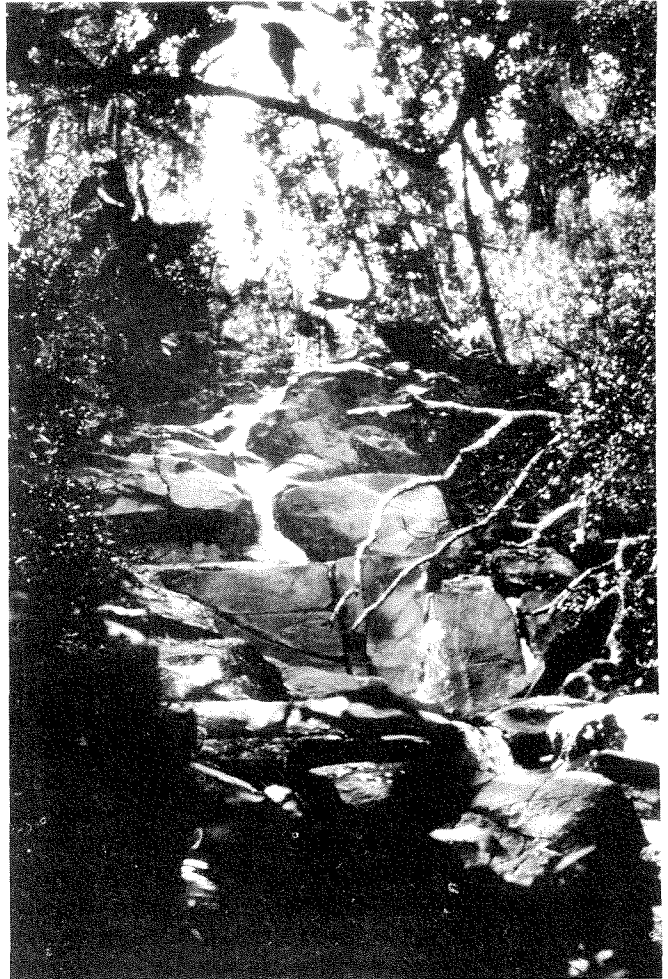
### Introduction

Research Natural Areas (RNA's) are tracts on which natural features and processes predominate and which are preserved for scientific or educational purposes (Federal Committee on Research Natural Areas 1968). The areas need not be pristine because this requisite would preclude many ecosystems that have suffered some level of human disturbance and which no longer exist in an undisturbed state (Dyrness and others 1975). However, if disturbed ecosystems are designated as RNA's, protective measures should be undertaken to restore them to their original condition through natural processes. Research Natural Areas may vary in size from a few to several thousand hectares and preferably are surrounded, or buffered, by other protected land.

Research Natural Areas are established to provide a baseline for comparison with areas influenced by human activity (Moir 1972). Research Natural Areas may include typical or unusual fauna and flora or may represent outstanding geologic, pedologic, or aquatic features or processes. They constitute reserves for the protection of rare or endangered organisms and serve as reservoirs for the conservation of genetic resources. Research on RNA's must be essentially nonmanipulative and reasonably consistent with the purpose and character of the surrounding land (Federal Committee on Research Natural Areas 1968). Deliberate manipulation simulating natural processes is occasionally allowed and, in some instances, encouraged to restore communities or organisms to their original state (Dyrness and others 1975).

It is imperative that the U.S. Department of Agriculture, Forest Service, exercise control over all research activities to assure that they comply with existing guidelines and do not negatively impact the resources in the RNA. The Forest Service must grant permission for all research activities and review them regularly. Research Natural Areas managed under the above guidelines serve scientists, resource managers, and the educational community, particularly at the university level.

The purpose of this report is to compile relevant environmental information on the Baño de Oro Research Natural Area (Baño de Oro) in Puerto Rico. Because research in the Luquillo Mountains has been extensive, much of the data was derived from published sources. Original inventories of fauna and flora, however, have been included to complement other information. Subsequent research will undoubtedly result in the identification of additional species and will require supplements to this text.



*Scenic Río Mameyes at 500 meters within the Baño de Oro Natural Area.*

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## Administrative Details

At the end of the Spanish-American War in 1898, the Crown lands of Puerto Rico passed from Spain to the United States. In 1903, the United States government proclaimed these lands as the Luquillo Forest Reserve, and since 1917 they have been managed by the Forest Service. In 1935, the Luquillo Forest Reserve was renamed the Caribbean National Forest (CNF) to include Federally purchased lands elsewhere in Puerto Rico. In 1939, the Tropical Forest Experiment Station (now the International Institute of Tropical Forestry) was established. In 1956, the CNF was also administratively designated as the Luquillo Experimental Forest (LEF) to recognize the growing importance of research in the forest. Although the terms CNF and LEF refer to the same land, the objectives of the Forest Service units that work in the forest are distinct. The CNF is responsible for management of the forest, or making it productive by demonstrating forest practices in a tropical setting. The LEF is responsible for forestry and forest-related ecological research. Throughout this publication this area will be referred to as the LEF.

The 745-ha Baño de Oro (located at 18°17'30" N. latitude and 65°45'30" W. longitude) in the Luquillo Mountains (fig. 1) was established by the Forest Service in 1949. Although comparatively small in size, the Baño de Oro encompasses the boundary areas of four municipalities: Rio Grande, Luquillo, Fajardo, and Ceiba.

The Baño de Oro was selected as an RNA for several reasons: (1) the land was surrounded by other Forest Service lands, (2) the terrain was unmodified by human activity, (3) the unit contained representative areas of the four forest types that characterize the Luquillo Mountains, and (4) the unit contained populations of the endemic Puerto Rican parrot (*Amazona vittata*), at that time confined to the upper slopes of the Luquillo Mountains. Since its proclamation, the Baño de Oro has been managed in accordance with RNA guidelines. In 1968, it was listed in a national directory of more than 300 RNA's set aside on Federal lands (Federal Committee on Research Natural Areas 1968). In 1976, the entire LEF was designated as part of the international network of Biosphere Reserves (Lugo 1987).

The Baño de Oro is roughly diamond shaped and oriented in line with the cardinal directions (fig. 1). The southwestern boundary extends along the ridge from the intersection of the Molindero and Pico del Este Roads to Pico del Oeste, approximately paralleling the Pico del Este Road, which was finished in 1962. The lower half of the northwestern boundary is about 100 m east of the Molindero Road. Where the northern part of the Molindero Road trends west, the boundary continues northeast on the same ridge intersecting the

Rio de la Mina at a 450-m elevation. From this point, the boundary is the Rio de la Mina to its confluence with the Rio Mameyes. A primitive trail parallels the Rio de la Mina and terminates at the Rio Mameyes. The northeastern boundary is the Rio Mameyes and its eastern fork for nearly half its distance after which the boundary follows along a ridge to a local high point at an elevation of 675 m and then descends along a divide to the Rio Fajardo. About 90 percent of the southeastern boundary is the eastern tributary of the Rio Fajardo from its confluence with the Rio Fajardo to its source just below Pico del Oeste. The remainder of the boundary follows the ravine above the river to Pico del Oeste.

Expansion of the Baño de Oro by more than 40 percent to encompass a total of 1,180 ha is being considered in the current forest management plan. The proposed new areas include Pico del Este, one of the wettest locales on the Island, areas above a 750-m elevation east of Pico del Este, and areas above a 700-m elevation south of the road to Pico del Este (fig. 1). A small area known locally as the "valley of the giants" because of the many large trees found there is also part of the proposed addition. It extends down to a 640-m elevation in the Icacos Valley, south of the Pico del Este road.

## Historical Perspective

Land clearing by pre-Columbian Indians appears to have affected only a small area in Puerto Rico, mainly on the coastal plain (Wadsworth 1950a). Land clearing by settlers began early in the northeastern part of the Island but did not ascend the slopes of the Luquillo Mountains for many years because Carib Indians lived there. Before 1876, the Spanish Crown did not grant concessions to people willing to settle in the mountains. In 1876, the Crown established forest reserves in Puerto Rico, including the LEF (Brown and others 1983). Subsequently, concessions to some mountainous lands were granted, but inaccessibility and the poor quality of the soil caused the core of the Luquillo Mountains to remain Crown land and to remain forested until the Treaty of Paris in 1898. In 1903, conservation of the region began with the proclamation of the Luquillo Mountains as a forest reserve.

The search for gold in the Luquillo Mountains was carried on from 1513 until the late 19th century (Wadsworth 1950a, 1970). During the 19th century, gold was discovered near the confluence of the Rio de la Mina and Rio Mameyes where the Luquillo Mine and the Monserrate Mine operated for a few years (Cardona 1984, Cox and Briggs 1973). Penetration into the upper slopes of the Luquillo Mountains via foot trails, however, was infrequent as late as 1905 (Wadsworth 1970). The foot trail to El Yunque was virtually impassable until a horse trail was finished in 1922. Route 191 from

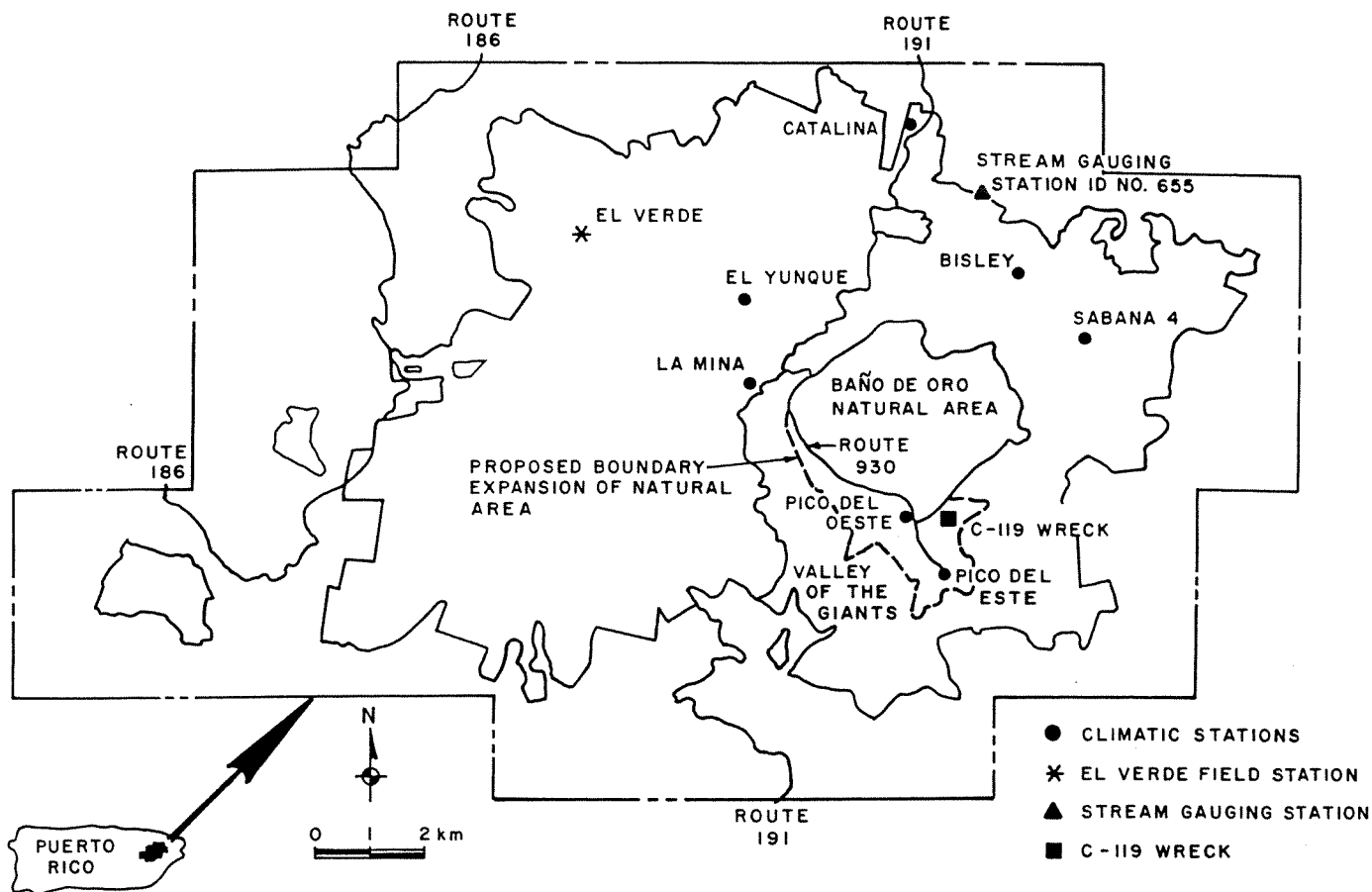


Figure 1.—Location of the Baño de Oro Natural Area within the Luquillo Experimental Forest. Climatic stations and reference sites are indicated.

the town of Mameyes to Rio Blanco, initiated in 1926, was not completed until 1942. Only 7 years later, the Forest Service established the Baño de Oro, located about 1 km east of the highway. At that time, less than 1 percent of Puerto Rico's land surface remained in pristine condition (Wadsworth 1950b), and the LEF, the largest contiguous undisturbed forest on the Puerto Rican mainland, surrounded the Baño de Oro.

There is no evidence of previous exploration or scientific collections in the Baño de Oro. Moreover, there is no evidence of logging, hunting, or diversion of water resources. Scattered banana plants and the remains of a house, however, are located near the confluence of the Rio de la Mina and Rio Mameyes, suggesting that the area had been occupied at least on an interim basis for some time.

### Objectives

The purpose of this report is to compile existing knowledge of the Baño de Oro to serve as a basis for further investigations. The main effort is to call attention to the nature of existing literature rather than to

review it in detail. Research activities conducted within the Baño de Oro are emphasized along with relevant ecological information gathered in the surrounding forests. All plant and animal species encountered within the Baño de Oro are listed in tables.

### OVERVIEW OF MAJOR FOREST RESEARCH

Numerous studies of the climate, flora, fauna, and ecology of the Luquillo Mountains have already been completed, ranking the LEF among the best studied tropical forests in the world. The citation of a few major references will indicate the extent of the investigations.

A bibliography with nearly 2,000 entries on Puerto Rican forestry research including texts, journal and newspaper articles, theses, proceedings, and reports, most written between the early 1880's and 1978, was compiled by the Institute of Tropical Forestry (now the International Institute of Tropical Forestry) library staff (Mosquera and Feheley 1983). Summarizing past research in the Luquillo Mountains, Wadsworth (1970)



*Effects of Hurricane Hugo in the Baño de Oro Natural Area.*

cited 118 references on the geography, climatology, geology, flora, fauna, ecology, archeology, agriculture, and forestry of the Luquillo Mountains. Both works also contain information on early botanical exploration of the mountains.

From 1939 through 1963, issues of the "Caribbean Forester" highlighted early Forest Service investigations in the mountains. Between the early 1960's and mid-1970's, the arborescent vegetation of Puerto Rico and the U.S. Virgin Islands was described based on past research and numerous field observations (Little and others 1974, Little and Wadsworth 1964).

A compendium of information on forest plants, animals, and the environment, before and after radiation, was summarized for the El Verde tabonuco forest located only 5 km northwest of the Baño de Oro (Odum and Pigeon 1970). In 1983, the history of LEF research and opportunities for additional investigations were outlined (Brown and others 1983). In 1987, long-term ecological research dealing with the fauna, flora, and watershed dynamics was initiated in the Bisley watersheds only 2 km northeast of the Baño de Oro (Scatena 1989). Moreover, current research activities in the LEF are summarized in the "Annual Letter" of the International Institute of Tropical Forestry.

Beginning in 1966, and extending through the mid-1970's, the staff of the Arnold Arboretum (located in Cambridge, Massachusetts) studied the Baño de Oro's dwarf forest on Pico del Oeste. The results appeared as 17 research papers in the "Journal of the Arnold Arboretum." Study of the Puerto Rican parrot,

whose numbers had declined rapidly during the 1960's, was initiated in 1968 throughout the LEF (Snyder and others 1987). Parrot nesting boxes were installed at two locations in the upper reaches of the Baño de Oro during the 1970's (fig. 2) as part of the research program. Parrot observations and implementation of the parrot recovery program continue today.

Studies conducted in the Baño de Oro Natural Area are covered in more detail in subsequent chapters. To facilitate future investigations of the flora and fauna in the Baño de Oro, a list of select references has been prepared (appendix table 1).

## THE BAÑO DE ORO NATURAL AREA

The information provided in this section pertains mainly to the Baño de Oro. Relevant data from studies elsewhere in the LEF, particularly with reference to climate and vegetation, are also included.

### Geology

The geology of the Caribbean area and Puerto Rico is complex and has been a source of controversy among authors who favored explanations based on theories in vogue at the time. The summits of the Luquillo Mountains were first described as Cretaceous monadnocks, or residuals of old topography standing above a plain of subaerial erosion (Meyerhoff 1933). This interpretation was questioned (Mitchell 1954) because uparching and

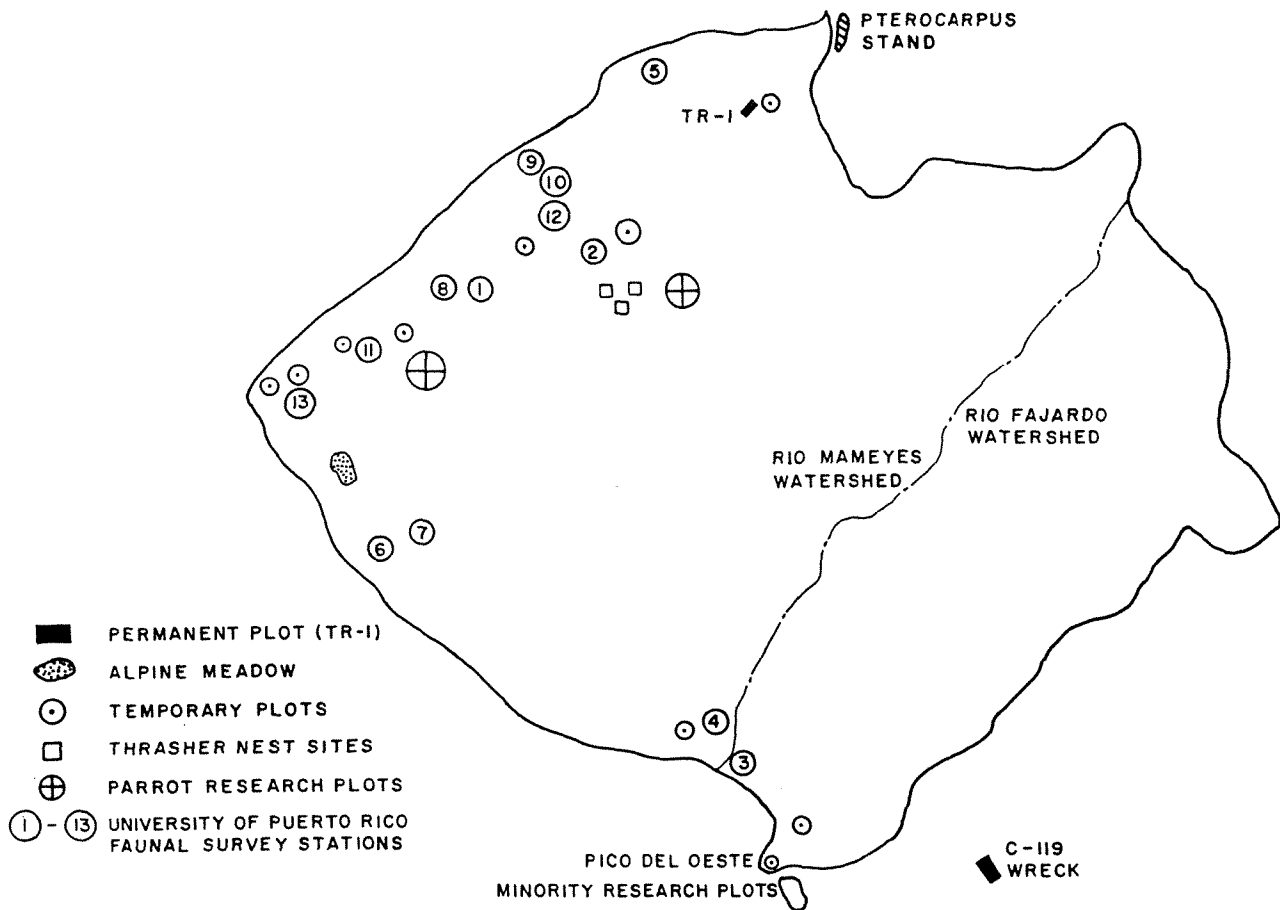


Figure 2.—Location of research plots in the Baño de Oro Natural Area. The plots surveyed in the University of Puerto Rico faunal study are numbered 1 through 13.

faulting provided a more logical explanation for the peak areas than erosion alone. In a summary of the Island's geologic history (Beinroth 1969), Puerto Rico's origin was attributed to a series of submarine volcanos formed during the Cretaceous Period. At the beginning of the Tertiary Period, mountain building and uplift occurred, followed by weathering and erosion, which reduced the Island to low hills. The central portion was then pushed upward, coastal areas sank, and limestone was deposited along the coasts. By the Miocene epoch, Puerto Rico was conceived as a nearly level plain with meandering streams. The entire area was uplifted again to over 1,000 m in elevation, and a new erosive cycle was initiated.

Recent explanations of geologic history in the Caribbean area rely on plate tectonics but still reflect controversy. North America, South America, and Africa began to diverge about 175 million years ago through a series of rifting episodes that created the Gulf of Mexico and the Caribbean Sea (Dillon and others 1987–88). Numerous geologic events, previously considered to be a variety of independent island arc systems formed at different places and times, now appear as a sequence of plate events reflecting a single great Caribbean Island arc system that was constructed in the Pacific and

migrated into the Atlantic (Burke 1988). A simple model involving the rotation of a tectonic block containing Puerto Rico within the broad strike-slip boundary of the Caribbean plate is proposed to account for the Island's major tectonic features (Masson and Scanlon 1991).

The Baño de Oro is underlain by a complexly faulted and folded terrain composed chiefly of Cretaceous volcanic rocks, subordinate Cretaceous and/or Tertiary intrusive bodies, and minor lower Tertiary volcanic and sedimentary rocks (Seiders 1971a). The underlying rocks are largely tuff, volcanic breccia, and tuffaceous sandstone and siltstone, chiefly marine (Cox and Briggs 1973). Lava probably constitutes more than 15 percent of the 10,000 m or deeper section and is chiefly concentrated in the lower part and locally in the middle part. Limestone occurs sporadically in the upper part of the section. In the Baño de Oro, five major geologic mapping units have been identified (fig. 3). Of the stratified deposits, unnamed volcanoclastic rocks, which included marine-deposited andesitic to what is thought to be basaltic volcanic sandstone, and fine volcanic breccia with subordinate cherty mudstone, occupy slightly more than half the area. Cherty mudstone lies in a thin strip in the southeastern



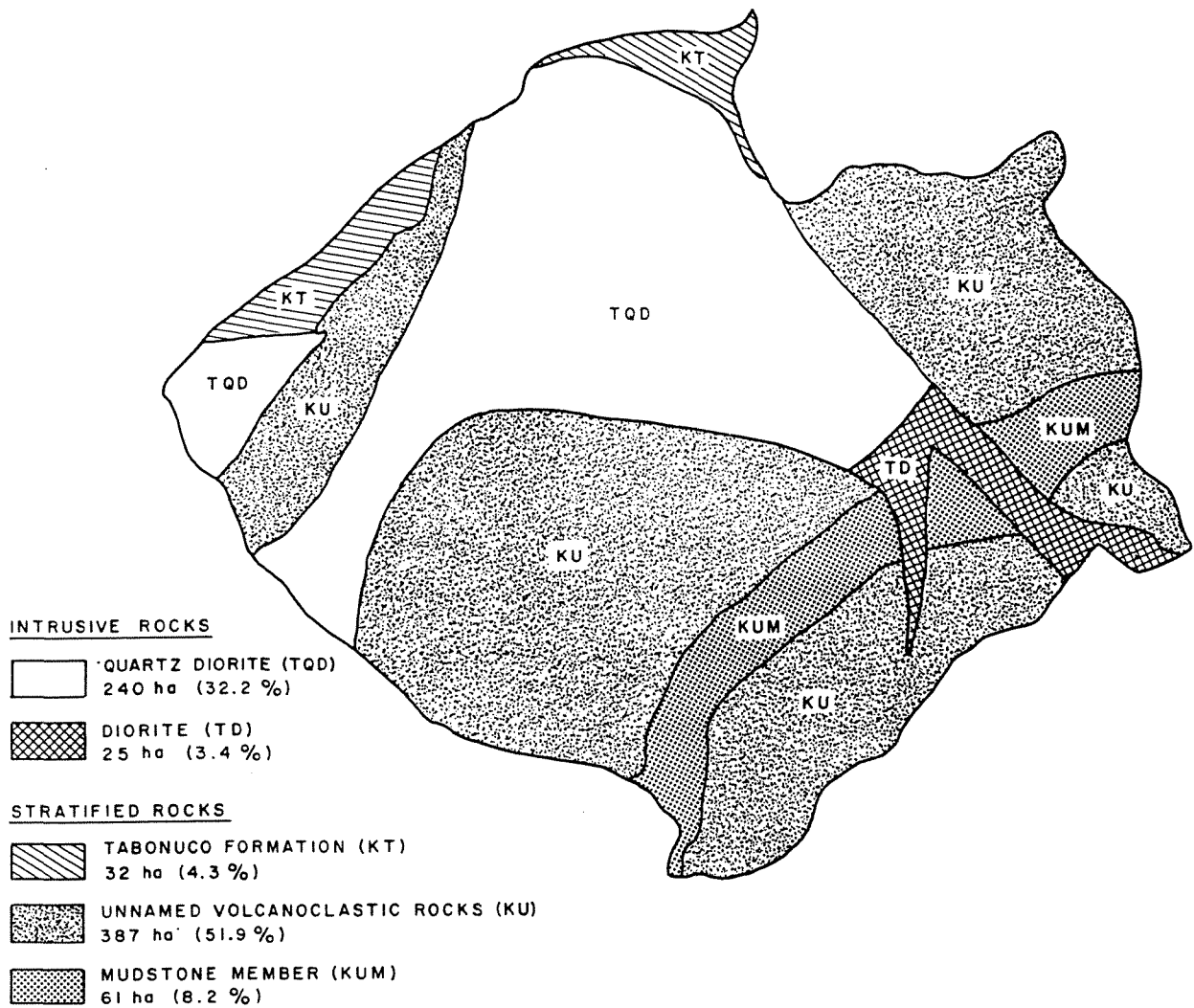


Figure 3. — Geologic map of the Baño de Oro Natural Area (Seiders 1971a, 1971b).

portion. The tabonuco formation, composed of andesitic to basaltic volcanic sandstone (about 60 percent), mudstone (about 30 percent), and volcanic breccia and conglomerate (about 10 percent), lies along the north and northwestern periphery.

Of the intrusive rocks, nearly one-third of the area is composed of quartz diorite in which quartz accounts for about a quarter of the mineral composition. A zone of contact metamorphism surrounds the quartz diorite, which exhibits metamorphosed volcanoclastic rocks typically harder and darker than unmetamorphosed equivalents. Hornblende diorite and quartz diorite are also found in the east central part of the Baño de Oro. More detailed descriptions of the mapping units are provided by Seiders (1971b).

### Physiography

The Baño de Oro measures 3.55 km from north to south and 4.15 km from east to west (fig. 4). Total relief is 780 m, ranging from 1,025 m on Pico del Oeste on

the south to 245 m in elevation where the Rio Mameyes flows out to the north. The average gradient between the high and low points in the watershed is 220 m/km.

Two main ridges are evident within the Baño de Oro. The first trends northeast from Pico del Oeste to a 685-m high point on the northeastern border of Baño de Oro, never descending below a 490-m elevation. This ridge separates the upper portions of the Rio Mameyes and Rio Fajardo watersheds. The Rio Fajardo flows out the eastern border of the Baño de Oro at an elevation of 350 m. The second ridge, trending northwest from Pico del Oeste along Route 930, descends gradually to about 700 m at the western edge of the Baño de Oro.

Nearly 71 percent of the Baño de Oro lies between 400 and 700 m in elevation, with about 11 percent < 400 m and 18 percent > 700 m in elevation (fig. 4). The terrain is steep. About 47 percent of the 745 ha is in slopes > 60 percent, with 48 percent in slopes between 30 and 60 percent, and only 5 percent in slopes < 30 percent (fig. 5).

ELEVATIONS (m)

250 – 300	10 ha ( 1.6 %)
300 – 400	70 ha ( 9.4 %)
400 – 500	210 ha (28.2 %)
500 – 600	172 ha (23.1 %)
600 – 700	147 ha (19.7 %)
700 – 800	90 ha (12.1 %)
800 – 900	32 ha ( 4.3 %)
900 – 1,000	13 ha ( 1.7 %)
> 1,000	1 ha ( 0.01%)

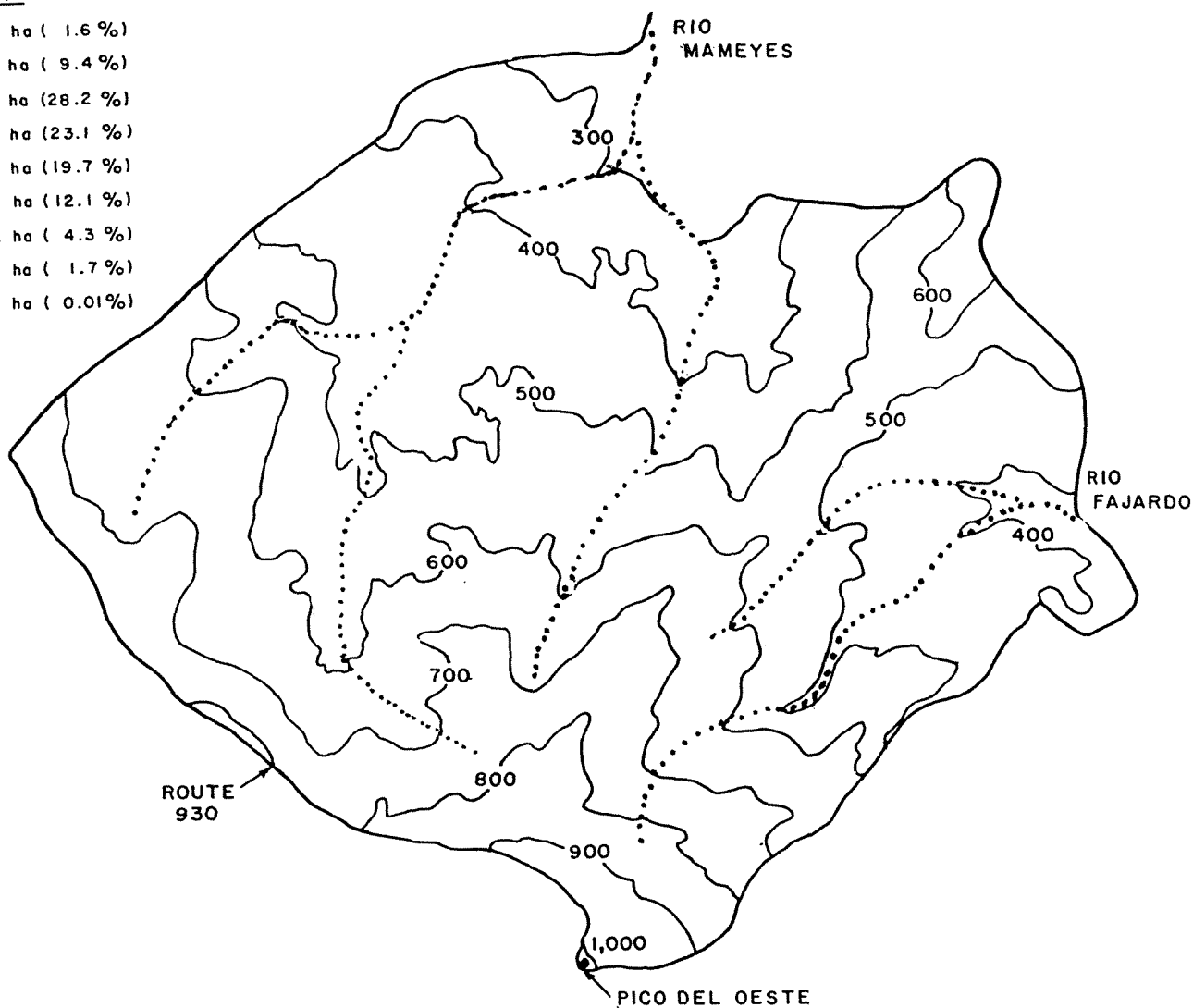


Figure 4.—Topographic map of the Baño de Oro Natural Area.

### Soils

Most of the Baño de Oro is inaccessible, and only limited information is available regarding soils. Ultisols, occupying about one-third of the 745 ha, and Inceptisols, occupying the remaining areas, are the only major soil orders that have been identified (fig. 5). In general, the Ultisols are confined to the largest river valleys below 600 m in elevation. The Inceptisols, in contrast, occupy the main ridges and adjacent terrain down to 300 m in elevation.

The Soil Conservation Service tentatively classified the entire area as the Los Guineos-Guayabota rock land association (Boccheciamp 1977). This area is characterized by shallow to deep, well-drained to poorly drained, strongly sloping to very steep soils on volcanic uplands in tropical rain forests. The specific units

recognized were Guayabota-Ciales-Picacho association on very steep land, Los Guineos-Yunque-Stoney rock land association on steep land, and the Utuado-Picacho-Stony rock land association on very steep land.

Subsequently, an effort was made to develop soil mapping units for the LEF (fig. 6). The largest unit classified was the Yunque-Los Guineos Complex, occupying nearly 40 percent of the Baño de Oro (fig. 6). The next largest unit, accounting for 25 percent of the Baño de Oro, was the Picacho-Utuado Complex.

Soils of Pico del Oeste's dwarf forest, designated as lithic tropaquentes, have a mucklike surface 25 to 30 cm thick with organic matter up to 50 percent (Lyford 1969). A distinctly mottled gray gleyed horizon lies below, and this is underlain by massive, plastic, non-sticky clay with weathered rock fragments in places. The pH throughout the horizons ranges between

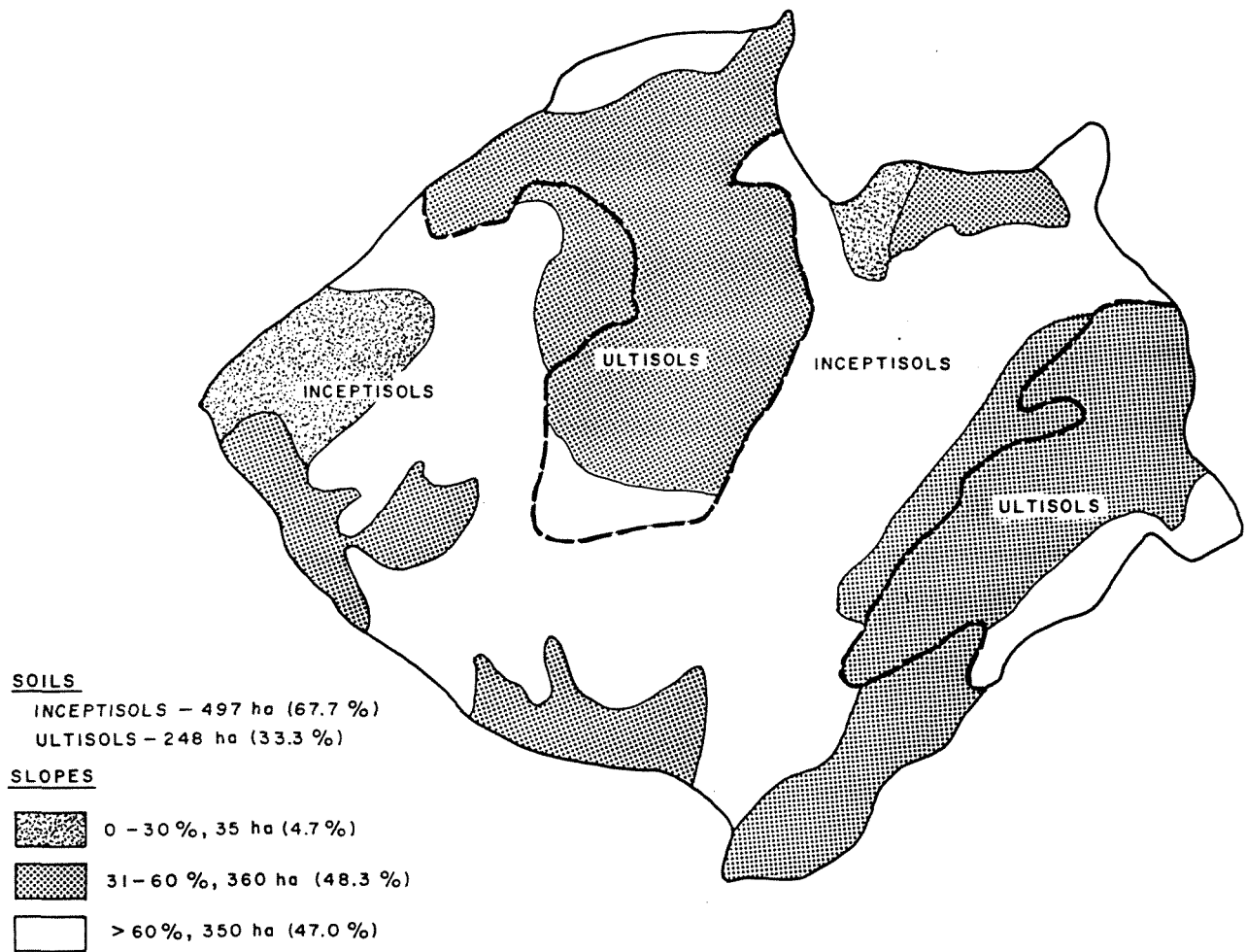


Figure 5.—Soil orders and slopes in the Baño de Oro Natural Area (Institute of Tropical Forestry files).

4.3 and 4.9. Seepage water entered from all horizons when trenches were dug into the soil.

The roots of dwarf forest vegetation are found in four general habitats: the soil, immediately above the soil in cryptogams or litter, appressed to trunks and branches, or hanging freely (Gill 1969). About 80 to 90 percent of the woody roots are just under the forest litter or within 2 to 10 cm of the soil surface. Tree stems are covered not only with epiphytes and roots but also with a soillike material high in organic matter derived from the decomposition of epiphytic material and trapped leaves.

### Climate

Puerto Rico, situated in the northeast trade wind belt about 1,800 km from the Equator, has a tropical marine climate (Calvesbert 1970). The longest day (about 13.2 hours) varies only about 2 hours in length from the shortest day (about 11.0 hours). The LEF, located in the northeastern part of the Island, presents the first obstacle to the trade winds crossing the

Atlantic. The abrupt elevational gradient from the base of the mountains to the summits profoundly influences local climate.

Four major systems may be superimposed on the trade wind regime influencing local weather (Odum and others 1970): polar troughs (temperate, low pressure troughs moving southeastward); easterly waves (low pressure troughs moving westward); shear lines (remnants of cold fronts that reach tropical latitudes in the winter); and tropical storms (low pressure centers, with closed isobars and circular converging airflow, moving westward). Tropical storms, particularly if moving slowly, may cause torrential rainfalls (Calvesbert 1970). The Island is also located within the hurricane belt of the Caribbean and occasionally experiences the high winds and heavy rains that accompany these storms.

No permanent climatic stations are located within the Baño de Oro. Climatic data are available from one temporary station situated on Pico del Oeste and from six other LEF sites located at short distances from the Baño de Oro (table 1) (fig. 1). Station records vary with

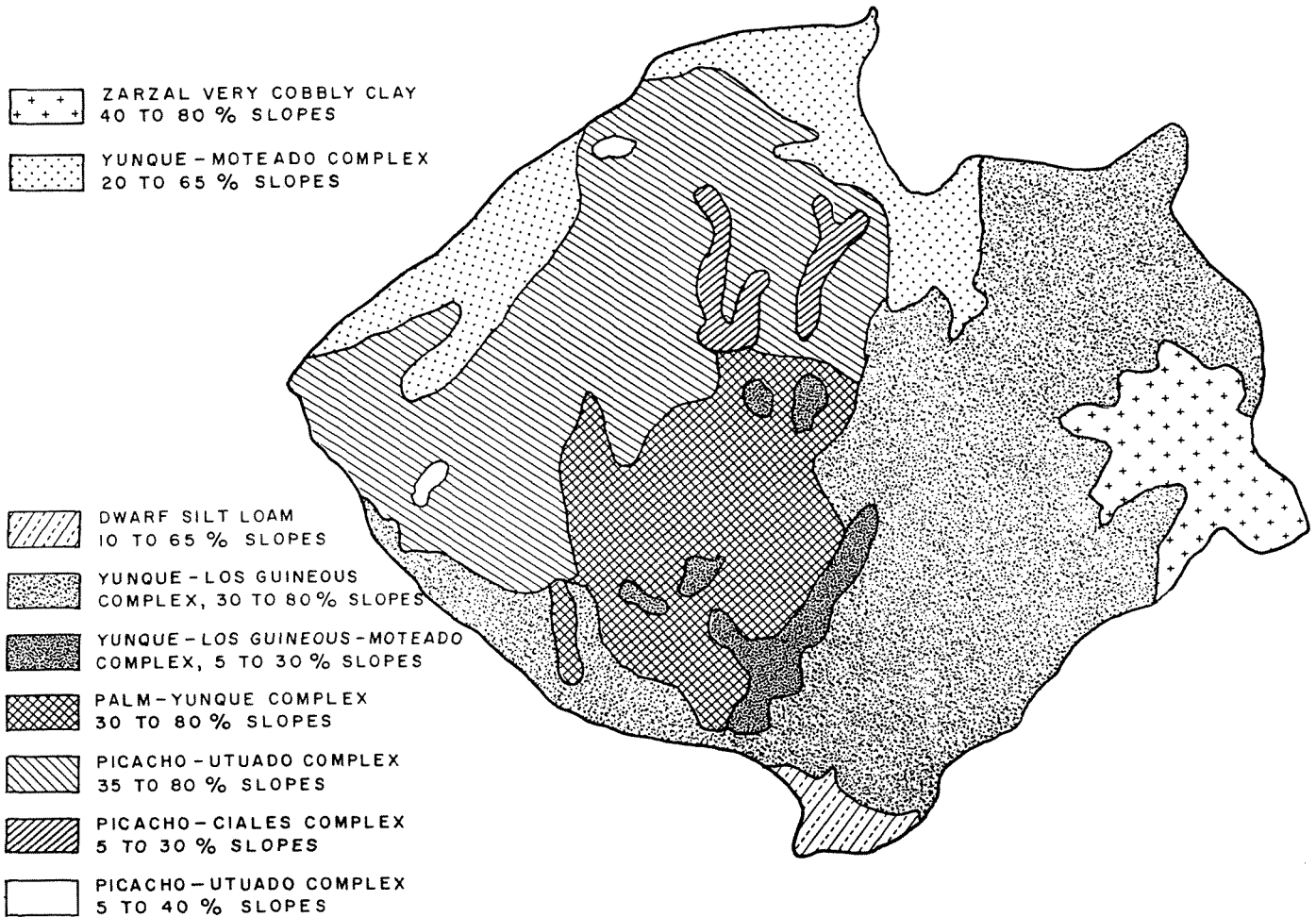


Figure 6.—Soil mapping units in the Baño de Oro Natural Area (Huffaker [In press]).

Table 1.—Mean annual climatic data for several sites in and around the Baño de Oro Natural Area\*

Site	Elevation	Rainfall	Temperature	Relative humidity	Solar radiation
	<i>Meters</i>	<i>Millimeters</i>	<i>°C</i>	<i>Percent</i>	<i>l day<sup>†</sup></i>
Catalina <sup>‡</sup>	150	2450	23.9	88	.... <sup>§</sup>
Sabana 4	300	3560 <sup>¶</sup>	21.7 <sup>‡</sup>	79 <sup>‡</sup>	....
Bisley	350	3000 <sup>**</sup>	....	....	....
La Mina <sup>††</sup>	715	4600	21.1	....	....
Pico del Oeste <sup>#</sup>	1036	4530	18.6	98	262
Pico del Este	1050	4450 <sup>§§</sup>	18.7 <sup>§§</sup>	98 <sup>¶¶</sup>	....
El Yunque <sup>‡</sup>	1065	4000	18.3	98	262

\*Dates and durations of records vary by site and parameter. See figure 1 for locations of climate stations.

<sup>†</sup>1 = langley = 1 calorie/cm<sup>2</sup>.

<sup>‡</sup>Record 1958–62 (Briscoe 1966).

<sup>§</sup>Blank field indicates missing data.

<sup>¶</sup>Crow and Weaver 1977.

<sup>\*\*</sup>Record 1973–79 (Snyder and others 1987) and 1985–87 (Bosch, unpublished) cited by Scatena 1989.

<sup>††</sup>Record 1935–43 (Wadsworth 1948).

<sup>#</sup>Record 3/1/66 to 2/28/67 except relative humidity that was measured from 7 to 10/66 and 12/66 to 2/67 (Baynton 1968).

<sup>§§</sup>Record 1970–82 (U.S. Department of Commerce 1970–82).

<sup>¶¶</sup>Record 11/68 to 6/69 (Weaver 1972b).

regard to data collected, years sampled, and duration of measurements. They indicate trends, but comparisons among sites are tenuous. Data from most of the permanent and temporary climatic stations in and around the Luquillo Mountains were graphed and summarized in a previous report (Brown and others 1983). Salient observations from that report have been incorporated into the following text on climate.

**Precipitation.**—Much of Puerto Rico's rainfall is orographic, caused by the ascent of moisture-laden trade winds over mountain barriers (Calvesbert 1970). At Catalina, Sabana 4, and Bisley, between 150 and 350 m in elevation, mean rainfall varies between 2,450 and 3,560 mm/yr (table 1). The four remaining sites, located at 715- to 1,065-m elevations, south to west of the Baño de Oro, average  $\geq 4,000$  mm/yr.

Rainfall fluctuates considerably from year to year (Wadsworth 1948, 1970). At the La Mina station, the 9-yr mean of 4,600 mm/yr was exceeded twice by more than 37 percent, and during 1 year, it was 20 percent below the mean. Similar fluctuations in annual rainfall were evident from coefficients of variation between 15 and 38 percent for other climatic stations in and adjacent to the Luquillo Mountains (Brown and others 1983).

Rainfall also varies during the year (fig. 7). At Pico del Este and La Mina, February, March, and April are drier than the remaining months. The wettest months for Pico del Este are May, October, and November; the wettest months for La Mina are May and November. The drier months of February and March and the wetter month of May also characterize other climatic stations in and around the Luquillo Forest (Brown and others 1983). The highest recorded daily rainfall for the LEF, 485 mm, was observed during May on Pico del Este (Weaver 1972a).

Other informative rainfall data were summarized for the La Mina station (Brown and others 1983, Wadsworth 1948). Fifty days out of the year, La Mina received  $>2.54$  cm (1 inch) of rainfall. Typical rainfalls, however, lasted 0.5 hour, delivered 3 mm of rain, and occurred 1,625 times per year. The maximum rainfall recorded for 1 month was 1,030 mm.

The total duration of rainfall events varied during the year. The longest durations of rainfall occurred from November to January and in June, coinciding with periods of lower monthly rainfall. This indicates that during these months storm events are longer but of lower intensity. Short durations of rainfall occurred during July through October coinciding with periods of higher rainfall and indicating greater intensity of storms. The total duration of rainy weather during the year was about 22 days, or proportionately about 6 percent of the year. About 55 percent of this rain occurred between 6 a.m. and 6 p.m.

Hail is a relatively rare event in Puerto Rico, although incomplete records and personal accounts indicate that it has fallen at some time virtually everywhere (Calvesbert 1970). During February 1969, a hail-storm lasting about 15 minutes occurred on Pico del Este (author, personal observation). The hailstones were relatively small, averaging about 0.5 cm in size.

**Temperature.**—Mean temperatures in Puerto Rico characteristically have little variation between the warmest and coolest months, and between years (Calvesbert 1970). Mean annual temperature decreases from 22 to 18 °C with ascent from 300 to 1,065 m in elevation in the Luquillo Mountains (table 1). At Sabana 4, the mean annual temperature varies from 21 °C between December and March to 24 °C in August and September (Briscoe 1966). Mean annual temperatures on El Yunque and Pico del Este vary from 17 or

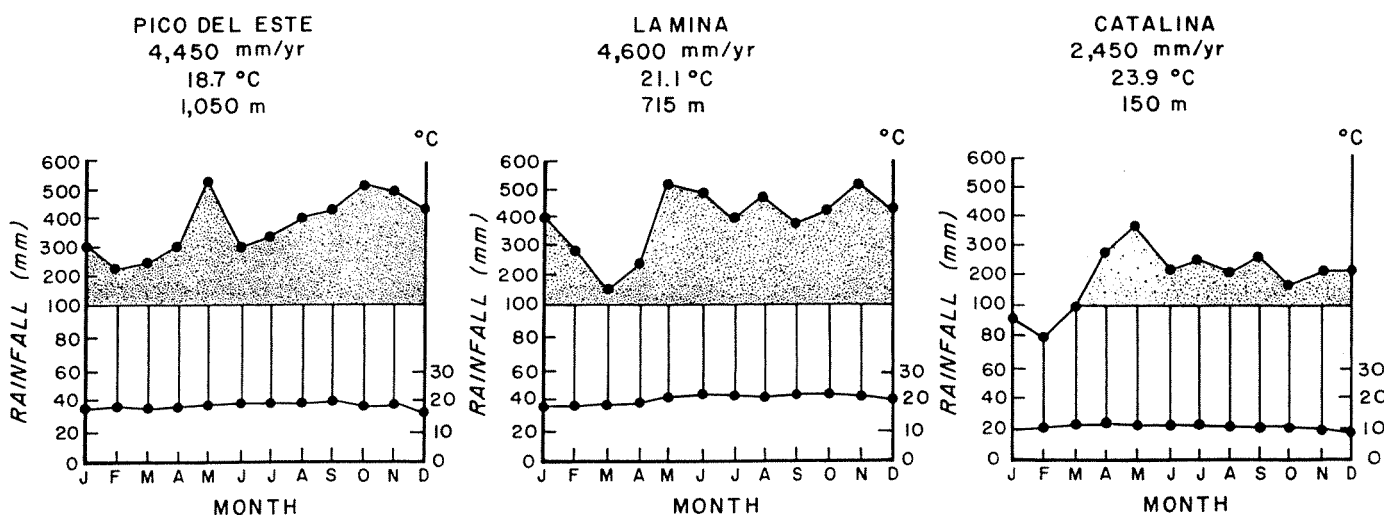


Figure 7.—Climatic diagrams for Pico del Este (U.S. Department of Commerce 1970-82), La Mina (Wadsworth 1948), and Catalina (Briscoe 1966). Mottled areas indicate rainfall  $>100$  mm/month, and striped areas indicate a water surplus.

18 °C between December and March to 19 or 20 °C between August and October (Briscoe 1966, U.S. Department of Commerce 1970-82). Diurnal temperature variation and temperature range in any given month are larger at lower elevations than at higher elevations (Brown and others 1983).

On Pico del Oeste, the highest and lowest recorded temperatures in 1966-67 were 26 and 13 °C (Baynton 1968). These temperatures corroborate observations on Pico del Este (author, personal observation). One might speculate that the maximum range of temperatures experienced in the Baño de Oro lies between 10 °C at the summits and slightly more than 30 °C at the lowest elevation. Freezing temperatures are unknown anywhere in Puerto Rico (Calvesbert 1970).

**Relative Humidity.**—The dewpoint temperature varies little over Puerto Rico, indicating that the overlying air mass is fairly constant with regard to moisture content during the year (Calvesbert 1970). For summit locations in the LEF, the mean annual relative humidity is >98 percent (table 1). Mean monthly relative humidity at El Yunque is near 100 percent for all months except February, when it decreases to about 90 percent. At lower elevations, Catalina and Sabana 4, the mean annual relative humidity varies between 79 and 88 percent. Individual mean monthly values range between 76 and 92 percent, with lows in March and highs in September through November (Brown and others 1983).

The diurnal variation in relative humidity at El Yunque is slight in comparison to that of the Catalina and Sabana 4 locations. At El Yunque, it is at or near 100 percent during the evening hours (from 6 p.m. to 8 a.m.). The low is at 1 p.m., when it averages about 95 percent. At Catalina and Sabana 4, the relative humidity is near 95 percent during the evening hours. During daylight hours, it decreases to 75 percent at Catalina and 70 percent at Sabana 4, at 2 p.m. and 1 p.m., respectively.

**Wind Velocity and Direction.**—The steadiness of the trade winds, blowing mostly from an easterly direction, is the outstanding feature of wind in Puerto Rico (Calvesbert 1970). On El Yunque, the prevailing mean monthly wind direction is from the northeast. In January and September, however, winds are from the south, and in December, from the east. In contrast, at the base of the mountains in Catalina, winds are more variable, blowing from the south in January, from the east-northeast in February and March, from the east from April through August, from the south in September, and from the northeast from October through December. The trade winds, particularly closer to the coast, are modified by land and sea breezes (Calvesbert 1970).

Mean monthly wind velocity ranged from 8 to 18 km/hr at El Yunque and from 2 to 6 km/hr at Catalina (Briscoe 1966, Brown and others 1983). Peaks in wind

velocity from 14 to 18 km/hr were recorded at El Yunque in December, January, April, and September. At Catalina, peaks from 4 to 6 km/hr were observed in April and from July through September.

Diurnal variation in wind velocity showed interesting contrasts. On El Yunque, depending on the month, maximum velocities from 14 to 16 km/hr occurred from 4 a.m. to 10 a.m., with minimum velocities between 11 and 14 km/hr from 12 noon to 4 p.m. (Briscoe 1966, Brown and others 1983). At Catalina, maximum wind velocities from 4 to 6 km/hr occurred between 10 a.m. and 4 p.m. and minimum wind velocities from 2 to 3 km/hr at other hours.

**Cloud Cover and Solar Insolation.**—Cloud cover increases with elevation in the Luquillo Mountains where the summits are frequently enveloped in clouds when the surrounding lowlands are clear. February and March are the months when the peaks are most likely to be cloud free. On Pico del Oeste, contrasting conditions were observed during 1 year of measurement. Two notable periods, one of 16 days in June 1966 and the other of 15 days in January 1967, were recorded during which cloud cover enveloped the peak continuously (Baynton 1968). During November 1966, however, a 3-week period averaging 15 hours per day of cloud-free weather was observed.

Pico del Este was one of 10 North American sites where cloud water was considered an important input to local ecosystems (Weathers and others 1988). Between May 1984 and November 1985, cloud water and rainfall samples were collected on an event basis and chemically analyzed for concentrations of  $\text{Ca}^{2+}$ ,  $\text{Mg}^{2+}$ ,  $\text{K}^+$ ,  $\text{Na}^+$ , ammonium, sulfate, nitrate, and  $\text{Cl}^-$ . The pH was determined, and at a few sites, trace metals (Pb, Cu, and Zn) and organic compounds were sampled.

The sea salt component, variable between events, contributed to a high mean ionic strength of samples from Pico del Este (Weathers and others 1988). The variability was related to wind velocity and its influence on aerosol production. Comparably high nitrate concentrations were attributed to the oxidation of reduced nitrogen gases from the rain forest or from local pollution. Ammonium concentrations, also considered high, may have been associated with the rapid decomposition of organic matter from the surrounding rain forest. One cloud sample was visibly contaminated with a reddish material, possibly dust from the Sahara Desert. More recent work assessed the influence of sea salt aerosols on precipitation chemistry at El Verde, located in the LEF's tabonuco forest (McDowell and others 1990).

Cloud cover affects incoming solar radiation. Mean annual solar radiation on El Yunque and Pico del Oeste averages 262 langley's/day, or 60 percent of that received at sea level on the northeastern coast of Puerto Rico (Baynton 1968, Briscoe 1966). Because the

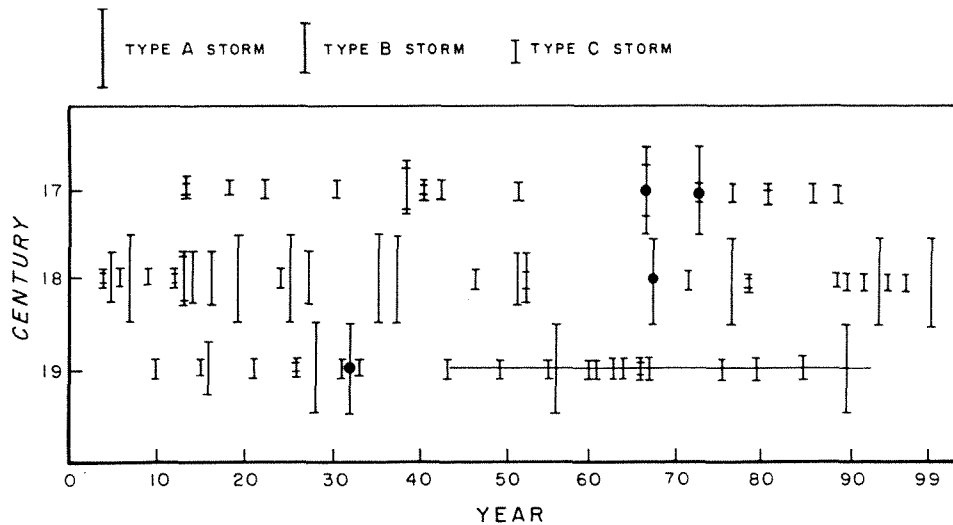


Figure 8. — Hurricane record for Puerto Rico from 1700 to 1970 (Salivia 1972) updated to 1992: type A storm, vortex of hurricane passed directly over the Island with hurricane force winds; type B storm, vortex of hurricane may or may not have passed over the Island, but only part of the Island experienced hurricane force winds; type C storm, vortex passed at some distance from the Island, which experienced high winds (not hurricane force) and heavy rains; double I bar, two storms in the same year with intensity of second storm indicated by position of second I bar within the first; horizontal line from 1943 to 1992, years of measurement of tree growth in the Luquillo Forest; black circle, type A storms that passed directly over the Luquillo Forest.

spectral composition of light changes little with cloudiness, light energy available for photosynthesis on the Luquillo Mountain summits is also reduced to 60 percent of that received in coastal areas (Baynton 1968).

The mean monthly totals of incoming solar radiation for the coast and summits parallel each other. At the summits, mean monthly solar insolation peaks between 320 and 380 langley/day during March and April and is lowest at 175 langley/day during December. Diurnal insolation patterns are also similar and peak near 1 p.m. (Briscoe 1966, Brown and others 1983).

Radiation fog may occur during the early morning hours in interior valleys throughout Puerto Rico, including those of the LEF. Often seen as blankets of cloud cover concentrated in low areas, these rapidly dissipate as the day progresses.

**Hurricanes.** — September is the month of most frequent hurricane occurrence followed by August and July (Salivia 1972). About 80 storms have occurred in Puerto Rico since the early 1700's (fig. 8), many of which probably caused localized damage to vegetation in the Luquillo Mountains. Of these, 15 were A storms (vortex of the hurricane passed directly over the Island with hurricane-force winds), and 12 were B storms (vortex of the hurricane may or may not have passed over the Island, but only part of the Island experienced hurricane-force winds), for an average of one storm over at least part of the Island every 12 years (fig. 9). Of the A storms, four had trajectories directly over the

Luquillo Mountains (fig. 8, 9). Based on existing data, hurricanes may be expected to pass directly over the LEF once every 62 years and to pass within 60 km once every 22 years (Scatena 1989). The LEF, then, could expect some damage from type A hurricanes at least once every 20 to 30 years.

The effects of Hurricane San Felipe of 1928, as reported for the Luquillo district, included defoliation and breakage of branches, later followed by an abnormal production of seeds (Bates 1929). Hurricane San Cipriano of 1932 passed directly over the LEF and must have done considerable damage to the forest based on compositional and structural changes observed during recovery (Crow 1980; Weaver 1986a, 1989). Hurricane Santa Clara of 1956 had very little effect on the LEF (Wadsworth and Englerth 1959). Hurricane Hugo of 1989, the first to have a major impact on the Luquillo Forest since San Cipriano of 1932, passed over the northeastern tip of Puerto Rico. Sustained winds were in excess of 225 km/hr, and the total 3-day rainfall ranged up to 34 cm (Larsen 1989, Matos 1989). More than 200 landslides were detected within the mountains of northeastern Puerto Rico (Larsen 1989). Defoliation, stripping of branches, and tree fall were evident throughout the Baño de Oro, which was well exposed to the storm. Hurricanes are of biological interest because of the long-term effects they have on forests and wildlife (Crow 1980; Walker and others 1991; Weaver 1986a, 1989).

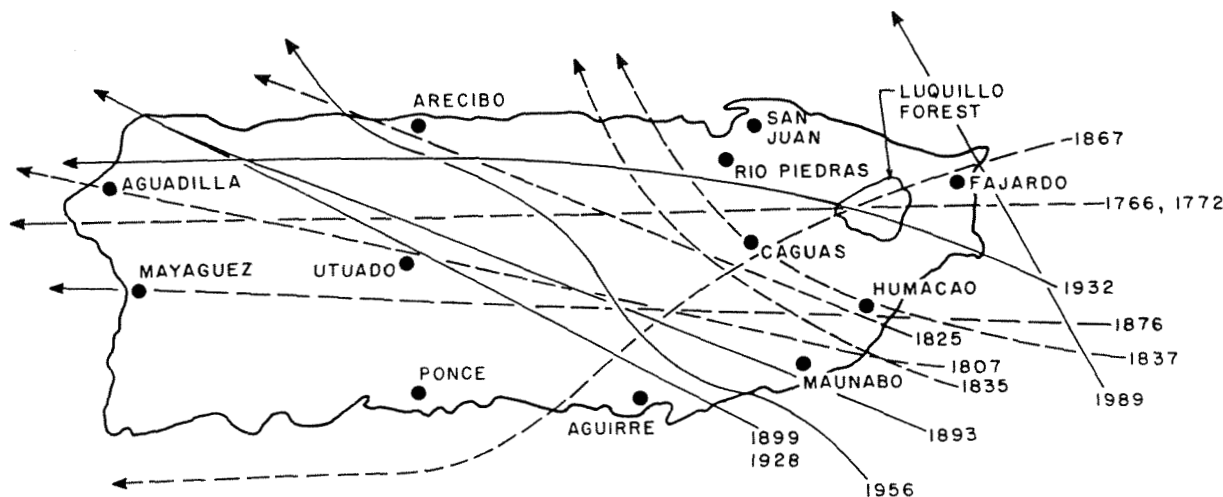


Figure 9.—Path of type A hurricanes with trajectories directly over Puerto Rico from 1700 to 1970. Solid lines are known trajectories and dashed lines are assumed trajectories based on descriptions (adapted from Salivia 1972). Hurricane Hugo of 1989 passed just east of Fajardo.

## Hydrology

Two major rivers, the Rio Mameyes and the Rio Fajardo, have their headwaters in the Baño de Oro (figs. 2 and 4). The Rio Mameyes, made up of three tributaries with a combined river length of about 12 km, flows north draining two-thirds of the Baño de Oro. The Rio Fajardo, with one tributary, has a combined river length of 7 km. It flows north and then east, draining the remainder of the Baño de Oro.

A gauging station (I.D. No. 655) is situated at an 84-m elevation on the Rio Mameyes at the border of the LEF (fig. 1). Records span periods from August 1967 to December 1973 and from June 1983 to the present (Curtis and others 1989). A 6-year record of annual discharge for the station ranged between 200 and 500 cm, with a mean and standard error of  $300 \pm 44$  cm. The mean discharge of total dissolved solids associated with this flow was 3,324 t/yr and was linearly related to river discharge (Brown and others 1983). The mean rates of monthly discharge are the lowest and with the least variability between February and April (fig. 10). They peak in May and October, with the greatest variability in October. Water quality parameters are shown in table 2.

A second gauging station, situated at a 42-m elevation on the Rio Fajardo, has experienced flood damage on several occasions. Low and peak flow discharges were sometimes recorded in 1960-61; water discharge, however, has been recorded from March 1961 to the present (Curtis and others 1989). The average discharge over the 28-year period is 1.98 m<sup>3</sup>/s. The maximum discharge for the same period occurred during Hurricane Hugo, September 18, 1989, when 665 m<sup>3</sup>/s

were recorded. Minimum discharge, 0.86 m<sup>3</sup>/s, occurred on May 3, 1984. Records are rated as fair with low flow affected by diversions for water supply.

Flooding is most likely to occur between May and November, the time of maximum rainfall expectancy. The combination of heavy rainfalls and steep slopes sometimes concentrates runoff into flows that exceed stream channels for short periods. Flooding is most likely to be associated with major rain-producing events such as tropical storms, cold fronts, or hurricanes (Calvesbert 1970). Flooding in the upper headwaters of the Rio Mameyes and Rio Fajardo, however, is localized and of short duration because of the steep topography.

## FLORA

### Major Forest Types

Three sets of nomenclature are commonly used to refer to the forests of the LEF, and each serves a particular audience: local names in Puerto Rico (Wadsworth 1951), Beard's (1944, 1949) terminology in the Caribbean, particularly the Lesser Antilles, and Holdridge's (1967) life zone system commonly used in Central and South America and the Greater Antilles.

The Baño de Oro is divided into two life zones (Ewel and Whitmore 1973): the subtropical rain forest and the subtropical lower montane rain forest (fig. 11). In Puerto Rico, these life zones are confined to the Luquillo Mountains. The subtropical rain forest is located at intermediate elevations to the windward



Table 2.—Mean water quality parameters for the Rio Mameyes for the period 1969–74\*

Parameter	Values <sup>†</sup> (mean ± SE)	
Temperature (°C)	22.9	(0.2)
Specific conductance (μs) <sup>‡</sup>	85.3	(17.1)
pH	7.2	(0.10)
Alkalinity (mg/L) <sup>§</sup>	32.8	(2.7)
Ca (mg/L)	10.5	(0.4)
Mg (mg/L)	2.5	(0.03)
Na (mg/L)	6.7	(0.2)
K (mg/L)	0.60	(0.04)
Cl (mg/L)	8.4	(0.2)
SO <sub>4</sub> (mg/L)	4.0	(0.4)
NO <sub>3</sub> (mg/L)	0.20	(0.05)
Dissolved PO <sub>4</sub> (mg/L)	0.30	(0.3)

\*Brown and others 1983, based on U.S. Geological Survey records.

<sup>†</sup>SE = standard errors (in parentheses); number of observations = 34; elevation = 84 m.

<sup>‡</sup>μs = microsiemens per centimeter at 25 °C (measure of water's capacity to conduct a current).

<sup>§</sup>mg/L = milligrams per liter.

where it occupies 1,420 ha, or 13 percent of the LEF. Twenty-seven percent of the 1,420-ha total, or 385 ha, is in the Baño de Oro. The second life zone is concentrated on windward slopes and summits and occupies 1,180 ha, or about 10 percent of the LEF. Thirty percent of the 1,180-ha total, or 360 ha, is in the Baño de Oro.

Four of Beard's forest types are recognized in the Baño de Oro: lower montane rain forest, montane rain forest, palm brake, and dwarf forest. Locally, these forests are known as tabonuco, colorado, palm, and dwarf forests, respectively. For convenience, local names will be used hereafter in the text.

General descriptive information for the four forest types is provided in table 3. The tabonuco forest, extending to about a 600-m elevation in the LEF, occupies 56 percent of the Baño de Oro (fig. 11). It is dominated by *Dacryodes excelsa*, *Sloanea berteriana*, and *Manilkara bidentata* in the overstory. The colorado forest, which lies between 600 and 900 m in elevation, is dominated by *Cyrilla racemiflora*, *Micropholis chrysophylloides*, and *M. garciniaefolia* in the overstory. The dwarf forest, a gnarled, epiphyte-laden, and dense forest type, occupies the slopes and summits above 900 m in elevation. *Tabebuia rigida*, *Ocotea spathulata*, and *Eugenia borinquensis* are the most common species. Finally, the palm forest, dominated by *Prestoea montana*, the sierra palm, is concentrated on steep slopes and in ravines above a 500-m elevation.

### Other Vegetation Types

There is an alpine meadow in the dwarf forest of the Baño de Oro (fig. 2). Its soil is characterized by a hardpan 60 to 70 cm below the surface (Odum 1970).

The origin of the meadow is uncertain but may be related to site disturbance such as a landslide during heavy rains or a major hurricane (Guariguata 1990, Larsen 1989), followed by soil changes (Weaver 1990). Once formed, the hardpan prevents percolation and may retard the penetration of tree roots.

A *Pterocarpus* stand extends behind the eastern bank of the Rio Mameyes at the confluence of the Rio de la Mina (fig. 2). The stand, occupying <1 ha, borders the Baño de Oro. Its location at a 245-m elevation in the LEF is notable because most *Pterocarpus* forests in the Caribbean are situated in intermittently flooded coastal lowlands.

The stand was studied in detail as part of a thesis program (Alvarez-Lopez 1990, Alvarez Ruiz 1982). Several of the larger trees range from 40 to 80 cm in diameter, and the tallest is 32 m. Seedling regeneration is abundant. Detailed structural information is available for the stand, including species importance values, a species-area curve, a complexity index, a stand profile, phenological observations, root biomass, soil profile, litter standing crop, and soil organic matter storage.

### Tree Species Distribution

The LEF has 225 species of native trees in 144 genera and 59 plant families. The closest botanical affinities are with Hispaniola and Cuba, but South America appears to have been the source of the first immigrants (Little 1970). Forty-one percent of the LEF's tree species are also found on the mainlands of South America, Central America, Mexico, and Florida. Moreover, 28 percent are found in the West Indies but not on the continents, and 31 percent are endemic to Puerto Rico (Little and Woodbury 1976).

Of the 88 species classified as endemic or rare in the LEF, 23 species are endemic only to the LEF, another 45 species are endemic to Puerto Rico and found in the LEF, and 20 species are classified as rare in Puerto Rico but also native to areas outside of Puerto Rico.

### Pico del Oeste Flora

Between 1966 and 1977, staff members of the Arnold Arboretum and collaborators published the results of 17 studies conducted in the dwarf forest of Pico del Oeste. An introduction, objectives, and general description of the dwarf forest program were outlined by Howard (1968, 1970b). The work encompassed studies of species composition (vascular plants, mosses, leafy Hepaticae, and algae), which are reported below.

**Vascular Plants.**—A survey of the vegetation for the entire Pico del Oeste summit area disclosed 97 species of vascular plants, 85 of which were considered to be the principal species (table 4). Of the latter, 31 were species of ferns, 14 were Monocotyledoneae, and

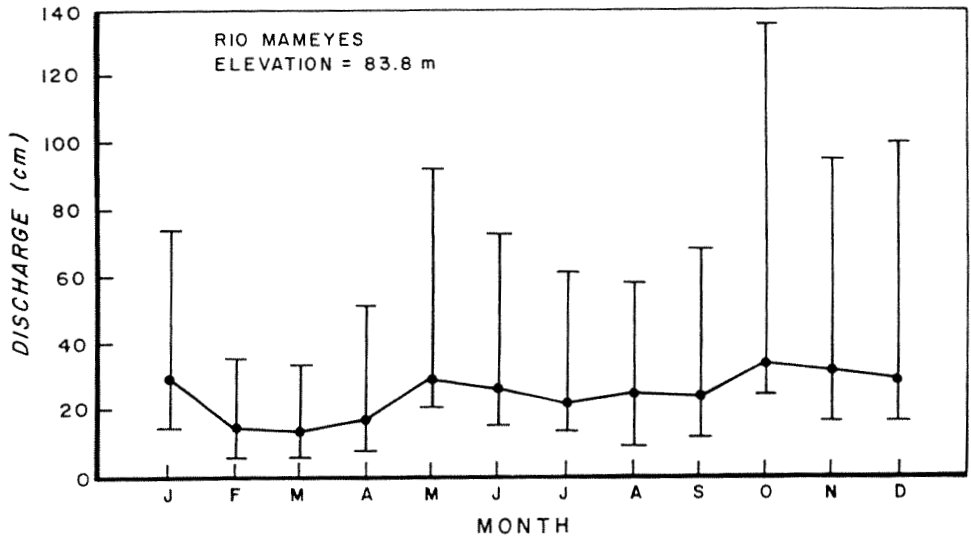


Figure 10.— Mean monthly discharge from the Río Mameyes (in black circles) and range of monthly discharges (bars) (Brown and others 1983).

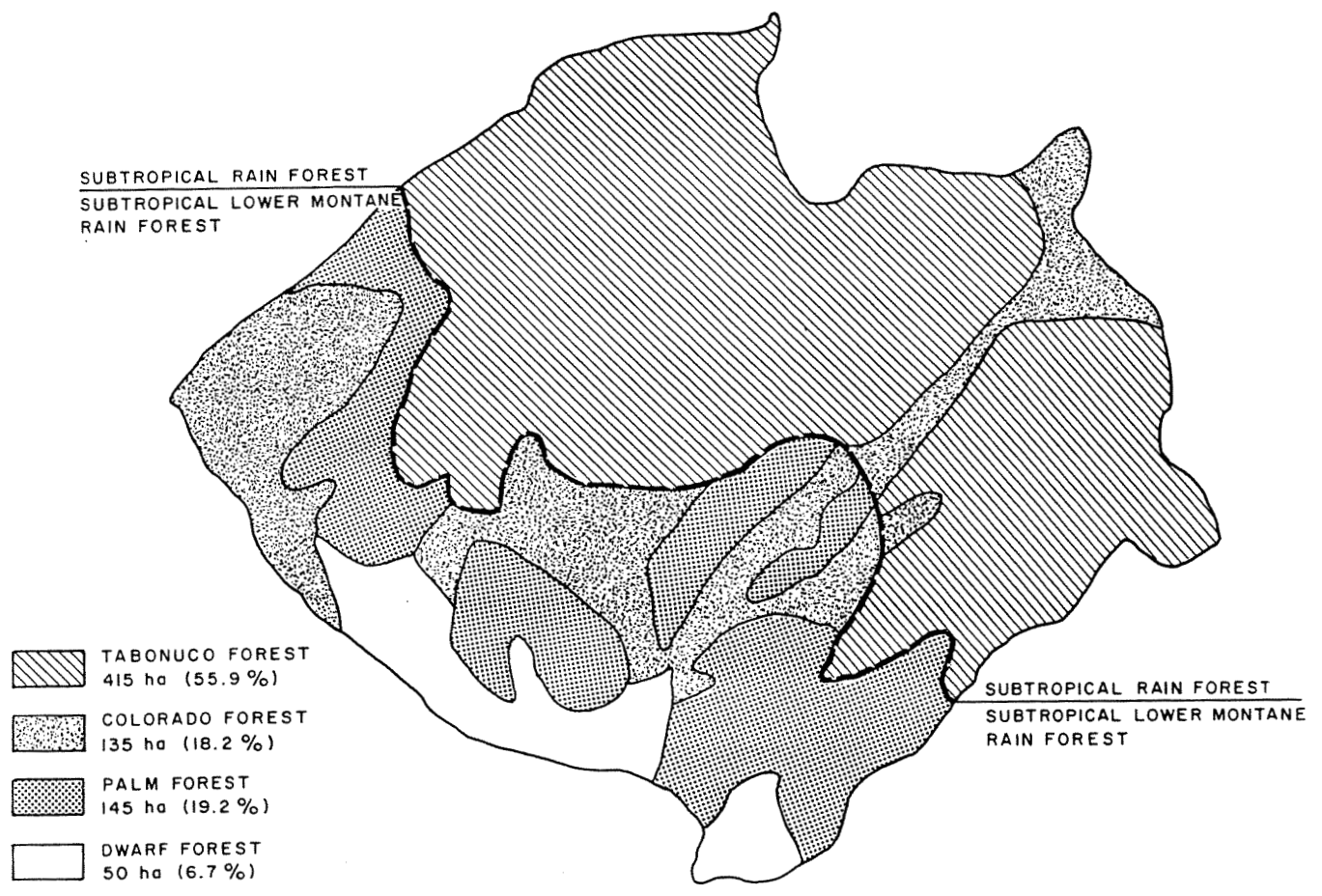


Figure 11.— Life zone and forest type map of the Baño de Oro Natural Area (Institute of Tropical Forestry files).

Table 3.—Forests of the Baño de Oro Natural Area

Forest type	Area		Tree species*		Tree height	Elevation
	Hectares	Percent	Total	No./ha		
Tabonuco	416	56	153	50	>30	<600
Colorado	136	18	101	35–40	15	600–900
Palm	143	19	26	<20	15	>500 (steep slopes and arroyos)
Dwarf	50	7	43	<15	5–7	>900 (exposed slopes and summits)
Total	745	100	225			

\*Little and Woodbury 1976. Species data refer to entire LEF and are not additive because of overlap among forest types. The number of species in the natural area is unknown.

Table 4.—Vascular plant species list for Pico del Oeste in the Baño de Oro Natural Area\*

Nomenclature
<b>Lycopodiophyta</b>
Lycopodiaceae
<i>Lycopodium cernuum</i> L.
<i>L. taxifolium</i> Sw.
Selaginellaceae
<i>Selaginella krugii</i> Hieron
<i>S. substipitata</i> Spring
<b>Polypodiophyta</b>
Cyatheaceae
<i>Cyathea borinquena</i> (Maxon) Domin
<i>C. pubescens</i> Mett. ex Kuhn
<i>Lophosoria quadripinnata</i> (Gmel.) C. Chr.
Polypodiaceae
<i>Blechnum divergens</i> (Kunze) Mett
<i>B. lineatum</i> (Sw.) Hieron
<i>B. underwoodianum</i> (Broadh.) C. Chr.
<i>Cochlidium minus</i> (Jenm.) Maxon
<i>C. seminudum</i> (Willd.) Maxon
<i>Diplazium centripetale</i> (Baker) Maxon
<i>D. grandifolium</i> Sw.
<i>D. l'herminieri</i> Hieron
<i>D. striatum</i> (L.) Presl
<i>Elaphoglossum firmum</i> (Mett.) Urban
<i>G. hessii</i> (Maxon) Alain
<i>G. serrulata</i> (Sw.) Sw.
<i>G. taenifolia</i> (Jenm.) Proctor
<i>Lindsaea stricta</i> (Sw.) Dryand
<i>Oleandra articulata</i> (Sw.) Presl
<i>Peltapteris peltata</i> (Sw.) Morton
<i>Polybotrya cervina</i> (L.) Kaulf
<i>Polypodium chnoodes</i> Spreng
<i>P. loriceum</i> L.
<i>Thelypteris decussata</i> (L.) Proctor
Hymenophyllaceae
<i>Hymenophyllum lincaire</i> Sw.
<i>H. macrothecum</i> Fee
<i>Trichomanes crispum</i> L.
<i>T. rigidum</i> Sw.

Table 4. – Vascular plant species list for Pico del Oeste in the Baño de Oro Natural Area\* – Continued

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Nomenclature

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**Magnoliophyta-Liliatae**

Gramineae

- Andropogon bicornis* L.
- Arthrostylidium sarmentosum* Pilger
- Ichnanthus pallens* (Sw.) Munro
- Isachne angustifolia* Nash

Cyperaceae

- Carex polystachya* Sw. ex Wahlenb
- Eleocharis yunquesis* Britton
- Fimbristylis dichotoma* (L.) Vahl
- Scleria secans* (L.) Urban

Palmae

- Prestoea montana* (R. Grah.) Nichols

Araceae

- Anthurium dominicense* Schott

Bromeliaceae

- Guzmania berteroniana* (R. & S.) Mez
- Vriesia sintenisii* (Baker) Smith & Pittend

Dioscoreaceae

- Rajania cordata* L.

Zingiberaceae

- Renealmia antillarum* (R. & S.) Gagnep

Orchidaceae

- Brachionidium parvum* Cogn
- Dilomilis montana* (Sw.) Summerhayes
- Epidendrum nocturnum* Jacq
- E. pallidiflorum* Hook

**Magnoliophyta-Magnoliatae**

Piperaceae

- Peperomia emarginella* (Sw.) DC .
- P. hernandiifolia* (Vahl) A. Dietr

Chloranthaceae

- Hedyosmum arborescens* Sw.

Moraceae

- Cecropia peltata* L.

Urticacea

- Pilea krugii* Urban
- P. obtusata* Liebm
- P. yunquensis* (Urb.) Britt. & Wils.

Lauraceae

- Ocotea spathulata* Mez

Magnoliaceae

- Magnolia splendens* Urban

Cunoniaceae

- Weinmannia pinnata* L.

Table 4. — Vascular plant species list for Pico del Oeste in the Baño de Oro Natural Area\*—Continued

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Nomenclature

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Meliaceae

*Trichilia pallida* Sw.

Aquifoliaceae

*Ilex sintenisii* (Urb.) Britton

Celastraceae

*Torrabasia cuneifolia* (C. Wr. ex Griseb.)  
Krug & Urban ex Segui

Ochnaceae

*Sauvagesia erecta* L.

Marcgraviaceae

*Marcgravia sintenisii* Urban

Theaceae

*Cleyera albopunctata* (Griseb.) Krug & Urban

Guttiferae

*Clusia grisebachiana* (Planchon & Triana) Alain  
*C. gundlachii* Stahl

Begoniaceae

*Begonia decandra* Pav. ex A. DC.

Thymelaeaceae

*Daphnopsis philippiana* Krug & Urban

Myrtaceae

*Calyptranthes krugii* Kiaersk.  
*Eugenia borinquensis* Britton

Melastamataceae

*Calycogonium squamulosum* Cogn  
*Mecranium amygdalinum* (Desr.) C. Wright ex Sauv  
*Miconia foveolata* Cogn  
*M. pachyphylla* Cogn  
*M. pycnoneura* Urban  
*M. sintenisii* Cogn

Ericaceae

*Gonocalyx portoricensis* (Urb.) A. C. Sm.  
*Hornemannia racemosa* Vahl.

Myrsinaceae

*Ardisia luquillensis* (Britton) Alain  
*Grammadenia sintenisii* (Urb.) Mez  
*Wallenia yunquensis* (Urb.) Mez

Sapotaceae

*Micropholis garciniaefolia* Pierre.

Symplocaceae

*Symplocos micrantha* Krug & Urban

Oleaceae

*Haenianthus salicifolius* Griseb. var. *obovatus* (Krug & Urb.) Knobl

Convolvulaceae

*Ipomoea repanda* Jacq.

Table 4.—Vascular plant species list for Pico del Oeste in the Baño de Oro Natural Area\*—Continued

Nomenclature
Boraginaceae <i>Cordia borinquensis</i> Urban
Bignoniaceae <i>Tabebuia rigida</i> Urban
Gesneriaceae <i>Alloplectus ambiguus</i> Urban <i>Gesneria sintenisii</i> Urban
Acanthaceae <i>Justicia martinsoniana</i> Howard
Rubiaceae <i>Hillia parasitica</i> Jacq. <i>Psychotria berteriana</i> DC. <i>P. guadalupensis</i> (DC.) Howard <i>Rondeletia portoricensis</i> Krug & Urban
Campanulaceae <i>Lobelia portoricensis</i> (Vatke) Urban
Compositae <i>Clibadium erosum</i> (Sw.) DC. <i>Mikania pachyphylla</i> Urban

\*Source: Howard 1968.

40 were Dicotyledoneae (Howard 1968). Of the species sampled on Pico del Oeste, 32 percent were endemic to Puerto Rico, 40 percent were restricted to the Greater and Lesser Antilles, and 28 percent were found in the Antilles and in continental areas (Howard 1968).

**Mosses.**—Twenty-three species of mosses were identified (table 5) (Russell and Miller 1977). Most species grow at the base of trees with about half occurring at other levels. Species growing on the forest floor have a lower resistance to desiccation than those in treetops, whereas the latter are more tolerant of higher light intensities.

**Leafy Hepaticae.**—Although the dwarf forest is sometimes called “mossy,” leafy Hepaticae comprise most of the bryophyte flora. Fifteen families, 34 genera, and 62 species were identified on Pico del Oeste (table 6) (Fulford and others 1970, 1971). Considerable differences in species composition were observed for hepatic flora on different peaks within the LEF.

**Algae.**—Some 123 species of epiphytic algae were identified with their vascular hosts on Pico del Oeste (table 7) (Foerster 1971). Sampling disclosed that they were not uniformly distributed but were segregated into various intergrading synusia. A general shift from Bacillariophyta- to Cyanophyta- to Chlorophyta-

dominated synusia was observed, a phenomenon apparently related to an increase in height and changes in host material. Moreover, a vertical shift of algae, or seasonal response to environmental utilization, is evident during the year, probably as a reaction to greater cloud cover during the wet season than in the dry season.

Other studies of the flora on Pico del Oeste included the following topics: stem growth, form, and leaf structure (Howard 1969); chromosome numbers and flowering cycles of dwarf forest species (Nevling 1969, 1971); transpiration rates and leaf temperatures (Gates 1969); soil and roots, including aerial roots (Gill 1969, Lyford 1969); phytochemical screening and chemistry of colored leaves (Persinos and others 1970, Wagner and others 1969); and the occurrence and growth of *Marcgravia* (Howard 1970a) and *Gonocalyx* (Nevling 1970).

**Other Dwarf Forest Studies.**—The dwarf forest on Pico del Oeste, at virtually the same elevation and <2 km distant from Pico del Oeste, has also been studied (Weaver 1972a, 1972b). Twenty-eight species of endemic plants and 28 species of vertebrate fauna were identified. The arborescent vegetation contained only a few tree species characterized as small in stature and high in stem density and basal area.

Table 5.—Moss species list for Pico del Oeste in the Baño de Oro Natural Area\*

Nomenclature

*Acroporium acrostegium*  
*A. pungens*  
*Callicostella depressa*  
*Campylopus cygneus*  
*Hemiragis aurea*  
*Hookeriopsis acicularis*  
*H. obsoletinervis*  
*Hypnella filiformis*  
*Isodrepanium lentulum*  
*Lepyrodontopsis trichophylla*  
*Leucobryum crispum*  
*L. martianum*  
*Leucoloma serrulatum*  
*L. shwaneckeanum*  
*Leucophanes calymeratum*  
*Macromitrium perichaetiale*  
*M. schwaneckeanum*  
*M. scoparium*  
*Pilotrichum evanescens*  
*Syrrhopodon prolifer*  
*Thuidium urceolatum*  
*Trichosteleum sentosum*  
*Vesicularia* sp.

\*Source: Russell and Miller 1977.



*Cyrrilla racimiflora* regeneration on an overturned tree after Hurricane Hugo within the Baño de Oro Natural Area.

Table 6. — *Leafy Hepaticae species list for Pico del Oeste in the Baño de Oro Natural Area\**

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Nomenclature

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Trichocoleaceae

- Trichocolea brevifissa* Steph.
- T. elliotii* Steph.
- T. filicaulis* Steph.
- T. flaccida* (Spr.) Jack & Steph.

Isotachidaceae

- Neesioscyphus bicuspidatus* (Steph.) Grolle

Herbertaceae

- Herberta divergens* (Steph.) Herz.
- H. elliotii* Spr.
- H. juniperoidea* (Sw.) Grolle
- H. pensilis* (T. Tayl.) Spr.

Lepidoziaceae

- Bazzania bidens* (Nees) Trevis.
- B. breuteliana* (Lindenb. & Gott.) Trevis.
- B. cubensis* (Gott.) Pagán
- B. eggersiana* (Steph.) Pagán
- B. gracilis* (Hampe & Gott.) Steph.
- B. hookeri* (Lindenb.) Trevis.
- B. longa* (Nees) Trevis.
- B. longistipula* (Lindenb.) Trevis
- B. roraimensis* (Steph.) Fulf.
- B. schwaneckiana* (Hampe & Gott) Trevis.
- B. stolonifera* (Sw.) Trevis.
- Lepidozia patens* Lindenb.
- Microlepidozia capillaris* (Sw.) Fulf.
- Micropterygium carinatum* (Grev.) Reim.
- M. exalatum* Steph.
- Telaranea sejuncta* (Angstr.) S. Arnell

Calypogeiaceae

- Calypogeia caespitosa* (Spr.) Steph.
- C. cellulosa* (Spreng.) Steph.
- C. crenulata* Bischl.
- C. cyclostipa* (Spr.) Steph.
- C. elliotii* Steph.
- C. laxa* Gott. & Lindenb.
- C. lophocoleoides* Steph.
- C. peruviana* Nees & Mont.

Cephaloziaceae

- Cephalozia caribbeana* Fulf.
- C. crassifolia* (Lindenb. & Gott.) Fulf.
- C. subforficata* Herz.
- Nowellia caribbeana* Fulf.
- N. dominicensis* Steph.

Odontoschismaceae

- Albiellopsis dominicensis* (Spr.) Fulf.
- Odontoschisma denudatum* (Nees) Dum.
- O. longiflorum* (T. Tayl.) Steph.
- O. prostratum* (Sw.) Trevis.

Regredicaulaceae

- Arachniopsis coactilis* Spr.

Zoopsidaceae

- Zoopsis antillana* Steph.

Albiellaceae

- Albiella husnoti* (Gott.) Schiffn.

Paracromastigaceae

- Leucosarmentum portoricense* Fulf.



Table 6. – Leafy Hepaticae species list for Pico del Oeste in the Baño de Oro Natural Area\* – Continued

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Nomenclature

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Lophocoleaceae

- Heteroscyphus elliottii* (Steph.) Pagán
- Leptoscyphus gibbosus* (T. Tayl.) Mitt.
- Lophocolea guadeloupensis* Steph.
- L. martiana* Nees

Lophoziaceae

- Syzygiella perfoliata* (Sw.) Spr.
- S. rubricaulis* (Nees) Steph.

Jungermanniaceae

- Jungermannia dominicensis* Spr.

Adelanthaceae

- Adelanthus decipiens* (Hook.) Mitt.

Plagiochillaceae

- Plagiochila abrupta* Lehm. & Lindenb.
- P. adiantoides* (Sw.) Dum.
- P. amoena* Steph.
- P. arcuata* Lindenb.
- P. bicornis* Hampe & Gott.
- P. bidens* Gott.
- P. breuteliana* Lindenb.
- P. bursata* (Desv.) Lindenb.
- P. chinantlana* Gott.
- P. confundens* Lindenb. & Gott.
- P. distinctifolia* Lindenb.
- P. divaricata* Lindenb.
- P. dominicensis* T. Tayl.
- P. jamaicensis* Lindenb. & Hampe
- P. rutilans* Lindenb.
- P. simplex* (Sw.) Dum.
- P. subbidentata* T. Tayl.
- P. tamariscina* Steph.
- P. ? tenuis* Lindenb. scraps

Scapaniaceae

- Scapania portoricensis* Hampe & Gott.

Radulaceae

- Radula fendleri* Gott.
- R. inflexa* Gott. ex Steph.
- R. kegelii* Gott. ex Steph.
- R. longifolia* Steph.
- R. saccatiloba* Steph. spp.

Frullaniaceae

- Frullania atrata* (Sw.) Dum.
- F. brasiliensis* Raddi
- F. exilis* T. Tayl.
- F. kunzei* Lehm. & Lindenb.
- F. subtilissima* (Nees & Mont) Lindenb.

Lejeuneaceae

- Anoplolejeunea conferta* (Meissn.) Evans
- Archilejeunea viridissima* (Lindenb.) Steph.
- Ceratolejeunea brevinervis* (Spr.) Evans
- C. cornuta* (Lindenb.) Steph.
- C. cubensis* (Mont.) Schiffn.
- C. flagelliformis* (Steph.) Fulf.
- C. maritima* (Spr.) Steph.
- C. patentissima* (Hampe & Gott.) Evans
- C. rubiginosa* Steph.

Table 6. — Leafy Hepaticae species list for Pico del Oeste in the Baño de Oro Natural Area\* — Continued

Nomenclature

- C. spinosa* (Gott.) Steph.  
*C. valida* Evans scraps  
*Cheilolejeunea decidua* Spr.  
*C. polyantha* Evans  
*Colura clavigera* (Gott. ex Schiffn.) Jovet-Ast  
*C. rhynchophora* Jovet-Ast  
*Crossotolejeunea bermudiana* Evans  
*C. boryana* (Mont.) Steph.  
*Cyclolejeunea accedens* (Gott.) Evans  
*C. angulistipa* (Steph.) Evans  
*C. chitonia* (T. Tayl.) Evans  
*C. convexistipa* (Lehm. & Lindenb.) Evans  
*Cyrtolejeunea holostipa* (Spr.) Evans  
*Cystolejeunea lineata* (Lehm. & Lindenb.) Evans  
*Diplasiolejeunea brachyclada* Evans  
*D. pellucida* (Meissn.) Schiffn.  
*D. unidentata* (Lehm & Lindenb.) Schiffn.  
*Drepanolejeunea anoplantha* (Spr.) Steph.  
*D. crucianella* (T. Tayl.) Evans  
*D. evansii* Bischl.  
*D. fragilis* Bischl.  
*D. inchoata* (Meissn.) Schiffn.  
*D. lichenicola* (Spr.) Steph. scraps  
*Euosmolejeunea clausa* (Nees & Mont.) Evans  
*E. rigidula* (Nees & Mont.) Steph.  
*E. trifaria* (Nees) Schiffn.  
*Harpalejeunea heterodonta* Evans  
*H. subacuta* Evans  
*H. uncinata* Steph.  
*Hygrolejeunea* sp.  
*Lejeunea flava* (Sw.) Nees  
*Leptolejeunea elliptica* (Lehm. & Lindenb.) Schiffn.  
*L. hamulata* Schiffn.  
*Leucolejeunea xanthocarpa* (Lehm. & Lindenb.) Evans  
*Lopholejeunea howei* Evans  
*L. mülleriana* (Gott.) Schiffn.  
*L. sagraeana* (Mont.) Schiffn.  
*Macrolejeunea subsimplex* (Nees & Mont.) Schiffn.  
*Marchesinia brachiata* Schiffn.  
*Microlejeunea acutifolia* Steph.  
*M. bullata* (T. Tayl.) Steph.  
*M. laetevirens* (Nees & Mont.) Evans  
*M. monoica* Bischl.  
*Neurolejeunea breutelii* (Gott.) Evans  
*Odontolejeunea lunulata* (Web. ) Schiffn.  
*Omphalanthus filiformis* (Sw.) Nees  
*Prionolejeunea aemula* (Gott.) Evans  
*P. aequitexta* Evans  
*P. exauriculata* Evans  
*P. helleri* Evans  
*P. innovata* Evans scraps  
*Ptychocoleus polycarpus* (Nees) Trevis.  
*Pycnolejeunea schwaneckii* (Steph.) Schiffn.  
*Rectolejeunea berteriana* (Gott.) Evans  
*R. phyllobola* (Nees & Mont.) Evans  
*Stictolejeunea squamata* (Willd.) Steph.  
*Strepsilejeunea involuta* Steph.  
*Symbiezidium barbiflorum* (Lindenb. & Gott.) Evans  
*S. laceratum* Evans.  
*S. transversale* (Sw.) Trevis.  
*Taxilejeunea obtusangulata* (Spr.) Evans.  
*T. sulphurea* (Lehm. & Lindenb.) Steph.  
*Trachylejeunea inflexa* Steph.

\*Sources: Fulford and others 1970, 1971.

Table 7.—Algae species list for Pico del Oeste in the Baño de Oro Natural Area\*

## Nomenclature

## Cyanophyta

## Chroococcales

- Aphanocapsa biformis* A. Br.  
*A. grevillei* (Hass.) Rabenh.  
*A. roeseana* DeBary  
*Aphanothece clathrata* W. & G. West  
*A. microscopica* Näg.  
*A. saxicola* Näg.  
*Chroococcus dispersus* (Keissler) Lemm.  
*C. dispersus* var. *minor* G. M. Sm.  
*C. giganteus* W. West  
*C. limneticus* Lemm.  
*C. minor* (Kütz.) Näg.  
*C. minutus* (Kütz.) Näg.  
*C. pallidus* Näg.  
*C. turgidus* (Kütz.) Näg.  
*C. varius* A. Br.  
*Dactylococcopsis fascicularis* Lemm.  
*D. smithii* R. & F. Chodat  
*Gloeocapsa aeruginosa* (Carm.) Kütz.  
*G. polydermatica* Kütz.  
*Gloeothece linearis* var. *composita* G. M. Sm.  
*G. palea* (Kütz.) Näg.  
*G. palea* (Kütz.) Rabenh.  
*Merismopedia aeruginea* Bréb. ex Kütz.  
*M. elagans* A. Br. ex Kütz.  
*M. glauca* (Ehrenb.) Näg.  
*M. punctata* Meyen  
*M. tenuissima* Lemm.  
*Microcystis aeruginosa* Kütz.  
*M. elabens* (Breb) Kütz.  
*M. incerta* Lemm.  
*M. ramosa* Braradw.  
*M. orissica* (?) W. West.  
*Pelogloea bacillifera* Lauterborn  
*Rhabdoderma* sp.  
*Synechococcus aeruginosus* Näg.

## Chamaesiphonales

- Chamaesiphon confervicola* A. Br.  
*C. rostaffinskii* Hansg.

## Nostocales

- Anabaena anomala* Fritsch  
*A. circinalis* Rabenh.  
*A. laxa* (Rabenh.) A. Br.  
*Anabaena* sp.  
*A. oryzae* Fritsch  
*A. oscillarioides* Bory ex Born. & Flah.  
*Aulosira fritschii* Bharadw.  
*A. prolifica* (?) Bharadw.  
*A. prolifica* Bharadw.  
*Calothrix epiphytica* W. & G. West  
*C. weberi* Schmidle  
*Coelosphaerium dubium* Grun.  
*Cylindrospermum catenatum* (?) Ralfs  
*Gloeotrichia echinnulata* (J. E. Sm.) Richter  
*G. longiarticulata* G. S. West  
*Lyngbya limnetica* Lemm.  
*Microchaete uberrima* Carter  
*Nostoc muscorum* C. Ag.  
*Oscillatoria agardhii* Gom.  
*O. annae* van Goor  
*O. foreaui* Frémy

Table 7. – *Algae species list for Pico del Oeste in the Baño de Oro Natural Area\**

Nomenclature

*O. geitleriana* Elenkin  
*O. limnetica* Lemm. sp.  
*Oscillatoria* sp.  
*O. subbrevis* Schmidle  
*Phormidium tenue* (Menegh.) Gom.  
*Pseudanabaena catenata* Lauterb.  
*P. constricta* (Szäfer) Lauterb.  
*Schizothrix ericetorum* Lemm.  
*Scytonema amplum* W. & G. West  
*S. burmanicum* Skuja  
*S. hofmannii* C. Ag. ex Born. & Flah.  
*S. javanicum* (?) (Kütz.) Born  
*S. schmidtii* (?) Gom.  
*S. stuposum* (Kütz.) Born. ex Born. & Flah  
*S. tolypothricoides* Kütz. ex Born. & Flah.  
*Scytonematopsis kashyapii* (Bharadw.) Geitler  
*Spirulina subtilissima* Kütz.  
*Tolypothrix distorta* Kütz. ex Born. & Flah.

Pleurocapsales

*Myxosarcina spectabilis* Geitler  
*Xenococcus kernerii* Hansg.

Stigonematales

*Camptylonema indicum* Schmidle  
*Hapalosiphon delicatulus* W. & G. West  
*H. fontinalis* (Ag.) Born.  
*H. hibernicus* W. & G. West  
*H. inteolus* W. & G. West  
*H. intricatus* W. & G. West  
*H. luteolus* W. & G. West  
*H. stuhlmannii* Hieron.  
*H. welwitschii* W. & G. West  
*Nostochopsis lobatus* Wood em. Geitler  
*Plectonema indica* Dixit  
*Stigonema aerugineum* Tilden  
*S. dendroideum* Frémy  
*Stigonema hormoides* (Kütz.) Born. & Flah.  
*S. informe* Kütz.  
*S. mesentericum* Geitler  
*S. minutum* (C. Ag.) Hass.  
*S. panniforme* Harv. ex Born. & Flah.  
*S. turfaceum* (Berk.) Cooke ex Born. & Flah.

**Chlorophyta**

Chaetophorales

*Cephaleuros virescens* Kunze  
*Protococcus viridis* C. Ag.  
*Stigeoclonium polymorphum* (?) (Franke) Heering  
*Trentepohlia aurea* var. *tenuior* Brühl & Biswas  
*T. aurea* (L.) Martius  
*T. iolithus* (L.) Wallroth  
*T. torulosa* De Wildeman  
*T. umbrina* (Kütz.) Born.

Chlorococcales

*Ankistodesmus falcatus* (Corda) Ralfs  
*Characium stipitatum* (Bachm.) Wille  
*C. obtusum* (?) Braun  
*Chlorella ellipsoidea* Gern.  
*C. vulgaris* Beyerinck  
*Chlorococcum humicola* (Näg.) Rabenh.  
*Crucigenia quadrata* Morren  
*Oocystis borgei* Snow

Table 7. – *Algae species list for Pico del Oeste in the Baño de Oro Natural Area\**

Nomenclature

*O. pyriformis* Prescott  
*O. submarina* Lagerheim  
*Pediastrum muticum* var. *crenulatum* Prescott  
*P. muticum* Kütz.  
*Quadrigula chodatii* (Tanner-Füllemann) G. M. Sm  
*Q. lacustris* (Chod.) G.M. Sm  
*Scenedesmus arcuatus* var. *platydisca* G.M.Sm.  
*Tetraedron tumidulum* (Reinsch) Hansg.  
*Trochiscia granulata* (Reinsch) Hansg.

Cylindrocapsales

*Cylindrocapsa conferta* W. West  
*C. geminella* Wolle

Oedogoniales

*Oedogonium* sp.  
*Pithophora oedogonia* (Mont. ) Wittr.

Sphaeropleales

*Sphaeroplea annulina* (Roth) C. Ag.

Tetrasporales

*Gloecystis major* Gerneck  
*G. vesiculosa* Näg.  
*Sphaerocystis schroeteri* (?) Choat

Tribonematales

*Tribonema utriculosum* (Kütz.) Hazen

Ulotrichales

*Geminella interrupta* Turpin  
*Stichococcus subtilis* (Kütz.) Klercker  
*Ulothrix aequalis* Kütz.  
*U. variabilis* Kütz

Zygnematales

*Cosmarium dentatum* Wolle  
*Cosmarium* sp.  
*Cylindrocystis brebissonii* var. *minor* W. & G. West  
*Euastrum* sp.  
*Hyalotheca undulata* Nordst.  
*Micrasterias denticulata* (?) Breb.  
*M. caimani* Transeau  
*M. floridana* Transeau  
*Mougeotia globulispota* Jao  
*Netrium digitus* (Ehrenb.) Itzigos. & Rothe  
*Temnogametum transeai* Prescott  
*Zygnemopsis desmidioides* (W. & G. west) Transeau  
*Zygogonium ericetorum* Kütz.

**Chrysophyta**

Heterococcales

*Peroniella planctonica* G. M. Sm.  
*Pleurogaster lunaris* Pascher  
*Tetragoniella gigas* Pascher

Rhynchrysidales

*Chrysidiastrum catenatum* Lauterb.  
*Lagynion reductum* Prescott

Table 7.—Algae species list for Pico del Oeste in the Baño de Oro Natural Area\*

## Nomenclature

## Bacillariophyta

## Centrales

- Biddulphia alternans* (bail.) Van Heurck  
*B. favus* (Ehrenb.) Van Heurck  
*Campylodiscus echeneis* (?) Ehrenb.  
*Coccinodiscus lacustris* (?) Grun.  
*Cyclotella bodanica* (?) Eulenst.  
*C. glomerata* Bachm.  
*Melosira crenulata* (Ehrenb.) Kütz.  
*M. granulata* (Ehrenb.) Ralfs  
*M. varians* C. Ag.  
*Triceratium semicirculare* Brightw.  
*T. undulatum* Ehrenb.

## Pennales

- Achanthes hauckiana* Grun.  
*A. microcephala* (Kütz.) Grun.  
*Amphora ovalis* Kütz.  
*Anomoeoneis costata* (?) (Kütz.) Hust.  
*Cymbella ventricosa* Kütz.  
*Dentivula* sp.  
*Diatoma hiemale* (Roth) Heib.  
*D. hiemale* var. *mesodon* (Ehrenb.) Grun.  
*D. tenue* var. *elongatum* Lyngb.  
*Diatoma vulgare* Bory  
*Diatomella balfouriana* Grev.  
*Diploneis oculata* (Breab.) Cl.  
*Eunotia exigua* (?) (Bréb.) Rabenh.  
*E. fallax* Cleve-Euler  
*E. naegelii* Mig.  
*E. pectinalis* f. *elongata* van Huerck  
*E. pectinalis* var. *minor* (Kütz.) Rabenh.  
*E. perpusilla* (?) Grun.  
*E. praerupta* Ehrenb.  
*E. soleirolii* (Kütz.) Rabenh.  
*Eunotia* sp.  
*E. tenella* (Grun.) Hust.  
*Fragilaria brevistriata* Grun.  
*F. lapponica* Grun.  
*Frustulia rhomboides* var. *capitata* (Mayer) Patr.  
*F. rhomboides* var. *saxonica* (Rabenh.) DeToni  
*F. rhomboides* var. *viridula* (Bréb.) Cl.  
*Hantzschia amphioxys* (Ehrenb.) Grun.  
*Isthmia enervis* Ehrenb.  
*Navicula carniolensis* (?) Hust.  
*N. cineta* (Grun.) Cl.  
*N. contenta* Grun.  
*N. crucicula* (?) (W. Smith) Donk  
*N. cryptocephala* (?) Kütz.  
*Navicula* spp. (3 separate species)  
*N. tenelloides* Hust.  
*Nitzschia biacrula* (?) Hohn & Hellerman  
*N. dissipata* (Kütz.) Grun.  
*N. hantzschiana* Rabenh.  
*N. ignorata* Krasske  
*N. parvula* Lewis  
*N. tryblionella* Hantzsch.  
*Pinnularia sudentica* Hilse  
*P. viridis* var. *minor* Cleve  
*Rhopalodia gibberula* (Ehrenb.) Mueller  
*R. ventricosa* (Kütz.) Mueller  
*Stauroneis ignorata* (?) Hust.  
*Surirella ovata* Kütz.  
*Tropidoneis* sp.

Table 7. – *Algae species list for Pico del Oeste in the Baño de Oro Natural Area\**

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Nomenclature

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**Pyrrophyta**

Dinococcales

*Cystodinium cornifax* (Schilling) Klebs

**Euglenophyta**

Euglenales

*Euglena elastica* (?) Prescott

*E. polymorpha* Dangeard

*Glenodinium kulczynskii* (?) (Wolosz.) Schiller

*Trachelomonas charkowiensis* (?) Swirenko

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\*Source: Foerster 1971



*Tree fall gap with regeneration of Cecropia peltata in the Baño de Oro Natural Area.*

Transpiration rates of dwarf forest trees were observed to be relatively low when compared to other environments (Medina and others 1981, Weaver and others 1973). Different rates were detected between primary and secondary species and between sun and shade exposures (Weaver 1975). Moreover, rates were negatively correlated with the amount of cloud cover on the peaks.

Tree diameter increment averaged 0.03 cm/yr, and aboveground biomass accumulation was estimated at 0.45 t/ha/yr (Weaver and others 1986). Litterfall averaged 3.1 t/ha/yr, 79 percent of which was leaf litter, 9 percent wood litter, and 12 percent miscellaneous material. Leaf herbivory was estimated at 5.5 percent, or 0.13 t/ha/yr (Benedict 1976). These data yield an estimate of aboveground primary productivity of nearly 3.7 t/ha/yr (Weaver and others 1986).

Dwarf forest succession after disturbance was observed for nearly 20 years near Pico del Este. Recovery after 6 years was characterized mainly by woody sprouts, ferns, and grasses, whereas seedlings of woody species were scarce (Byer and Weaver 1977). After nearly 20 years, nine primary forest species comprised 75 percent of the trees and 85 percent of the biomass (Weaver 1990). Recovery was slow, and at the observed rate would span about two centuries before the initial aboveground biomass would be restored.

### Vegetation Gradient

Thirty plots, 50 by 10 m in size (or 1.5 ha in total), were systematically sampled in the Baño de Oro to provide data on forest structure and species composition for all trees  $\geq 4.1$  cm in d.b.h. The plots ranged in elevation from 350 to 1,025 m and were stratified in

groups of three according to topography (ridge, slope, and valley) at each elevation. Height of the dominant and codominant stems decreased along the gradient from 23 m at a 350-m elevation to 5 m at a 1,025-m elevation, with the most and least pronounced decreases apparent on ridge and valley topography, respectively (fig. 12). Although variation in tree height is considerable, the tallest trees in the tabonuco forest ( $\leq 600$  m) are on ridges, and the tallest trees in the dwarf forest ( $\geq 900$  m) are found in valleys.

The diameters of the largest recorded stems in the dwarf, colorado, and tabonuco forests were about 50 cm, 100 cm, and 95 cm, respectively. Only 32 percent of the dwarf forest trees are  $>10$  cm in d.b.h., whereas the comparable figures for the colorado and tabonuco forest are 60 and 65 percent, respectively (fig. 13). The tallest trees in the dwarf, colorado, and tabonuco forests measured about 15 m, 21 m, and 28 m. Only 10 percent of the dwarf forest trees were  $>9$  m tall, whereas comparable data for the colorado and tabonuco forests were 44 percent and 54 percent (fig. 14).

The mean basal area for all plots combined was  $44 \pm 3$  m<sup>2</sup>/ha, and the mean total aboveground biomass, based on regression equations, was  $205 \pm 27$  t/ha. Basal area and biomass estimates for the respective forests are biased, especially for ridge plots at lower elevations, because the sampling procedure used small, closed-canopy plots. These plots tend to have a greater number of stems than larger areas, which include natural breaks, or gaps, in the canopy.

Species composition according to elevation, topography, and forest type is tentatively presented in table 8. Given that the entire sample of the area was limited to only 1.5 ha, this table is not intended to be used

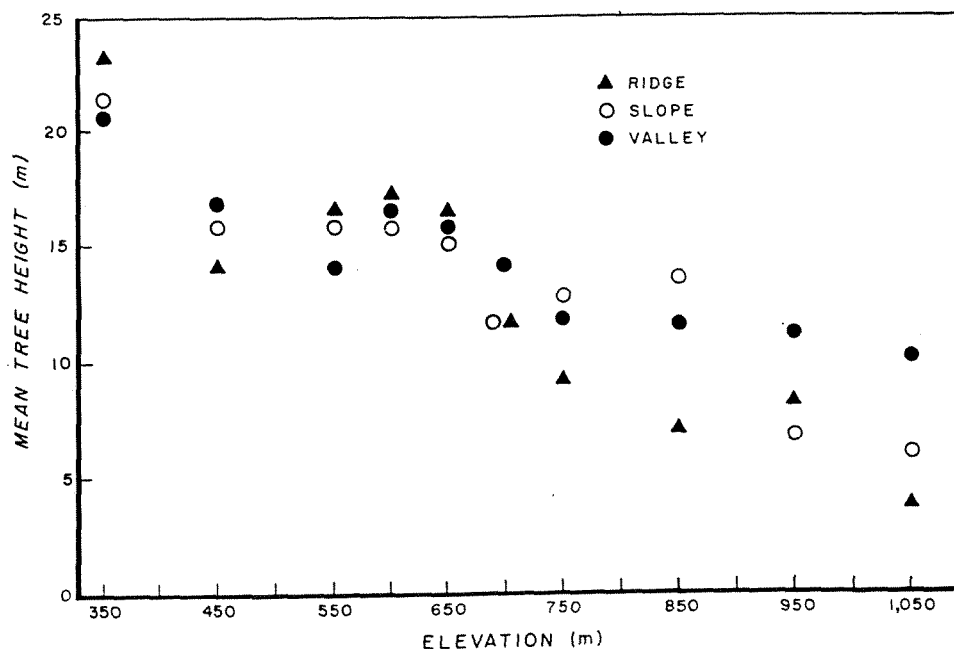


Figure 12.—The height of dominant and codominant trees by topography and elevation on closed canopy 50- by 10-m plots in the Baño de Oro Natural Area.





Walking *Clusia grisebachiana* possibly the result of past hurricane impacts in the Baño de Oro Natural Area.

rigorously to determine species distributions, but rather is to be used as a guide. In general, the first 30 species ranging from *Pterocarpus officinalis* through *Alchornea latifolia* are principally tabonuco forest species. The 12 species from *Haenianthus salicifolius* through *Ternstroemia luquillensis* are mainly dwarf forest species. The remaining 27 species in between are principally colorado forest species, or are well distributed throughout the Baño de Oro.

Among the larger shade tolerant species, *Prestoea montana*, *Micropholis garciniaefolia*, and *Calyco-gonium squamulosum* are well distributed in all three forest types. *Cecropia peltata*, a shade-intolerant species, is also well distributed. Among the smaller tree species, *Ocotea leucoxylon* and *Psychotria berteriana* are found throughout the area. *Ocotea spathulata* and *Tabebuia rigida*, shade-tolerant species normally confined to the upper two forest types, are also present in the tabonuco forest. This is probably due to the high rainfall that characterizes the Baño de Oro.

Information borrowed from several other LEF studies outside of the Baño de Oro provides insights regarding changes in forest structure and dynamics over the gradient from the 150-m LEF border to the 1,050-m mountain summits. Future studies may confirm similar relationships within the Baño de Oro.

Structurally, the number of trees per unit area and the soil organic matter content increase with elevation (table 9). In contrast, specific leaf area, canopy height, typical d.b.h. range, forest volume and biomass, leaf area index, and species richness all decrease with an increase in elevation.

Forest dynamics also show changes with elevation (table 10) (Weaver and Murphy 1990). Mortality rates in palm and tabonuco forests measured over 30 years exceeded ingrowth, while in the colorado forest mortality rates measured over 35 years were equal to ingrowth. These differences may be due to more rapid growth and competition among stems in the lower forests. Loose litter tends to increase with elevation except in the dwarf forest. In contrast, litterfall decreases with elevation except in the palm forest (Frangi and Lugo 1985). Litter turnover rate also decreases with elevation. Standing herbivory and herbivory rate records are incomplete and thus difficult to compare. It appears, however, that both decrease with an increase in elevation. Diameter, volume, and biomass increment all decrease with elevation as does aboveground net primary productivity.

The structural and floristic impoverishment of forests with an increase in elevation on small, wet, tropical mountains, such as the isolated, coastal mountains in the West Indies, has been attributed to the Masenerhebung effect, a phenomenon first recorded in the European Alps. Many investigators have proposed ideas to account for this phenomenon in Puerto Rico and elsewhere, among them, saturated soils and reduced root respiration (Holdridge 1967), impeded soil drainage (Wadsworth and Bonnet 1951), high winds in summit areas, leaching of the soils combined with high fog incidence (Baynton 1969), reduced transpiration rates (Beard 1944, Leigh 1975, Odum 1968), and fog, high soil water content, and reduced mineralization of organic matter (Grubb 1971).

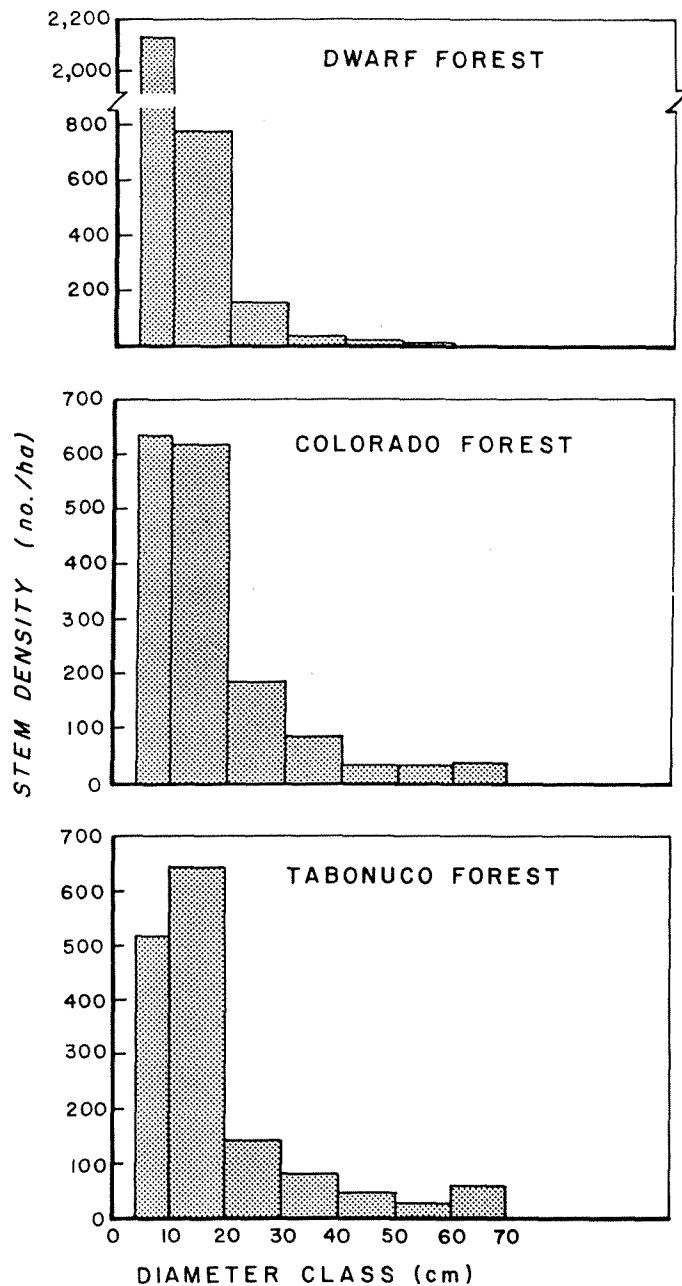


Figure 13.—Diameter class distributions of trees on closed canopy 50-by-10-m plots in the tabonuco, colorado, and dwarf forests of the Baño de Oro Natural Area.

**Current Research Activities**

**Long-Term Monitoring on TR-1.**—Known forestry research activities began in the Baño de Oro with the 1937 timber cruise. The cruise records were used to characterize species composition and forest structure and are still available at the International Institute of Tropical Forestry.

Beginning in the mid-1940's, only a decade after the passage of Hurricane San Cipriano directly over the

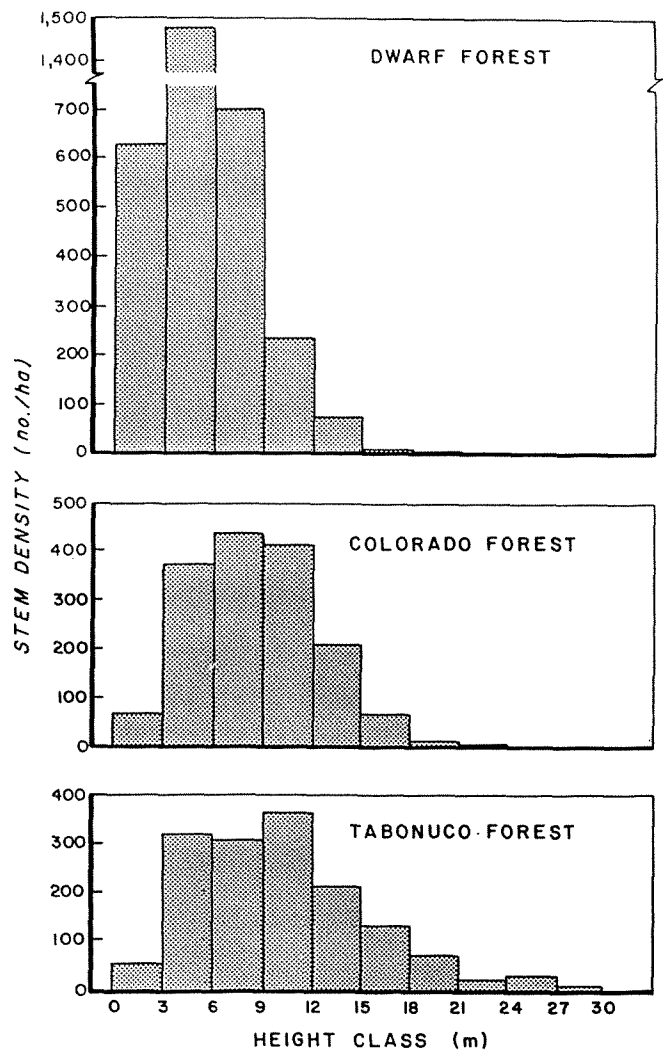


Figure 14.—Height class distributions of trees on closed canopy 50-by-10-m temporary plots in the tabonuco, colorado, and dwarf forests of the Baño de Oro Natural Area.

LEF, several permanent plots were established throughout the forest to determine species compositions and diameter growth rates (Crow 1980, Lugo and Brown 1981, Wadsworth 1950a, Weaver 1983). One of these, TR-1, is located at a 350-m elevation in the northern part of the Baño de Oro. The 0.4-ha plot is centered on a ridge and contains tree species characteristic of the tabonuco, colorado, and dwarf forests. First sampled in 1946, the plot was remeasured in 1951, 1956, 1966, 1977, and again in 1988 and 1990, just before and immediately after the passage of Hurricane Hugo in September 1989. With the passage of time, the plot record has become a valuable chronology of changes in species composition, forest structure, and dynamics in response to Hurricane San Cipriano of 1932 (table 11) (Weaver 1983).

Table 8.—Occurrence of tree species in the Baño de Oro Natural Area by elevation, topography, and forest type.\* Species are ranked from those most common at lower elevation to those most common at higher elevation

Species	Elevation (Meters)										Total		Percent by topography			Percent by forest type†		
	350	450	550	600	650	700	750	850	950	1050	No.	Percent	Valley	Slope	Ridge	Tabonuco	Colorado	Dwarf
<i>Pterocarpus officinalis</i>	1										1		100		100			
<i>Andira inermis</i>	1										1		100				100	
<i>Guatteria caribaea</i>	1										1			100		100		
<i>Ixora ferrea</i>	1										1				100	100		
<i>Laplacea portoricensis</i>	2										2	0.1			100	100		
<i>Phyllanthus nobilis</i>	1										1				100	100		
<i>Buchenavia capitata</i>	1										1				100	100		
<i>Rneedia portoricensis</i>	2										2	0.1			100	100		
<i>Mecranium amygdalinum</i>	1										1				100	100		
<i>Hirtella rugosa</i>	6										6	0.2			100	100		
<i>Inga laurina</i>	8										8	0.3	12	62	26	100		
<i>Manilkara bidentata</i>	13										13	0.4		77	23	100		
<i>Meliosma herbertii</i>	2										2	0.1			100	100		
<i>Cassipourea guianensis</i>	2										2	0.1		50	50	100		
<i>Guarea guidonia</i>	1	2									3	0.1	100			100		
<i>G. ramiflora</i>	1	1									2	0.1		50	50	100		
<i>Antirhea obtusifolia</i>	2	1									3	0.1		67	33	100		
<i>Tabebuia heterophylla</i>	3	1									4	0.1	25		75	100		
<i>Homalium racemosum</i>	2	1									3	0.1	67		33	100		
<i>Drypetes glauca</i>	3	3									6	0.2		83	17	100		
<i>Menendezia urbanii</i>	10	7									17	0.6	18	35	47	100		
<i>Cordia sulcata</i>		1									1		100			100		
<i>Myrcia deflexa</i>		1									1		100			100		
<i>Ocotea moschata</i>		1									1		100			100		
<i>Eugenia stahlia</i>		1									1				100	100		
<i>Palicourea riparia</i>		1									1				100	100		
<i>Sloanea berteriana</i>	26	1		1							28	0.9	65	21	14	97	3	
<i>Dacryodes excelsa</i>	25			2							27	0.9		45	55	93	7	
<i>Didymopanax morototoni</i>	6		1	1							8	0.3			100	88	12	
<i>Alchornea latifolia</i>	3			1	1						5	0.2		17	83	60	40	
<i>Miconia tetrandra</i>		5								1	6	0.2	33	50	17	83	17	
<i>Daphnopsis philippiana</i>		45	5	11	6	12	26		1		106	3.5	19	44	37	47	52	1
<i>Croton poecilanthus</i>		22	17	7	14	27	15				102	3.4	80	13	7	38	62	
<i>Ditta myricoides</i>		1	1	1	2	1					6	0.2	17	50	33	33	67	
<i>Cyrilla racemiflora</i>		13	23	19	15	14	30				114	3.8	6	39	55	32	68	
<i>Sapium laurocerasus</i>		1				1					2	0.1	50	50		50	50	
<i>Rondeletia portoricensis</i>		1					1				2	0.1	50	50		50	50	
<i>Magnolia splendens</i>	1	2	4	5	7	7	11				37	1.2	8	30	62	19	81	
<i>Cordia borinquensis</i>	2	8	7	2	17	12	5	1			54	1.8	31	54	15	31	67	2
<i>Prestoea montana</i>	28	87	51	51	48	17	24	35	11		352	11.7	65	21	14	47	40	13

Table 8.—Occurrence of tree species in the Baño de Oro Natural Area by elevation, topography, and forest type.\* Species are ranked from those most common at lower elevation to those most common at higher elevation—Continued.

Species	Elevation (Meters)										Total		Percent by topography			Percent by forest type†			
	350	450	550	600	650	700	750	850	950	1050	No.	Percent	Valley	Slope	Ridge	Tabonuco	Colorado	Dwarf	
	----- Number of stems -----																		
<i>Ocotea leucoxydon</i>	1	4	3		1	4	2	3	1		19	0.6	37	10	53	42	37	21	
<i>Cecropia peltata</i>	1	1			3	2		4	1		12	0.4	84	8	8	17	42	41	
<i>Citharexylum caudatum</i>					1						1		100				100		
<i>Miconia laevigata</i>						4					4	0.1		100			100		
<i>Eugenia eggersii</i>							1				1				100		100		
<i>Xylosma schuaneckeanum</i>						1	1				2	0.1	50		50		100		
<i>Miconia prasina</i>						1					1			100			100		
<i>Torrabasia cuneifolia</i>				1	1	3	3				8	0.3		12	88		100		
<i>Ardisia luquillensis</i>						2	2				4	0.1		25	75		100		
<i>Micropholis garciniaefolia</i>	2	40	37	32	30	48	82	4	20	30	325	10.8	10	42	48	24	59	17	
<i>Psychotria berteriana</i>		3	2	1	1	1	4	10	5		27	0.9	26	30	44	19	26	55	
<i>Clusia krugiana</i>		3	4	1	2	7	16	3	10	6	52	1.7	31	23	46	13	51	36	
<i>Calyconium squamulosum</i>	6	26			2	27	11	98	15	10	195	6.4	29	38	33	16	21	63	
<i>Hedyosmum arborescens</i>			1				4			2	7	0.2	29		71	14	58	28	
<i>Byrsonima wadsworthii</i>	1			4	8	2	6				21	0.7	14	38	48	5	95		
<i>Myrcia fallax</i>				1	1	5	2	5			14	0.5	7	28	65		64	36	
<i>Miconia pachyphylla</i>						3				2	5	0.2		60	40		60	40	
<i>Haenianthus salicifolius</i>	1		2	5	7	10		40	1	2	68	2.2	10	62	28	4	33	63	
<i>Marliera sintenisii</i>						3		5			8	0.3		25	75		38	62	
<i>Tabebuia rigida</i>		19	14	8	13	16	32	16	75	210	403	13.4	7	42	51	8	17	75	
<i>Grammadenia sintenisii</i>						1			1		2	0.1		50	50		50	50	
<i>Ocotea spathulata</i>	4	3	12	13	18	34	29	32	101	216	462	15.3	11	37	52	4	20	76	
<i>Cyathea arborea</i>						1				1	2	0.1		50	50		50	50	
<i>Ilex sideroxyloides</i>			1							8	9	0.3		11	89	11		89	
<i>Eugenia borinquensis</i>			1		1			12	36	86	136	4.5	19	35	46	1	1	98	
<i>Calyptranthes krugii</i>								5	3	28	36	1.2	17	53	30			100	
<i>Alsophila bryophila</i>								8	126	122	256	8.5	30	60	10			100	
<i>Miconia sintenisii</i>									2		2	0.1	100					100	
<i>Ternstroemia luquillensis</i>										4	4	0.1			100			100	
Number of stems	171	306	186	167	199	266	308	281	410	726	3020	100.0							
Number of stems/ha	1140	2040	1240	1113	1327	1773	2053	1873	2733	4840	3227								
Number of species	35	31	18	20	22	28	22	16	17	13	70								
Species per forest	(-----53-----)			(-----38-----)				(-----24-----)											

\*Survey conducted on 30 temporary plots 50 by 10 m in size.

†Forest types: tabonuco, 350 to 500 m; colorado, 600 to 750 m; and dwarf 850 to 1050 m. Percentages refer to proportions of species found on each topographic position or forest type.

Table 9.—Comparison of stand structure for four forests within the Luquillo Mountains\*

Structural characteristics	Forest type			
	Tabonuco	Palm	Colorado	Dwarf
Trees/ha	1750 <sup>†</sup>	1620 <sup>†</sup> (3050) <sup>‡</sup>	1850	21,900 <sup>†</sup>
Canopy height (m)	20–30	17	8–20	3–5
Typical d.b.h. range (cm)	4–50	4–30	4–30	4–15
Basal area (m <sup>2</sup> /ha)	40–45 <sup>†</sup>	30 <sup>†</sup> (42) <sup>‡</sup>	40	45–65 <sup>†</sup>
Aboveground volume (m <sup>3</sup> /ha)	350 <sup>†</sup>	210 <sup>†</sup>	220	120
Aboveground woody biomass (t/ha)	190	174 <sup>‡</sup>	130	80
Leaf biomass (t/ha)	7.9	25.1 <sup>‡</sup>	5.8	2.9
Leaf area index (m <sup>2</sup> /m <sup>2</sup> )	6–7	3.3 <sup>‡</sup>	3–5	2–3.5
Specific leaf area (cm <sup>2</sup> /g)	127	..... <sup>§</sup>	91	47
Standing herbivory (percent)	7	.....	5	.....
Total tree species	170	50	90	40
Tree species/ha	50	30	40	15
Soil organic matter (t/ha)	155 <sup>¶</sup>	316 <sup>**</sup>	328 <sup>††</sup>	550

\*Benedict 1976; Crow 1980; Frangi and Lugo 1985; Medina and others 1981; Odum 1970; Odum and Ruiz-Reyes 1970; Ovington and Olson 1970; Wadsworth 1950a; Weaver 1972a, 1983; Weaver and Murphy 1990.

<sup>†</sup>All trees ≥ 4 cm in diameter.

<sup>‡</sup>All trees ≥ 1 cm in diameter.

<sup>§</sup>Blank fields indicate missing data.

<sup>¶</sup>Top 25 cm of soil.

<sup>\*\*</sup>Top 100 cm of soil.

<sup>††</sup>Top 50 cm of soil.

Table 10.—Comparison of stand dynamics for four forests within the Luquillo Mountains\*

Dynamic feature	Forest type <sup>†</sup>			
	Tabonuco	Palm	Colorado	Dwarf
Ingrowth (stems/ha/yr)	21	12	20	..... <sup>‡</sup>
Mortality (stems/ha/yr)	32	23	20	.....
Litterfall (t/ha/yr)	8.61	8.8	6.8	3.1
Leaf	4.94	6.26	5.05	2.45
Wood	1.38	0.86	1.22	.....
Flower	0.17	0.18		
Fruit	0.34	1.14	(0.23) <sup>§</sup>	(0.65) <sup>§</sup>
Miscellaneous	1.78	0.36	0.30	.....
Loose litter (t/ha)	6.0	5.4	8.76	4.34
Herbivory rate (t/ha/yr)	0.38	.....	0.25	0.13
Litter turnover rate	1.20	1.62	0.78	0.70
Mean d.b.h. growth (cm/yr)	0.15	0.23	0.10	0.03
Total aboveground growth				
Woody volume (m <sup>3</sup> /ha/yr)	2.26	.....	0.93	0.70
Woody biomass (t/ha/yr)	2.5	3.3	0.57	0.45
Total aboveground net primary productivity (r/ha/yr)	10.5	19.5	7.66	3.70

\*Adapted from: Benedict 1976; Briscoe and Wadsworth 1970; Frangi and Lugo 1985; Odum 1970; Reagan and others 1982; Wadsworth 1951, 1952; Weaver 1983; Weaver and Murphy 1990; Weaver and others 1986.

<sup>†</sup>Plot elevations: tabonuco, 450 m; palm, 750 m; colorado 750 m; and dwarf 1,000 m.

<sup>‡</sup>Blank fields indicate missing data.

<sup>§</sup>Flowers and fruits combined.

Table 11. — Stand table-ranking of species by density and basal area (BA) dominance on permanent plot TR-1 from 1946 through 1976 on a hectare basis

Species	1946		Ingrowth 1946-76		Mortality	1976	
	No. of stems	BA	No. of stems	BA	No. of stems	No. of stems	BA
		Meters		Meters			Meters
<i>Dacryodes excelsa</i>	215	20.93	5	0.01	30	190	24.30
<i>Melastomataceae</i> spp.	208	1.04	....*	....	120	88	1.80
<i>Prestonea montana</i>	195	3.36	28	.37	40	183	3.30
<i>Micropholis garciniaefolia</i>	120	3.22	2	.00	27	95	2.90
<i>Octoea moschata</i>	105	1.14	10	.01	55	60	.64
<i>Calycogonium squamulosum</i>	95	.50	5	.01	45	55	.40
<i>Sloanea berteriana</i>	82	1.00	10	.03	40	52	.31
<i>Didymopanax morototoni</i>	75	.75	....	....	20	55	2.10
<i>Cordia borinquensis</i>	70	.21	5	.01	55	20	.07
<i>Hirtella rugosa</i>	62	.25	22	.04	13	71	.30
<i>Psychotria berteriana</i>	60	.12	....	....	60	....	....
<i>Cordia sulcata</i>	52	.19	....	....	34	18	.12
<i>Laplacea portoricensis</i>	50	.32	....	....	38	12	.13
<i>Cecropia peltata</i>	48	.45	....	....	38	10	.36
<i>Meliosma herbertii</i>	32	.27	12	.02	4	40	.37
<i>Inga laurina</i>	28	.31	....	....	13	15	.44
<i>Alchornea latifolia</i>	28	.30	....	....	12	16	.60
<i>Magnolia splendena</i>	25	2.51	....	....	12	13	2.60
<i>Rheedia portoricensis</i>	25	.10	15	.02	2	38	.11
<i>Manilkara bidentata</i>	25	.08	2	.00	2	25	.18
<i>Tabebuia heterophylla</i>	22	.11	5	.01	14	13	.09
<i>Matayba domingensis</i>	18	.20	....	....	....	18	.77
<i>Cyrilla racemiflora</i>	15	2.91	....	....	4	11	3.10
<i>Buchenavia capitata</i>	12	1.30	....	....	2	10	2.50
<i>Homalium racemosum</i>	12	.44	....	....	....	12	.87
<i>Cyathea arborea</i>	10	.07	....	....	10	....	....
<i>Eugenia borinquensis</i>	8	.40	....	....	....	8	.50
<i>Byrsonima wadsworthii</i>	8	.35	....	....	....	8	.40
<i>Andira inermis</i>	8	.09	....	....	3	5	.10
<i>Tetragastris balsamifera</i>	8	.03	....	....	....	8	.07
<i>Myrcia splendens</i>	8	.02	....	....	8	....	....
<i>Hedyosmum arborescens</i>	8	.01	....	....	8	....	....
<i>Alchorneopsis portoricensis</i>	5	.10	....	....	....	5	.45
<i>Casearia sylvestris</i>	5	.01	2	.00	5	2	.00
<i>Daphnopsis philippiana</i>	5	.01	2	.00	5	2	.00
<i>Beilschmiedia pendula</i>	2	.37	....	....	....	2	1.00
<i>Guatteria caribaea</i>	2	0.16	....	....	....	2	0.18
<i>Solanum rugosum</i>	2	.02	....	....	2	....	....
<i>Croton poecilanthus</i>	2	.01	....	....	....	2	.03
<i>Byrsonima coriacea</i>	2	.01	....	....	....	2	.02
<i>Sapium laurocerasus</i>	2	.01	....	....	2	....	....
<i>Phyllanthus nobilis</i>	2	.01	....	....	....	2	.00
<i>Myrcia deflexa</i>	2	.00	....	....	2	....	....
<i>Quararibaea turbinata</i>	2	.00	2	0.00	....	4	.01
<i>Guarea ramiflora</i>	2	.00	....	....	....	2	.00
<i>Ocotea leucoxylon</i>	2	.00	....	....	2	....	....
<i>Byrsonima coriacea</i>	2	.00	....	....	2	....	....
<i>Antirhea obtusifolia</i>	2	.00	....	....	....	2	.00
<i>Oxandra laurifolia</i>	....	....	8	.01	....	8	.01
<i>Guarea guidonia</i>	....	....	2	.00	....	2	.00
Unknown	....	....	2	.00	....	2	.00
Mean total	1778	43.69	139	0.54	729	1188	51.13

\*Blank fields indicate missing data.

The 30-year partial record shows stand composition in 1946 and 1976. Mortality exceeded ingrowth, and the number of stems decreased considerably over the period of measurement. Small secondary trees such as the *Melastomataceae* and *Psychotria berteriana* disappeared completely. Larger secondary species such as *Cecropia peltata* and *Didymopanax morototoni*, and several *Melastomataceae*, decreased considerably in numbers. Table 12 shows a 30-year record of diameter growth by species for all stems that survived the period. A gradual slowing of growth is apparent as the trees age and the stand closes during recovery.

Diameter class distributions also indicate changes over time (fig. 15). Stems in the smallest two d.b.h. classes, between 4.1 and 19.9 cm, decreased by 58 percent and 21 percent, respectively, between 1946 and 1988. In contrast, the stems in the next two largest d.b.h. classes, between 20.0 and 39.9 cm, increased 23 percent and 57 percent, respectively. Fluctuations in classes  $\geq 40$  cm are less evident. These structural changes reflect growth after the 1932 hurricane. After Hurricane Hugo, the number of stems decreased in all diameter classes, most notably in those between 4.1 and 19.9 cm (fig. 15).

Table 12. — Mean annual d.b.h. increment by species from 1946 through 1976 on permanent plot TR-1 for all trees that survived the entire period and range of d.b.h. by species in 1946

Species	Mean annual diameter increment					CV*	No. of stems	D.b.h. range 1946
	1946–51	1951–56	1956–66	1966–76	1946–76			
	Centimeters/year					Percent†		Centimeters
<i>Dacryodes excelsa</i>	0.22	0.13	0.14	0.16	0.16	87	74	4–96
<i>Melastomataceae</i> spp.	.31	.22	.24	.14	.21	69	35	4–25
<i>Prestoea montana</i>	.03	.01	.02	.02	.01	175	62	10–20
<i>Micropholis garciniaefolia</i>	.11	.02	.06	.04	.05	98	37	6–37
<i>Ocotea moschata</i>	.14	.07	.08	.05	.08	67	19	4–28
<i>Calycogonium squamulosum</i>	.10	.05	.08	.03	.06	110	20	4–22
<i>Sloanea berteriana</i>	.10	.08	.12	.06	.09	84	17	4–9
<i>Didymopanax morototoni</i>	.62	.42	.28	.12	.31	64	22	5–22
<i>Cordia borinquensis</i>	.02	.00	.02	.02	.01	118	6	4–10
<i>Hirtella rugosa</i>	.03	.02	.03	.02	.02	98	20	4–13
<i>Cordia sulcata</i>	.06	.02	.05	.04	.04	130	7	4–11
<i>Laplacea portoricensis</i>	.24	.09	.12	.08	.11	90	5	4–12
<i>Cecropia peltata</i>	.80	.25	.38	.15	.35	16	4	6–15
<i>Meliosma herbertii</i>	.10	.06	.09	.04	.07	100	11	4–23
<i>Inga laurina</i>	.15	.15	.22	.10	.14	92	6	6–21
<i>Alchornea latifolia</i>	.49	.29	.24	.03	.21	99	6	7–19
<i>Magnolia splendens</i>	.10	.12	.05	.08	.07	73	5	7–67
<i>Rhedia portoricensis</i>	.03	.00	.03	.02	.02	140	9	4–9
<i>Manilkara bidentata</i>	.12	.08	.15	.08	.10	54	9	5–9
<i>Tabebuia heterophylla</i>	.02	.02	.01	.05	.02	107	3	5–15
<i>Matayba domingensis</i>	.50	.38	.42	.25	.36	36	7	5–20
<i>Cyrilla racemiflora</i>	.22	.21	.18	.18	.19	64	4	39–74
<i>Buchenavia capitata</i>	.79	.62	.45	.38	.51	34	4	27–56
<i>Homalium racemosum</i>	.38	.21	.32	.16	.25	84	5	8–37
<i>Eugenia borinquensis</i>	.12	.08	.15	.02	.09	87	3	23–29
<i>Byrsonima wadsworthii</i>	.02	.02	.10	.02	.04	58	3	11–34
<i>Andira inermis</i>	.15	.02	.10	.05	.08	24	2	12–15
<i>Tetragastris balsamifera</i>	.07	.02	.07	.20	.11	42	3	5–12
<i>Alchorneopsis portoricensis</i>	.85	.65	.80	.35	.61	7	2	7–21
<i>Beilschmiedia pendula</i>	.60	.80	.58	1.43	.92	....	1	43
<i>Guatteria caribaea</i>	.05	.10	.12	.00	.06	....	1	28
<i>Croton poecilanthus</i>	.10	.10	.22	.16	.16	....	1	7
<i>Byrsonima coriacea</i>	.15	.00	.15	.10	.10	....	1	7
<i>Phyllanthus nobilis</i>	.05	.05	.02	.08	.05	....	1	6
<i>Quararibaea turbinata</i>	.05	.05	.00	.00	.02	....	1	5
<i>Guarea ramiflora</i>	.00	.00	.02	.00	.01	....	1	5
<i>Antirhea obtusifolia</i>	.05	.00	.02	.02	.02	....	1	4
Mean/Total‡	0.125 0.134	0.075 0.085	0.085 0.095	0.058 0.065	0.080 0.088	.... 138	418 356	4–96 4–96

\*CV = coefficient of variation.

†Blank fields indicate missing data.

‡Top row includes plam *Prestoea montana*; bottom row excludes palm.

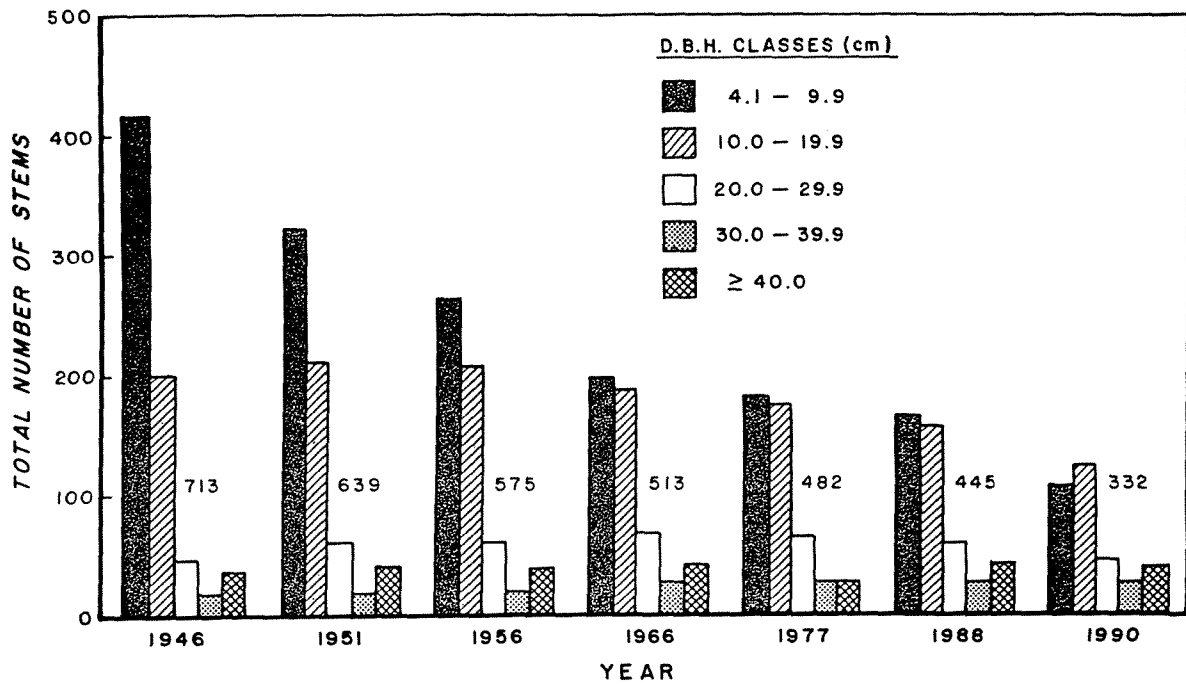


Figure 15.— Diameter class distributions in 7 different years on long-term plot TR-1 in the Baño de Oro Natural Area. The numbers in the declining sequence from 713 to 332 refer to total stems in the plot.

**Phenology Trail.**— A trail was established through the east fork of the Rio Mameyes in February 1987 to monitor the phenology of colorado forest vegetation. Ninety-eight individual plants were originally selected: 14 were *Marcgravia sintinisii* or *Clusia gundlachi*, common forest vines, and 84 were of 15 tree species with d.b.h.'s between 4.3 and 110.0 cm (table 13).

Monitoring is done twice monthly. The quantity of flowers, leaves, and fruits, each rated from 1 through 4, are recorded for each plant. Fruit size and ripeness are also noted, as are the number of individuals of each bird species found using the plants. Unfortunately, several plants were damaged by Hurricane Hugo. These should be replaced to maintain the initial representation of plants.

**Ring Formation in *Cyrilla Racemiflora*.**— A study was initiated in January 1989 to determine the nature of ring formation in *Cyrilla racemiflora*. One of the four sites selected for the study borders the Baño de Oro. Among the parameters being monitored at the Baño de Oro site are rainfall, temperature, branch elongation, flowering and fruiting, leaf formation and leaf drop, xylem water potential, and xylem cell formation. The study spanned one dry season extending from January to late June 1989, with further monitoring in October and December 1989 and in June 1990. As sampling continues and the patterns observed in the first year are tested against future growth, the periodicity of growth ring formation should become clearer.

In December 1990, the study was expanded to include trees on a permanent plot that had been disturbed by Hurricane San Cipriano in 1932 and thinned in 1946. Increment borings and ring counts of trees on sites with known past disturbance will be used as an additional test of the hypothesis that the number of rings is indicative of tree age in *Cyrilla*. Simultaneous monitoring of carbon dioxide exchange of *Cyrilla* leaves along with that of xylem water potential is being done to clarify the relationship between these parameters.

**Minority Research Program.**— Eight separate experiments aimed at determining the influences of climate, soil fertility, and genome on plant productivity are being conducted in the dwarf forest near the border of the Baño de Oro (fig. 2). The research consists of: tree growth in fertilized versus control plots, understory responses to fertilization, fine root biomass and production observations, litterfall and litter chemistry, nutrient cycling via throughfall, nitrogen mineralization and nitrification, wind damage to forest trees, and a transplant experiment.

The tree growth in fertilized versus control plots was originally designed to evaluate the effect of nutrient availability (N-P-K plus micronutrients) on forest productivity such as diameter increment, twig growth, and new leaf development. Given that Hurricane Hugo damaged the plots, the experiment now deals with a forest recovering from disturbance rather than with a mature forest. The revised experimental design places



Table 13. — Species included in the phenological study in the East Fork watershed of the Rio Mameyes

Species	Number of individuals	D.b.h.*	
		Minimum	Maximum
		----- Centimeters -----	
<i>Calycogonium squamulosum</i>	1	12.0	12.0
<i>Clusia gundlachii</i> <sup>†</sup>	2	....	....
<i>Dacryodes excelsa</i>	10	26.0	85.0
<i>Eugenia stahlii</i>	2	24.0	25.0
<i>Haenianthis salicifolius</i>	5	8.0	55.0
<i>Inga laurina</i>	5	16.0	75.0
<i>Laplacea portoricensis</i>	1	13.0	13.0
<i>Magnolia splendens</i>	10	41.0	85.0
<i>Marcgravia sintenisii</i> <sup>†</sup>	12	....	....
<i>Matayba domengensis</i>	5	34.0	43.0
<i>Micropholis garciniaefolia</i>	11	22.0	55.0
<i>Ocotea portoricensis</i>	1	18.0	18.0
<i>O. spathulata</i>	3	19.0	40.0
<i>Prestoea montana</i>	10	11.5	19.0
<i>Psychotrai berteriana</i>	1	4.3	4.3
<i>Rheedia portoricensis</i>	8	5.0	14.0
<i>Sloanea berteriana</i>	11	15.0	110.0
Total	98		

\*Blank fields indicate missing data.

<sup>†</sup>Vines; all remaining species are trees.

greater emphasis on indices of productivity such as canopy recovery (leaf area index), sprouting, and recruitment and growth of seedling and saplings.

Understory responses to fertilization are being assessed on treatment and control quadrats located within the fertilized and control plots. Vegetation cover, height, and basal diameters of marked tree seedlings are being measured every 6 months.

Fine root biomass and production are being observed on the treatment and control plots. Six cores are sequentially taken in the upper 10 cm of mineral soil and litter layers on each plot at 2-month intervals. Changes in the live and dead fine root mass between sampling dates are used to determine root production, mortality, and decomposition in each experimental plot.

Litterfall and litter chemistry are being examined to determine the influence of nutrient availability on the production of canopy litter, its nutrient concentrations, and the efficiency of nutrient use. Litter derived as a result of the hurricane is also being examined in the same manner. Litter baskets are sampled every 2 weeks, and the collections are sorted into fractions and analyzed for nutrients. Fresh leaf samples of a common dwarf forest tree, *Tabebuia rigida*, are simultaneously collected on each plot.

Nutrient cycling via throughfall is being assessed by using 3-day sampling periods twice monthly on the treatment and control plots. Nitrogen mineralization and nitrification are being estimated by in situ incubation of intact soil cores every 6 months.

Wind damage to trees is being assessed on forest plots established before Hurricane Hugo to answer four questions: (1) Can damage be predicted by either abiotic factors (for example, aspect) or biotic factors (for example, tree diameter)? (2) Is initial tree recovery related to damage? (3) Do tree species recover from damage at different rates? (4) Does the forest recover via species turnover and succession or via direct regeneration of canopy species?

The transplant experiment is designed to explore two questions: (1) Are there genetic differences in growth characteristics between populations of tropical plant species growing at low and high elevations? (2) Does wind affect the growth of plants in the dwarf forest? Reciprocal transplants of clones of key forest species are used to detect genetically determined differences in productivity between seedlings in the dwarf forest and those at lower elevations in the LEF. The effect of wind on productivity in the dwarf forest is being examined by comparing growth in plots protected by barriers versus growth in exposed plots.

**Water Chemistry.** — Weekly sampling of streamflow was initiated just above the USGS (U.S. Geological Survey) gauge at Puente Roto in May 1989 as part of the long-term ecological research in the LEF. The purpose of the study is twofold: first, to quantify dissolved and fine particulate exports from the Rio Mameyes watershed, which includes the Bisley experimental watersheds, and drainage from the Baño de Oro; and second, to determine the effects of watershed scale on exports by comparing the Puente Roto data with those

from smaller watersheds in the same basin. The dissolved chemistry parameters being measured are: pH, ortho-PO<sub>4</sub>, NO<sub>3</sub><sup>-</sup>, NH<sub>4</sub><sup>+</sup>, organic C, organic N, Cl<sup>-</sup>, SO<sub>4</sub><sup>-2</sup>, SiO<sub>2</sub>, Na<sup>+</sup>, K<sup>+</sup>, Ca<sup>+2</sup>, and Mg<sup>+2</sup>. Particulate measures include N, C, and total sediments. Observations will continue for several years.

### FAUNA

From August 31, 1984, through February 8, 1985, a general survey of animal species was conducted in the Baño de Oro by the University of Puerto Rico Biology Department. The purpose was to determine the diversity and distribution of the fauna in each of the four forest types and in the streams. Samples were collected in each of the four forest types and from the streams flowing out of the upper reaches of the Rio Mameyes. The results, based on observations made at 13 sampling stations (fig. 2), are shown in tables 14 and 15.

### Vertebrates

One species of fish was observed but not identified. This was probably the green stream goby (*Sicydium plumieri*), a diadromous fish reported to be in the headwaters of the Rio Mameyes (Erdman 1986, Wiley and Bauer 1985). The goby is common in streams of the West Indies (Erdman 1961).

Eleven of the 14 amphibians reported for the LEF (Brown and others 1983) were collected. These included 1 toad and 10 endemic frogs of the genus *Eleutherodactylus*. Of the 13 reptiles identified, 2 were geckos, 8 were lizards (mainly of the genus *Anolis*), and 3 were snakes. *Epicrates inornatus*, the Puerto Rican boa, is classified as a rare and endangered species.

Twenty-one of the 66 species of birds on the LEF checklist (Wiley and Bauer 1985) were observed during the survey. Other species reported by qualified personnel have been added to the list (table 15). Two introduced mammals, the mongoose and the black rat, were

Table 14.—Animal species recorded in the Baño de Oro Natural Area (except bird species)

Classification	Endemic*	Habitat type†				
		T	C	P	D	W
Phylum Platyhelminthes						
Class Turbellaria						
Order Tricladida						
Family Geoplanidae						
1. <i>Geoplana</i> sp.						X
Phylum Nematoda						
Class Adenophorea (Aphasmidea)						
Order Dorylaimida						
Family Dorylaimidae						
1. <i>Dorylaimus</i> sp.						X
Class Secernentea (Phasmidea)						
Order Tylenchida						
Family Aphelenchoididae						
2. <i>Aphelenchoides</i> sp.						X
Family Heteroderidae						
3. <i>Meloidogyne</i> sp.						X
Phylum Annelida						
Class Oligochaeta						
Order Haplotaxida						
1. Haplotoxid sp. 1 (giant form)		X				
2. Haplotoxid sp. 2 (violet form)		X	X	X		
3. Haplotoxid sp. 3. (white form)			X			
Class Hirudinea						
Order (?)						
Family (?)						
4. Hirudinid sp. 1. (terrestrial form)						X
Phylum Mollusca						
Class of Gastropoda						
Subclass Prosobranchia						
Order Archaeogastropoda						
Family Helicinidae						
1. <i>Alcadiata alta</i>	O			X		
2. <i>A. striata</i>	O	X	X	X	X	

Table 14.—Animal species recorded in the Baño de Oro Natural Area (except bird species)—Continued

Classification	Endemic*	Habitat type†				
		T	C	P	D	W
Order Mesogastropoda						
Family Cyclophoridae						
3. <i>Megalomastoma croceum</i>	0	X	X			
4. <i>M. verruculosum</i>	0					
Family Pomatiidae						
5. <i>Chondropoma yunkei</i>	0					
Subclass Pulmonata						
Order Stylommatophora						
Family Bulimulidae						
6. <i>Gaeotis nigrolineata</i>	0		X			X
Family Camaenidae						
7. <i>Caracolus caracolla</i>	0	X	X	X	X	
8. <i>Polydotes acutangula</i>	0	X		X		
9. <i>P. luquillensis</i>	0	X	X	X	X	
Family Clausiliidae						
10. <i>Nenia tridens</i>	0	X	X	X		
Family Haplotremidae						
11. <i>Austrosolenites alticola</i>	0	X		X	X	
Family Oleacinidae						
12. <i>Oleacina glabra</i>	0					X
13. <i>O. playa</i>	0					X
14. <i>Varicella portoricensis</i>	0	X				
Family Sagdidae						
15. <i>Platysuccinea portoricensis</i>	0		X			X
16. <i>Succinea hyalina</i>	0					X
Family Subulinidae						
17. <i>Obeliscus terebraster</i>		X		X		
Order Systellommatophora						
Family Veronicellidae						
18. <i>Vaginulus plebleius</i>				X		
Phylum Onychophora						
Family Peripatidae						
1. <i>Peripatus juanensis</i>	0	X	X			
Phylum Arthropoda						
Subphylum Chelicerata						
Class Arachnida						
Order Amblypygi						
Family Phrynidae						
1. <i>Phrynus longipes</i>	0	X				
Order Araneae						
Suborder Orthognatha						
Family Barychelidae						
2. <i>Psalistops corozali</i>	0	X	X	X		
Family Dipluridae						
3. <i>Accola spinosa</i>	0	X	X	X	X	
Family Theraphosidae						
4. <i>Avicularia laeta</i>	0		X			X
5. <i>Cyrtopholis portoricae</i>	0					X
6. <i>Ischnocolus culebrae</i>	0		X	X	X	
7. <i>Stichoplastus culebrae</i>	0	X				
Suborder Labidognatha						
Division Cribellata						
Family Uloboridae						
8. <i>Miagrammopes ciliatus</i>	0	X	X	X	X	
9. <i>M. molitus</i>	0	X				
Division Acribellata						
Family Anyphaenidae						
10. <i>Wulfila tropica</i>	0	X	X	X		
11. <i>W. macropalpus</i>	0	X		X		
Family Araneidae						
Subfamily Gasteracanthinae						
12. <i>Gasteracantha tetracantha</i>	0	X		X	X	

Table 14.—Animal species recorded in the Baño de Oro Natural Area (except bird species)—Continued

Classification	Endemic*	Habitat type†				
		T	C	P	D	W
Subfamily Araneinoe						
13. <i>Edricus crassicauda</i>		X				X
Subfamily Metinae						
14. <i>Leucage regni</i>	O	X	X	X		
15. <i>L. venusta</i>		X	X			
16. <i>Pseudometa hameta</i>		X		X		
Family Clubionidae						
17. <i>Corinna jayuyae</i>	O		X			X
18. <i>C. abnormis</i>	O		X			
Family Ctenidae						
19. <i>Oligoctenus ottleyi</i>	O			X		
Family Pholcidae						
20. <i>Modisimus cavaticus</i>	O		X	X	X	
21. <i>M. montanus</i>	O	X	X	X		
22. <i>M. sexoculatus</i>	O		X	X		
23. <i>M. signatus</i>	O	X	X	X	X	
Family Salticidae						
24. <i>Corythalia gloriae</i>	O	X	X	X		
25. <i>Emanthis portoricensis</i>	O	X	X	X	X	
Family Selenopidae						
Family Sparassidae						
27. <i>Pseudosparianthis jayuyae</i>	O			X		
28. <i>Stassina portoricensis</i>	O	X	X	X	X	
Family Tetragnathidae						
29. <i>Tetragnatha tenuissima</i>		X		X		
Family Theridiidae						
30. <i>Lithyphantes septemmaculatus</i>			X	X	X	
Family Theridiosomatidae						
31. <i>Wendilgardia theridionina</i>	O	X		X		
Family Zoridae						
32. <i>Zorid</i> sp. 1			X			X
Order Opiliones						
Suborder Laniatores						
Family Phalangodidae						
33. <i>Metapellobunus unicolor</i>	O					X
34. <i>Pseudomitraceras minutus</i>	O			X		X
Order Scorpiones						
Family Buthidae						
35. <i>Titus obtusus</i>	O	X	X	X		
Subphylum Crustacea						
Class Malacostraca						
Order Decapoda						
Family Atyidae						
1. <i>Atya lanipes</i>	O	X				X
2. <i>Micratya poeyi</i>		X				X
3. <i>Xiphocaris elongata</i>		X				X
Family Palaemonidae						
4. <i>Macrobrachium carcinus</i>		X				X
Family Pseudothelphusidae						
5. <i>Epilobocera sinuatifrons</i>	O	X				X
Order Isopoda						
Family Cubaridae						
6. <i>Sphaeroniscus portoricensis</i>			X			X
Family Oniscidae						
6. <i>Philocia richmondi</i>		X	X	X	X	X
7. <i>Synurops granulatus</i>		X	X	X	X	X
8. <i>Rhysotus turgifrons</i>			X	X	X	X
9. <i>Porcelloides pruinosus</i>						X
Subphylum Uniramia						
Class Chilopoda						
Subclass Anamorpha						
Order Scutigermorpha						
Family Scutigerae						
1. <i>Antillona portoricensis</i>	O	X		X		

Table 14.—Animal species recorded in the Baño de Oro Natural Area (except bird species)—Continued

Classification	Endemic*	Habitat type <sup>†</sup>				
		T	C	P	D	W
Subclass Epimorpha						
Order Scolopendromorpha						
Family Cryptopidae						
2. <i>Cryptops bivittatus</i>		X	X	X		
3. <i>Newportia longitarsis</i>		X				
4. <i>Newportia</i> n. sp. (M.S.)	O	X	X	X	X	
5. <i>Newportia</i> n. sp. (M.S.)	O		X	X		
6. <i>Newportia</i> sp. (juveniles)		X				
7. <i>Scolopocryptops ferrugineus</i>	O	X	X	X	X	
8. <i>S. melanostomus</i>	O	X		X		
Family Scolopendridae						
9. <i>Scolopendra alternans</i>		X	X			
10. <i>Otostigmus caraibicus</i>	O	X				
Order Geophilomorpha						
11. Geophilomorph sp. 1			X			
12. Geophilomorph sp. 2					X	
13. Geophilomorph sp. 3				X		
14. Geophilomorph sp. 4			X			
15. Geophilomorph sp. 5		X				
Class Diplopoda						
Subclass Penicillata						
Order Polyxenida						
Family Lophoproctidae						
1. <i>Lophoturus niveus</i>		X		X		
2. <i>Lophoturus</i> sp.	O					
Subclass Pentozonia						
Order Glomeridesmida						
Family Glomeridesmidae						
3. <i>Glomeridesmus marmoreus</i>	O	X	X	X	X	
Order Polydesmida						
Suborder Polydesmidea						
Family Pyrgodesmidae						
4. <i>Docodesmus vidalis</i>	O		X		X	
5. <i>Docodesmus</i> sp.		X		X		
6. <i>Iomus incisus</i>	O		X	X		
7. <i>Iomus</i> sp.					X	
8. <i>Liomus obscurus</i>	O		X			
9. <i>Liomus</i> sp.					X	
Family Chelodesmidae						
10. <i>Ricodesmus stejneri</i>	O	X	X	X		
Family Fuhrmannodesmidae						
11. <i>Cryptogonodesmus rolleis</i>	O				X	
Family Haplodesmidae						
12. <i>Cylindrodesmus caraibicus</i>	O	X		X	X	
Order Spirobolida						
Family Spirobolellidae						
13. <i>Spirobolellus richmondi</i>	O	X	X	X	X	
14. <i>Spirobolellus</i> n. sp. 1	O	X		X		
15. <i>Spirobolellus</i> n. sp. 2	O					
Order Spirostreptida						
Family Pseudononolenidae						
16. <i>Epinannolene trinidadensis</i>	O	X		X	X	
17. <i>Epinannolene</i> sp.	O			X		
18. <i>Epinannolene</i> sp.	O			X		
Order Stemmiulida						
Family Semmiulidae						
19. <i>Prostemmiulus</i> n. sp. 1	O					
20. <i>Prostemmiulus</i> n. sp. 2	O					
21. <i>Prostemmiulus</i> sp. 1		X	X	X		
Order Siphonophorida						
Family Siphonophoridae						
24. <i>Siphonophora portoricensis</i>	O		X	X		

Table 14.—Animal species recorded in the Baño de Oro Natural Area (except bird species)—Continued

Classification	Endemic*	Habitat type†				
		T	C	P	D	W
Class Symphyla						
Family Scutigereidae						
1. <i>Hanseniella</i> sp			X			
Class Insecta						
Order Orthoptera						
Family Blattidae						
5. <i>Pelmatosilpha coriacea</i>			X	X	X	
6. <i>Neoblatella borinquensis</i>		X	X	X	X	
Order Isoptera						
Family Termitidae						
19. <i>Nasutitermis costalis</i>				X		
Family Kaotermitidae						
21. <i>Glyptotermes rubescens</i>			X	X		
Order Hemiptera						
Family Notonectidae						
29. <i>Buenoa macrophthalma</i>		X			X	
Family Veliidae						
30. <i>Rhagovelia collaris</i>		X			X	
Order Coleoptera						
Family Scarabeidae						
31. <i>Phyllophaga yunqueana</i>		X	X	X		
Order Diptera						
Family Tachinidae						
<i>Ormia punctata</i>		X				
Order Lepidoptera						
Family Danaidae						
41. <i>Danaus plexippus</i>					X	
Family Megalopygidae						
43. <i>Megalopyge krugii</i>		X				
Family Satyridae						
44. <i>Calisto nubila</i>					X	
Family Sphingidae						
45. <i>Herse cingulata</i>					X	
Order Hymenoptera						
Family Apidae						
46. <i>Apis mellifera</i>					X	
Family Formicidae						
Subfamily Dolichoderinae						
47. <i>Iridomyrmex melleus</i>				X	X	
Subfamily Formicinae						
48. <i>Myrmelachista ramulorum</i>					X	
49. <i>Paratrechina longicornis</i>					X	
Subfamily Myrmicinae						
50. <i>Macromischa isabellae</i>					X	
53. <i>Solenopsis geminata</i>					X	
Subfamily Ponerinae						
57. <i>Ponera opaciceps</i> (Juan H. Opaciceps)			X			
Family Psammocharidae						
58. <i>Pepsi</i> sp.					X	
Phylum Chordata						
Class Osteichthyes						
Order						
Family						
1. Unidentified sp. obs.					X	
Class Amphibia						
Order Anura						
Family Bufonidae						
1. <i>Bufo marinus</i>		X			X	
Family Leptodactylidae						
2. <i>Eleutherodactylus coqui</i>	O	X	X	X		
3. <i>E. eneidae</i>	O			X		
4. <i>E. portoricensis</i>	O			X		
5. <i>E. richmondi</i>	O			X		
6. <i>Leptodactylus albilabris</i>	O				X	

Table 14.—Animal species recorded in the Baño de Oro Natural Area (except bird species)—Continued

Classification	Endemic*	Habitat type†				
		T	C	P	D	W
Class Reptilia						
Order Squamata						
Suborder Sauria						
Family Gekkonidae						
1. <i>Sphaerodactylus klauberi</i>	O					X
2. <i>S. macrolepsis grandisquamis</i>	O					X
Family Anguidae						
3. <i>Diploglossus pleei</i>	O	X				X
Family Iguanidae						
4. <i>Anolis c. cristatellus</i>		X		X		
5. <i>A. cuvieri</i>	O	X				X
6. <i>A. evermani</i>	O	X		X		X
7. <i>A. krugii</i>	O		X			X
8. <i>A. gundlachi</i>	O		X	X		
9. <i>A. stratulus</i>		X		X		
10. <i>A. occultus</i>	O			X		X
Suborder Serpentes						
Family Boidae						
11. <i>Epicrates inornatus</i>	O		X			
Family Colubridae						
12. <i>Alsophis portoricensis</i>	O		X			
13. <i>Arrhyton exiguum stahli</i>		X				
Class aves‡						
Class Mammalia						
Order Carnivora						
Family Viverridae						
1. <i>Herpestes javanicus</i>		X		X		
Order Rodentia						
Family Muridae						
2. <i>Rattus rattus</i>				X		

\*Species endemic to Puerto Rico indicated by O.

†Habitat types: T = tabonuco forest; C = colorado forest; P = palm forest; D = dwarf forest; and W = fresh water.

X indicates in which habitat species occurs.

‡Refer to Table 15.

also found. Eleven species of native bats are known to live in some part of the LEF (Brown and others 1983, Starrett 1962), but none were observed during the survey.

**Bat Study.**—One-half of Puerto Rico's 14 bat species are found in the tabonuco forest (Willig and Gannon 1991). *Stenoderma rufum*, a frugivorous species endemic to Puerto Rico and the U.S. Virgin Islands, comprises at least 25 percent of the individuals within the LEF's tabonuco forest. Other species include *Artibeus jamaicensis*, a frugivore, and *Monophyllus redmani*, a nectivore.

The foraging movements of bats are instrumental in the spatial and genetic structure of plant communities through the dispersal of seeds and pollen. Moreover, they respond to changes in the structure and species composition of the forest after major storm events. Hurricane Hugo had numerous effects on bat populations. *Artibeus jamaicensis* and *S. rufum* decreased in numbers and *M. redmani* increased. The major objective of the study was to determine the effects of the hurricane on bat ecology. Specifically, the community

composition, population levels, size of the home range, bat numbers, fidelity to feeding areas, commuting distances traveled, and demographic structure were investigated.

**Black Rat Study.**—Predation of Puerto Rican parrot eggs by black rats (*Rattus rattus*), observed years ago (Rodriguez-Vidal 1959), prompted an investigation of rat reproductive chronology, population fluctuations, and habitat use in the vicinity of active nesting sites between 1982 and 1985 (Walker Layton 1986, Zwank and Walker Layton 1989). Peak sexual activity occurred in June with peak populations observed from July through September. Density estimates ranged from 70 to 280 rats per hectare with the lows recorded in late winter and early spring prior to the breeding season.

Radio tracking and snap trapping in trees and on the ground indicated that rats appear to be primarily arboreal during daylight hours and spend time on the ground at night. Snap trapping at three different elevations in the Baño de Oro indicated denser rat populations in the dwarf forest than in either the colorado or tabonuco forests.

Table 15.—Checklist of birds in the Baño de Oro Natural Area

Common English name	Common Spanish name	Scientific Name	Status in LEF†	Occurrence in LEF‡	Habitat preference**
Green-backed heron	Martinete	<i>Butorides striatus</i>	T	C	T,C,[R]
Sharp-shinned hawk*	Halcón de Sierra	<i>Accipiter striatus</i>	R	U	T,C
Broad-winged hawk*	Guaraguao de Bosque	<i>Buteo platypterus</i>	R	C	T,C
Red-tailed hawk	Guaraguao Colirrojo	<i>B. jamaicensis</i>	R	C	T,C,P,(D)
Merlin	Halcón Migratorio	<i>Falco columbarius</i>	T	U	T,C,(P)
Peregrine falcon	Halcón Peregrinus	<i>F. peregrinus</i>	T	U	T,C,(P)
Spotted sandpiper	Playero Coleador	<i>Actitis macularia</i>	T	C	T,C,P, [R]
Scaly-naped pigeon	Paloma Turca	<i>Columba squamosa</i>	R	C	T,C,P,D
Ruddy quail-dove	Paloma Perdiz Rojiza	<i>Geotrygon montana</i>	R	C	T,C,P,Plant
Puerto Rican parrot†	Cotorra de Puerto Rico	<i>Amazon vittata</i>	R	R	T,C,P
Puerto Rican lizard-cuckoo†	Pájaro Bobo Mayor	<i>Saurothera vieilloti</i>	R	C	E,Plant, T,C,P,D
Puerto Rican screech-owl†	Múcaro de Puerto Rico	<i>Otus nudipes</i>	R	C	T,C,P,Plant
Black swift	Vencejo Negro	<i>Cypseloides niger</i>	T	C	T,C,P,D
Antillean mango	Zumbador Dorado	<i>Anthracothonax dominicus</i>	R	R	E,Plant
Green mango†	Zumbador Verde	<i>A. viridis</i>	R	C	T,(C)
Puerto Rican emerald†	Zumbadorcito de Puerto Rico	<i>Chlorostilbon maugaeus</i>	R	C	(T),C,P,D
Puerto Rican tody†	San Pedrito	<i>Todus mexicanus</i>	R	C	T,C,P,D
Puerto Rican woodpecker†	Carpintero de Puerto Rico	<i>Melanerpes portoricensis</i>	R	C	Plant,T,C,P,(D)
Gray kingbird	Pitirre	<i>Tyrannus dominicensis</i>	R	U	E,Plant
Cave swallow	Golondrina de Cuevas	<i>Hirundo fulva</i>	T	U	E
Red-legged thrush	Zorzal de Patas Coloradas	<i>Turdus plumbeus</i>	R	C	E,Plant,T,(C)
Pearly-eyed thrasher	Zorzal Pardo	<i>Margarops fuscatus</i>	R	C	Plant,T,C,P,D
Black-whiskered vireo	Julián Chivl	<i>Vireo altiloquus</i>	R	C	E,Plant,T,(C)
Golden-winged warbler	Reinita Alidorada	<i>Vermivora chrysoptera</i>	T	R	T,(C)
Northern parula	Reinita Pechidorada	<i>Parula americana</i>	T	C	E,Plant,T,C,P,D
Magnolia warbler	Reinita Manchada	<i>Dendroica magnolia</i>	T	U	Plant,T,C
Cape May warbler	Reinita Tigre	<i>D. tigrina</i>	T	U	Plant,T,C
Black-throated blue warbler	Reinita Azul	<i>D. caerulescens</i>	T	C	Plant,T,C,P,D
Elfin Woods warbler†	Reinita de Bosque Enano	<i>D. angelae</i>	R	U	C,P,D
Black-and-white warbler	Reinita Trepadora	<i>Mniotilta varia</i>	T	U	Plant,T,C,P,D
American redstart	Candelita	<i>Setophaga ruticilla</i>	T	C	Plant,T,C,P,D
Ovenbird	Pizpita Dorada	<i>Seiurus aurocapillus</i>	T	U	Plant,T,C
Louisiana waterthrush	Pizpita de Rlo	<i>S. motacilla</i>	T	C	T,C, P,[R]
Bananaquit	Reinita Común	<i>Coereba flaveola</i>	R	C	Plant,T,C,P,D
Antillean euphonia	Canario del Pais	<i>Euphonia musica</i>	R	C	T,C,P,D
Stripe-headed tanager	Reina Mora	<i>Spindalis zena</i>	R	C	Plant,T,C,P,D
Puerto Rican tanager†	Llorosa	<i>Nesospingus speculiferus</i>	R	C	(T),C,P,D
Black-faced grassquit	Gorrión Negro	<i>Tiaris bicolor</i>	R	U	(Plant),E
Puerto Rican bullfinch†	Come Name de Puerto Rico	<i>Loxigilla portoricensis</i>	R	C	Plant,T,C,P,D

\* = Endemic Subspecies.

† = Endemic Species.

‡LEF = Luquillo Experimental Forest; status: R = resident, T = transient or migratory.

§Occurrence in national forest: C = common; U = uncommon; R = rare.

\*\*Habitat preference: plant = plantation; E = edge of forest at interface with pastures, crop land or fallow land; T = Tabonuco Forest; C = Colorado Forest; P = Palm Forest; D = Dwarf Forest (Elfin Woodland); R = River edge; brackets [ ] denote specific habitat used within a forest zone; parentheses ( ) denote habitat where species is much less common than other areas given; underlined habitat type is area in which species is most often found.

**Puerto Rican Parrot Studies.**—A notable decline in the population of Puerto Rican parrots after the mid-1950's led to an intensive investigation of the species and its habitat. The West, Central, and East Fork watersheds of the Rio Mameyes, located in the upper reaches of the Baño de Oro, comprise traditional parrot habitat. Snyder (1978) disclosed that a lack of good nesting sites throughout the colorado forest forced the parrots to use inadequate sites, which subsequently led to reproductive losses. The Puerto Rican parrot monograph, summarizing nearly 20 years of continual

observations of their daily habits—territorial and feeding behavior using radio telemetry techniques, selection of nesting sites, egg laying, incubation, and fledging, among other topics—was recently published (Snyder and others 1987). Observations of the parrot and its habitat continue today.

Future studies of the Puerto Rican parrot will involve the foraging ecology of breeding and nonbreeding territorial pairs and observations of captive bred birds after their release. About 200 trees were identified with potential nesting cavities in the Baño de Oro





Parrot research blind and nesting boxes within the Baño de Oro Natural Area.

in the mid-1970's. The impact of Hurricane Hugo on parrot habitat in general, and on the availability of these tree cavities in particular, will be investigated as well.

**Other Bird Species Studies.**—Transect studies of birds were made along the Pico del Este Road and on the Rio de la Mina trail (Kepler and Kepler 1970) at the highest and lowest elevations in the Baño de Oro. Bird diversity in the LEF was considered to be lower than that in the dry Guanica Forest in southwestern Puerto Rico.

A new species of Parulidae (*Dendroica angelae*), endemic to Puerto Rico, was reported from the LEF's dwarf forest (Kepler and Parkes 1972). The species is confined to the LEF's upper forests, including the Baño de Oro, and has also been reported in Maricao Forest in western Puerto Rico. This bird's isolated habitat, restricted range, and similarity to the black-and-white warbler were factors responsible for its late discovery.

Recommended birding sites for the LEF include the Yokahu Tower and the Big Tree Trail on the Baño de Oro's western border, the Pico del Este Road along its southern highpoints, and the Bisley/Mameyes River Valley at the northern base of the Baño de Oro (Wiley and Bauer 1985). Additional bird species seen from these vantage points as well as by qualified observers elsewhere within the Baño de Oro have been incorporated into the survey list (table 15).

The pearly-eyed thrasher (*Margarops fuscatus*) was not abundant in the upper LEF prior to 1950 (Snyder and Taapken 1978). Presently, the thrasher is common

in colorado forests where it competes with the parrot for nesting sites. Several experiments with nest boxes of different depths, designs, and physical locations within parrot habitat provided guidelines for mitigating competition between the species.

One of the study sites for determining the effects of ectoparasites on the growth and development of pearly-eyed thrashers was located within the Baño de Oro (fig. 2). The reproductive success of the thrashers was greatly reduced as a consequence of warble fly (*Philornis deceptivus*) parasitism, which was heavy as a result of an apparent increase in the thrasher's density (Arendt 1983, Uhazy and Arendt 1986). Parasitized nestlings either died or demonstrated different growth patterns depending on the timing of the infestation and the extent of parasitic attack (Arendt 1985a). The impact of parasitic attacks was less on adults than on nestlings (Arendt 1985b).

Some of the observations on the breeding biology and diet of red-tailed hawks (*Buteo jamaicensis*) were also made in the Baño de Oro (Santana and Temple 1988). Observations on the biology of the sharp-shinned hawk (*Accipiter striatus*) continue today.

Beginning in September 1989, after the passage of Hurricane Hugo, point counts of forest bird species were initiated in the Baño de Oro. Fifteen stations 100 m apart are being used to tally North American migrants and determine their population densities and fluctuation over time.

**Anoline Lizard Studies.**—In the early 1960's, the distribution of anoline lizards was studied in the

vicinity of an 800-m elevation in the LEF (Rand 1964), probably just west of the Baño de Oro. Typical perch heights, perch diameters, and shade conditions were recorded for *Anolis evermanni*, *A. gundlachi*, and *A. krugi* to determine how differences in structural and microclimatic preferences result in spatial separation among species.

Today, the distribution of anoline lizards, as well as the effects of Hurricane Hugo on anoline lizard communities, are being studied along an elevational gradient from 500 to 1,000 m in the LEF. The 800- and 900-m sites are situated in the Baño de Oro. The main objectives of the study are to assess the composition, density, and diversity of anoline lizards, to determine structural niche dimensions for all species, and to measure niche breadth and overlap at each elevational level.

**Frog Diversity Study.**—Beginning in February 1989, a 200-m transect has been sampled for frog density and abundance in the vicinity of the southwestern boundary of the Baño de Oro. Regular monitoring for the most common species includes sampling for adult sizes, presence of juveniles, sex determination, and breeding activities, including assessment of egg clutches. An attempt will also be made to determine the effects of Hurricane Hugo on frog populations.

## Invertebrates

**Earthworm Study.**—Monthly samplings of earthworms were initiated in each of the Baño de Oro's forest types in July 1991. The objectives of the project are to identify earthworm species and to determine if correlations exist between their occurrence and environmental factors. Soil pits measuring 25 by 25 cm and 40 cm deep are being excavated at designated sites, and earthworm samples are being extracted from different depths. At each site, the date (season), altitude, and loose litter above the pit are noted along with several soil parameters such as depth, humidity, bulk density, nutrient status, and organic matter content.

**Studies of Other Organisms.**—A free-living flatworm, roundworms, nematodes, and numerous mollusks and arthropods were identified in the survey of the Baño de Oro (table 14). Much additional work needs to be done with these groups of organisms.

The nomenclature of the earthworms had not been resolved at the time of the University of Puerto Rico survey. Moreover, the centipedes found in the Baño de Oro could not be designated to corresponding families, genera, or species because only one specimen of each was encountered and dissection is required before they can be classified to family rank. Insect identification of Thysanoptera, Collembola, Orthoptera, and others was also impossible. Study of the insects will take considerable time and, undoubtedly, involve many investigators.

## Classified Plant and Animal Species

Several of the plant and animal species recorded in the Baño de Oro have been classified by the U.S. Fish and Wildlife Service, the Commonwealth Department of Natural Resources, or the Forest Service as rare, endangered, threatened, or sensitive. The Federal list of threatened and endangered species in Puerto Rico (Delgado-Mendoza and others 1990) contains the Puerto Rican parrot (*Amazona vittata*), the Arctic peregrine falcon (*Falco peregrinus tundrius*), and the Puerto Rican boa constrictor (*Epicrates inornatus*). Additional species listed by the Commonwealth Department of Natural Resources as threatened or endangered are the sharp-shinned hawk (*Accipiter striatus venator*) and two species of tree frogs, *Eleutherodactylus eneidae* and *E. karlschmidti* (Delgado-Mendoza and others 1990).

Animal species classified as sensitive by the U.S. Department of Agriculture, Forest Service (1990), include the three aforementioned species listed by the Commonwealth as well as the broad-winged hawk (*Buteo platypterus brunnescens*) and the elfin woods warbler (*Dendroica angelae*). Plant species on the sensitive list are: *Eugenia eggersii*, *Laplacea portoricensis*, *Marliera sintensii*, *Ternstroemia luquillensis*, and *Xylosma schwaneckeanum*.

## FUTURE ACTIVITIES

The Baño de Oro is unique within the LEF and Puerto Rico. As witnessed by the rain forest life zones that characterize it, the Baño de Oro is the wettest tract in the LEF, which in turn is the wettest area in Puerto Rico. The contiguous tract contains a good representation of all forest types undisturbed by humans, albeit recently disturbed by Hurricane Hugo. Continued human modification of forest land elsewhere in Puerto Rico may make the Baño de Oro more valuable with the passage of time.

The ecosystems represented are the products of centuries of evolution. The tract is sufficiently large to indefinitely support the flora and most of the fauna that it contains under current climatic conditions. Certain large animals such as the parrot, the broad-winged hawk, and the tanager could not persist if this area were managed in isolation. However, the entire Baño de Oro is surrounded by the LEF, which has been protected for over a century. Deliberate modification, such as extensive cutting, removal of plants or animals, or pollution of the waters, could have deleterious effects. In this respect, the Pico del Este road (Route 930), which borders the Baño de Oro, represents a potential problem. Discarding of refuse or disturbance of roadside vegetation could become matters of concern as the forest receives more visitors.

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The size, undisturbed nature, and diversity of the Baño de Oro make it an ideal site for ecological investigations. Soils range from deep alluviums in the narrow valleys to shallow, rocky ridges. Two life zones, four major forest types, and the rare *Pterocarpus* swamp are found within the area or bordering it. Numerous tree species, epiphytes, ferns, liverworts, and mosses characterize the vegetation. The Puerto Rican parrot, the Puerto Rican tanager, the broad-winged hawk, and the boa constrictor add to the Baño de Oro's diversity.

The Baño de Oro is accessible from the Pico del Este road at highest elevations and from the Bisley Trail and the Big Tree/Rio de la Mina trails at lowest elevations. The Big Tree/Rio de la Mina trail is particularly scenic, offering vistas of numerous waterfalls and exposed rock along the river. From the standpoint of educational opportunities, the fauna and flora of the mountains may be viewed more easily from other areas, suggesting that the Baño de Oro should not be used intensively for this purpose. Moreover, adequate recreational facilities already exist and will be amplified in other parts of the LEF; these areas have vistas and attractive watercourses like those of the Baño de Oro. The major uses of the Baño de Oro, then, should be for long-term ecological investigations.

Many of the intriguing aspects of faunal and floral relationships in diverse habitats such as that of the LEF cannot be answered without knowledge of past events. Only too often, ecological studies are exceedingly limited in this regard. Species compositions, structural features, and growth rates of the major forest types in the LEF have altered during the past 40 years. These changes were attributed to disturbance caused by Hurricane San Cipriano in 1932 and subsequent recovery of the forest. Likewise, animal populations dependent on the vegetation have most probably changed over time, although supportive information on this topic is lacking. Knowledge of floral and faunal dynamics, and periodic changes in environmental factors, such as rainfall, erosion rates, nutrient status, and others, can be attained only through carefully implemented, long-term ecological studies. Such studies take on even greater importance with the most recent disturbance of the Baño de Oro by Hurricane Hugo.

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Appendix Table 1. — *Select reference list for flora and fauna in Puerto Rico including the Baño de Oro Natural Area*

Topics	Sources
<b>Vegetation</b>	
Forest types	Beard 1944, 1949; Dansereau and Buell 1966; Ewel and Whitmore 1973; Little and others 1974; Little and Wadsworth 1991; Stehle 1945; Wadsworth 1951
Botany	Britton and Wilson 1923–30a, 1923–30b; Cook and Gleason 1928; Gleason and Cook 1927; Howard 1968
Trees/Seedlings	Duke 1970, Little 1970, Little and others 1974, Little and Wadsworth 1991, Little and Woodbury 1976, Longwood 1961, Smith 1970
Autecology (trees)	Bannister 1970; Burns and Honkala 1990*; Edmisten 1970; Francis, in press†; Frangi and Lugo 1985; Lebron 1977; Muñiz-Melendez 1978; Nieves 1979; Sastre de Jesus 1979; Silander 1979; Van Valen 1975; Weaver 1986b
Phenology (trees)	Estrada Pinto 1970, Nevling 1971
Ferns	Kepler 1975, Proctor 1989
Medicinal plants	Nunez Melendez 1982
Bryophytes	Crum and Steere 1957; Fulford and others 1970, 1971; Gradstein 1989; Miller and Russel 1975; Russel and Miller 1977
Mycology	Seaver and Chardon 1926, Seaver and others 1926
Algae	Foerster 1971
Lichens	Harris 1989
Myxomycetes	Alexopoulos 1970
<b>Animals</b>	
Mammals	Anthony 1925–26, Starrett 1962, Tamsitt and Valdivieso 1970
Birds	Biaggi 1970; Bond 1971; Danforth 1931; Leopold 1963; Raffaele 1983; Wetmore 1916, 1927; Wiley and Bauer 1985
Amphibians/Reptiles	Drewry 1970a, Rand 1964, Rivero 1978, Schmidt 1928, Stejneger 1904, Thomas 1966
Insects	Barber 1939; Comstock 1944; Curren 1928; Drewry 1970b; Forbes 1930, 1931; Klots 1932
Spiders	Martorell 1945; Osborn 1935; Petrunkevich 1929, 1930; Schauss 1940; Smith 1936; Wolcott 1923, 1936, 1948
Mollusks	Aguayo 1966, Van der Schalie 1948
Rare/Sensitive Species	Proctor 1991, Raffaele and others 1977, USDA FS 1990, Woodbury and others 1975

\*Contains descriptions of 20 tree species native or introduced to Puerto Rico.

†Contains descriptions of 71 tree species to date, many of them introduced to Puerto Rico.

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Weaver, Peter L. 1994. Baño de Oro Natural Area, Luquillo Mountains, Puerto Rico. Gen. Tech. Rep. SO-111. New Orleans, LA: U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station. 55 p.

Past and current research in the Baño de Oro Natural Area is summarized and used as a basis for further investigation. The current state of knowledge regarding the environment is outlined.

**Keywords:** Climate, fauna, flora.