

United States
Department of
Agriculture

Forest Service



**International Institute
of Tropical Forestry**

General Technical
Report IITF-44

The Luquillo Mountains: Forest Resources and Their History

Peter L. Weaver



The Author:

Peter L. Weaver, Research Forester,
Forest Service, U.S. Department of
Agriculture, International Institute of
Tropical Forestry, Jardín Botánico Sur,
Río Piedras, PR 00926-1119.

Cover Photos

LEFT: Recreation and Wildlife—The El Yunque hiking trail, one of the oldest, is a favorite for viewing flora and fauna. (Photo by Peter L. Weaver)
TOP RIGHT: Historic legacy—The construction of the Baño Grande bath house and bathing pool date to the late 1930s. (Photo from IITF files)
BOTTOM RIGHT: Water—Numerous streams provide pristine water supplies to surrounding communities. (Photo by Peter L. Weaver)

Product Disclaimer

The use of trade or firm names in this publication is for reader information and does not imply endorsement by the U.S. Department of Agriculture of any product or service.

November 2012

International Institute of Tropical Forestry

Jardín Botánico Sur
1201 Calle Ceiba
San Juan, PR 00926-1119

The Luquillo Mountains: Forest Resources and Their History

PETER L. WEAVER

Contents

LIST OF FIGURES	v
ABSTRACT	vi
FOREWORD	vii
INTRODUCTION	1
OBJECTIVES	6
CHAPTER 1. HISTORICAL PERSPECTIVE	7
Pre-Colonial Era	7
Spanish Arrival, Exploration, and Settlement	7
Forest Proclamation and Land Acquisition	9
Opening of the Forest	9
Management of the Forest	14
Research and Training in the Forest	16
CHAPTER 2. ENVIRONMENTAL SETTING	23
Geology	23
Physiography and Hydrology	25
Soils	26
Climate	29
CHAPTER 3. TREE DISTRIBUTIONS AND MAJOR FOREST TYPES	37
Tree Species Affinities and Geographic Distribution	37
Field Sampling and Permanent Plot Monitoring	37
Lower Montane Forest	43
Montane Forest	53
Palm Brake	56
Dwarf Forest	58
CHAPTER 4. ENVIRONMENTAL GRADIENTS	61
Tree Species Ranges in Luquillo Mountains	62
Tree Life Cycles and Longevity	63
MAJOR TYPES OF DISTURBANCE	66
Treefalls (Background Mortality)	66
Climatic Disturbances	66
Landslides	69
Human Activities—Settlement and Development	70
Accidents	71
Post-Disturbance Recovery	72
CHAPTER 6. OTHER VEGETATION	74
Tree Plantings and Plantations	74
Mahogany Line Planting	76
Mahogany Provenance Trial	77
Forest Service Arboretum (Caracoles)	78
Other Tree Species and Common Herbs	80
CHAPTER 7. VERTEBRATE FAUNA	81
Mammals	81
Birds	81
Reptiles	88
Amphibians	89
Fish	90

Contents

CHAPTER 8. SPECIES DIVERSITY—PLANTS AND ANIMALS	91
Plant Diversity	91
Animal Diversity	91
CHAPTER 9. CLASSIFIED SPECIES OF PLANTS AND ANIMALS	92
Classified Plants	92
Classified Animals	92
CHAPTER 10. OTHER RESOURCES	94
Water and Shrimp	94
Recreation	94
Scenery and Trails	95
Heritage	99
El Yunque Stories—Myth, Legend, and Curious Facts	103
CHAPTER 11. DESIGNATED LAND USES	106
The Baño de Oro Research Natural Area	106
Luquillo Experimental Forest Biosphere Reserve	107
Wild and Scenic Rivers	107
The El Toro Wilderness Area	108
Special Use Permits	109
CHAPTER 12. MAJOR FOREST RESEARCH SITES	110
El Verde Ecological Studies	110
Luquillo Forest Dynamics Plot (LFDP) at El Verde	111
Long Term Ecological Research (LTER) at Bisley	112
Riparian Palm Stand	113
Pico del Oeste Dwarf Forest	114
Pico del Este Dwarf Forest	114
CHAPTER 13. FOREST PLANNING AND MANAGEMENT	115
Primary Forest	116
Demonstration of Sustainable Timber Production	117
Wildlife	117
Water	118
Wild and Scenic Rivers	119
Wilderness	119
Recreation and Conservation Education Programs	120
Access (Roads, Trails, Acquisitions)	121
Research	122
EPILOGUE—<i>QUO VADIS?</i>	123
ACKNOWLEDGMENTS	124
ENDNOTES	125
LITERATURE CITED	126
APPENDIX A	138
APPENDIX B	147
APPENDIX C	148
APPENDIX D	151
APPENDIX E	154
APPENDIX F	158

List of Figures

Figure 1—Location of the Luquillo Experimental Forest in northeastern Puerto Rico. Major cities and towns (21) and municipalities (underlined town names) (8) surround the forest. Built up areas are shaded.	2
Figure 2—Ecological Life Zones within the Luquillo Experimental Forest.	5
Figure 3—Forest types within the Luquillo Experimental Forest.	5
Figure 4—Acquisition of properties (tracts) in the Luquillo Experimental Forest.	10
Figure 5—Roads and hiking trails in the Luquillo Experimental Forest.	14
Figure 6—Plantation sites in the Luquillo Experimental Forest in 1947.	16
Figure 7—Proposed timber production areas within the Luquillo Experimental Forest in 1950.	21
Figure 8—Geology of the Luquillo Experimental Forest.	24
Figure 9—Major peaks, rivers, watersheds, flow gages, and water intakes in and around the Luquillo Experimental Forest.	25
Figure 10—Soils of the Luquillo Experimental Forest.	28
Figure 11—Climatic diagrams for sites within the Luquillo Experimental Forest.	31
Figure 12—Hurricane trajectories over Puerto Rico since 1700.	33
Figure 13—Permanent and temporary plot locations, and major research sites within the Luquillo Experimental Forest.	42
Figure 14—Mean canopy heights per plot by elevation in the Luquillo Experimental Forest (linear trends for ridge, slope, and ravine).	44
Figure 15—Mean density of stems ≥ 4 cm d.b.h. per plot by elevation in the Luquillo Experimental Forest (linear trends for ridge, slope, and ravine).	44
Figure 16—Aboveground dry weight biomass per plot for stems ≥ 4 cm d.b.h. by elevation within the Luquillo Experimental Forest (linear trends for ridge, slope, and ravine).	45
Figure 17—Number of tree species per plot for stems ≥ 4 cm d.b.h. by elevation within the Luquillo Experimental Forest (linear trends for ridge, slope, and ravine).	45
Figure 18—Species-area curves for stems ≥ 4 cm d.b.h. by forest types within the Luquillo Experimental Forest.	46
Figure 19—Design of the arboretum in the Luquillo Experimental Forest.	75
Figure 20—Management areas and structures within the Luquillo Experimental Forest.	79
Figure 21—Major designated areas within the Luquillo Experimental Forest.	104

Abstract

This report presents an overview of the El Yunque National Forest, which is also designated as Luquillo Experimental Forest, in northeastern Puerto Rico. The principal topics include the environmental setting (geology, soils, and climate), environmental gradients, arborescent flora, vertebrate fauna, and forest management (i.e., plantations, silvicultural operations, planning, research, and designated land uses). A chronology from the time of European discovery to the present outlines major events in the Luquillo Experimental Forest, including an early presence of indigenous peoples, exploration for gold, timber extraction, farming, trail and road construction, and recreational developments.

Keywords: Disturbances, forest resources, gradients, history, Luquillo Mountains of Puerto Rico, management, research.

FOREWORD

The Luquillo Mountains of Puerto Rico bear a forest that, above all, is attractive. The attraction arises from a mysterious, magnificent, complex manifestation of nature: the mischievous laugh of a lizard cuckoo announcing forthcoming rain; the approaching roar of a torrent pounding on the forest canopy; weather-beaten palo colorados, invincible despite hundreds of hurricanes; deep shade beneath emergent tabonucos dripping with transpiration; understory trees obviously contented, including palms and ferns; dutiful yagrumos filling gaps; lianas thick with water; epiphytes with yellow-eyed lagartos; extended roots holding the mountain; the talkative approach of the San Pedrito; species nowhere else; streams of continuous clear forest water; and an incessant nocturnal symphony.

A world renowned forest ecologist, the late Dr. Leslie Holdridge, as a result of a 10-year introduction to the tropics in the Luquillo forest, despite a subsequent career in tropical forests throughout the hemisphere and living at a distance, requested that his bodily remains be left in the Luquillo forest. So did the late Angelito Torres, a bull-of-the-woods reputedly born within the forest and an indefatigable worker in its care during all of a very active life.

It is this attraction, after 43 years of Dr. Peter Weaver's study deep in the Luquillo forest, that brought an advanced academic degree and led him to bring a comprehensive story of the forest, much of it unknown or forgotten, to this book. Not content with a purely historic record, Dr. Weaver describes the present condition of the forest and its prospective uses. I am proud to have been a colleague of Dr. Weaver's during his life in the forest and in his preparation of this classic volume.

Frank H. Wadsworth

INTRODUCTION

The Luquillo Mountains of northeastern Puerto Rico, which contain the 11 310 ha El Yunque National Forest (EYNF) also administratively designated as the Luquillo Experimental Forest (LEF), are in essence an island within an island (fig. 1) (table 1). If sea level were to rise about 50 m, the valleys of the major rivers surrounding the mountains would flood and form an island comparable in size to many of the Lesser Antilles (Weaver 2002a). The mountains—steep, wet, and isolated at higher elevations—were not traversed by PR route 191 until 1942. A major landslide in the early 1970s blocked the road, which has remained closed for > 40 years.

The Luquillo Mountains rise abruptly from sea level at Las Cabezas de San Juan on the northeastern tip of Puerto Rico to 1074 m in elevation at El Toro Peak in the LEF. Over a distance of 20 km, annual rainfall increases from 900 mm along the coast through 2500 mm at the forest entrance to >4500 mm at the summits (Briscoe 1966). The gradient in elevation and moisture results in six distinct ecological life zones (Ewel and Whitmore 1973, Holdridge 1967). Subtropical dry forest grows along the northeastern coast and subtropical moist forest just inland. Ascending the mountains, subtropical

wet forest encircles most of the LEF along the forest border (fig. 2). Subtropical rain forest and subtropical lower montane rain forest are found to the windward of the mountain divide, and subtropical lower montane wet forest mainly to the leeward. A patch of subtropical moist forest lies in an isolated parcel to the southwest. Wet forest types account for about 75 percent of the land area within the LEF.

Four forest types known as lower montane rain forest, montane rain forest, dwarf forest, and palm brake occur in the Greater Antilles and in the mountainous Lesser Antilles between St. Kitts and Grenada (Beard 1949, Little and Wadsworth 1964, Seifriz 1943, Smith 1954). These four forest types are recognized with local names in the LEF: tabonuco forest between 150 and 600 m; colorado forest between 600 and 900 m; dwarf forest above 900 m; and palm brake on steep windward facing slopes and in drainages above 450 m (Wadsworth 1951) (fig. 3). The first two types cover about 80 percent of the LEF. In addition, four major vegetative communities have been described for the above forest types along the same gradient (1) *Dacryodes excelsa*-*Manilkara bidentata*, (2) *Cyrilla racemiflora*-*Micropholis garciniifolia*,



The Luquillo Mountains as viewed from PR route 2, which parallels the north coast. Part of the El Toro Wilderness Area extends left to right through the upper middle part of the photo. El Yunque rock is visible at the upper right. (Photo by Peter L. Weaver)

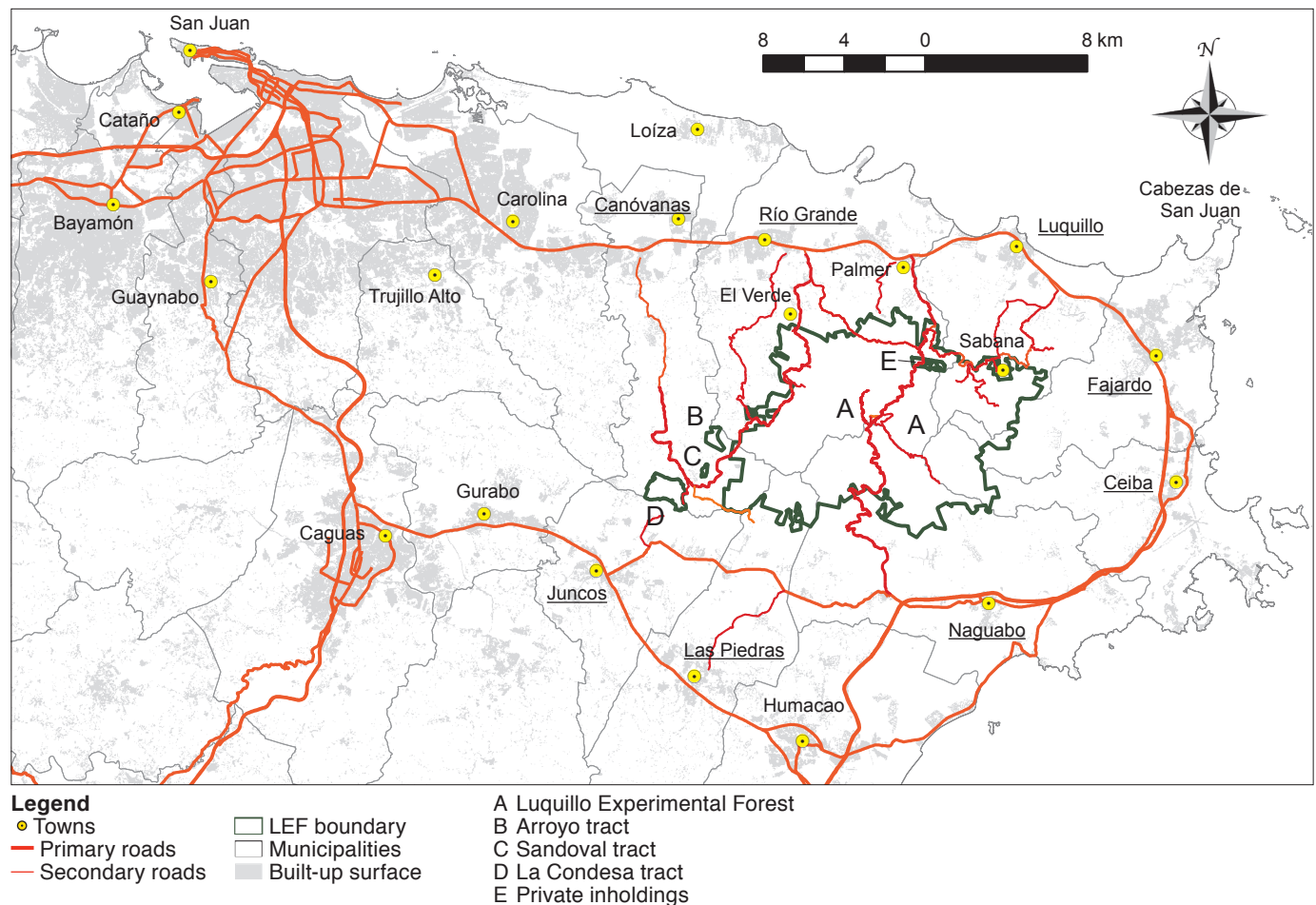


Figure 1—Location of the Luquillo Experimental Forest in northeastern Puerto Rico. Major cities and towns (21) and municipalities (underlined town names) (8) surround the forest. Built up areas are shaded.

(3) *Tabebuia rigida*-*Eugenia borinquensis*, and (4) *Prestoea montana*-*Cecropia schreberiana*, respectively (Gould and others 2006). Hereafter, Beard's terminology will be used and cited throughout the text as lower montane forest, montane forest, palm brake, and dwarf forest; however, Beard's complete terminology will be written out in figures and tables.

In 1876, the Spanish King Alfonso XII established forest reserves in Puerto Rico, including lands in the Luquillo Mountains, by means of the "La Ordenanza de Montes." However, it wasn't until 1880-81 that the lands in the Luquillo Mountains became known as the "Sierra de Luquillo." The King's declaration antedated the 1891 Land Revision Act that created the U.S. National Forest System (table 2) (appendix A). In 1898, after the Spanish-American War, Spain ceded Crown lands to the United States. In 1903, President Theodore Roosevelt proclaimed the lands in the Luquillo Mountains as the Luquillo Forest Reserve, a name that was retained until 1907. Subsequent administrative decisions led to name changes for the forest. From 1907 to 1935, the forest was called the Luquillo National Forest, the only tropical forest

within the National Forest System. From 1935 until 2007, it was referred to as the Caribbean National Forest to reflect lands held elsewhere in Puerto Rico, e.g., the Toro Negro Unit in the Central Mountains retained from 1935 until 1970. Finally, in 2007, the forest was designated as El Yunque National Forest, the traditional name used by island residents. Since 1956, the forest has also been designated as the LEF to administratively recognize its concurrent research activities. The administrative complexity of the forest was succinctly stated 60 years ago in the introduction to the forest atlas (Upton 1949, see endnotes):

"The Caribbean Forest in part is actually the oldest Forest Reserve, having been established by the Spanish Crown in 1876. It started as a Forest Reserve by Presidential Proclamation in 1903, took the general changeover in designation to a National Forest and then a change in its given name to include two Purchase Unit additions, and has been built up by purchase, donation, and transfer since 1931. It contains lands to which none of the general US land laws apply and is subject to special local laws

Table 1—Fascinating trivia about the Luquillo Experimental Forest^a

TOPIC	EXPLANATION
Forest Reserve	Set aside by Spanish Crown, 1876-1898
Spanish-American War	Spain passes crown lands in Puerto Rico to United States
National Forest	Forest Reserve proclaimed by Theodore Roosevelt in 1903, renamed as a national forest in 1907
Administration	Both a national forest and an experimental forest; also, occupies part of eight local municipalities
Size^b	When set aside, 5040 ha; today, 11 310 ha
Designated Areas	Research Natural Area (1949), Biosphere Reserve (1976), Wild and Scenic Rivers (2002), El Toro Wilderness (2005)
Major research sites^c	Permanent forest monitoring plots (scattered in LEF), El Verde LTER studies, Luquillo forest ecology and dynamics plot (El Verde), LTER (Bisley), riparian palm stand plot, dwarf forest (Pico del Este and Pico del Oeste)
Geology	Uplifted Cretaceous marine volcanoclastic rocks and Tertiary quartz diorite intrusive rocks
Topography	From 120 to 1074 m in elevation; 6 peaks >1000 m
Climate	Tropical maritime
Rainfall (mean annual)	Increases with elevation, about 3800 mm for the forest
Rainfall (total 1 day)	Recorded 485 mm on May 19, 1969 on Pico del Este
Showers per year	1,625 between 1938-1942 at La Mina
Temperature extremes	Minimum = 11 °C and maximum = 32 °C
Hurricanes (major)	About 15 passed near or over mountains since 1700
Hail	January 1969 for 10 minutes near Pico del Este
Water	
Sources	Ten watersheds and rivers within the LEF
Largest rivers	Headwaters of Río Grande de Loíza and Río Mameyes
River—free flow	Río Mameyes, only major LEF stream without a dam
Municipal water	35 intakes on forest streams supply ~750,000 people
Shrimp	11 migratory species live in forest streams
Trees	
Native tree species	225 in total; 41 percent shared with continents, 28 percent West Indian but not on continents, and 31 percent endemic to Puerto Rico and the U.S. Virgin Islands
Endemic tree species	8 species to the Luquillo Mountains alone; 60 species to Puerto Rico (and the Luquillo Mountains)
Planted tree species	144 (agriculture, arboretum, ornamental, and plantations)
Exotic tree species	113 planted but not all survived
Native conifer	<i>Podocarpus coriaceae</i> near El Yunque Peak
Coastal lowland species	<i>Pterocarpus officinalis</i> —rare Caribbean island occurrence at 250 m elevation
Most common	<i>Prestoea montana</i> from forest border to summits
Rarest	Uncertain— one of the dwarf forest endemics, possibly <i>Didymopanax gleasonii</i> or <i>Styrax portoricensis</i>
Range (greatest in LEF)	<i>Cecropia schreberiana</i> , <i>Henriettea squamulosa</i> , <i>Micropholis garciniifolia</i> , and <i>Prestoea montana</i>
Range (greatest in the Western hemisphere)	<i>Guarea guidonia</i> —Cuba to Argentina; <i>Cyrilla racemiflora</i> , eastern Virginia to Amazon River in Brazil
Range—also in Africa	<i>Andira inermis</i> , <i>Ceiba pentandra</i> , <i>Pterocarpus officinalis</i>
Largest (in diameter)	<i>Cyrilla racemiflora</i> previously recorded at 2.65 m in d.b.h.
Tallest (total height)	<i>Dacryodes excelsa</i> and <i>Manilkara bidentata</i> at >30 m
Oldest tree species	<i>Cyrilla racemiflora</i> and <i>Mangolia splendens</i> at ~1000 years
Densest native wood	<i>Clusia clusioides</i> , specific gravity at ~0.9 g cm ⁻³
Lightest native wood	<i>Ochroma pyramidale</i> , specific gravity at ~0.22 g cm ⁻³
Vertebrates^d	
Mammals	16 species, 11 native bats + 5 introduced pests
Birds	107 species (12 endemics, 2 endemic subspecies), 7 exotics
Reptiles	19 species (1 endemic), 18 natives, 11 lizards, 3 geckos (1 introduced), 5 snakes
Amphibians	15 species (11 endemics), 13 native, 2 introduced
Fish	7 species, 6 native and 1 introduced
Recreation	About 750,000 visitors annually
Major sites	El Portal Rain Forest Center; La Coca falls; Caimitillo, Palo Colorado, Río Cubuy, and Sierra Palm Picnic Areas; Baño Grande and Baño de Oro pools
Other sites	Quebrada Grande and Río Sabana picnic areas, La Mina falls
Trails	23 trails, 39 km recreational + 19 km administrative
Towers	El Yunque, Mt. Britton, and Yokahu
Forest vistas	El Yunque rock, Los Picachos, Pico del Este, Pico del Oeste, and above towers
Other vistas	Las Cabezas viewpoint, La Mina and El Toro peaks, Río Espíritu Santo bridge

^aSources: Data extracted from text and the literature.^bSource: U.S. Department of Agriculture, Forest Service (1995), see endnotes.^cLTER = Long term ecological research.^dEndemics to Puerto Rico

Table 2—Chronological designations of areas encompassing all or part of the Luquillo Mountains known today as the Luquillo Experimental Forest or El Yunque National Forest

Land unit designations	Year(s)	Size ha	Forest percent ^a
Pre-Columbian			
Yukiyú (Luquillo Mountains)	<1500	19 600	173.2
Spain^b			
Forest Reserve	1876-1898	10 058	88.9
USDA Forest Service			
Luquillo Forest Reserve ^c	1903-1907	5040	44.6
Luquillo National Forest ^c	1907-1935	5040	44.6
Caribbean National Forest ^d	1935-2007	6184	54.7
Baño de Oro Natural Area ^e	1949-present	745	6.6
Luquillo Experimental Forest ^{d,f}	1956-present	10 638	94.1
Biosphere Reserve ^f	1976-present	11 274	99.7
LTER—Bisley Watersheds ^g	1985-present	~363	3.2
LFDP—Ecological Grid ^g	1990-present	16	0.1
Wild and Scenic Rivers ^h	2002-present	525	6.6
Río Icacos—scenic ^h	2002-present	74	0.6
Río Mameyes—wild/scenic ^h	2002-present	100	0.9
Río de la Mina— scenic ^h	2002-present	38	0.3
El Toro Wilderness	2005-present	4050	35.8
El Yunque National Forest ^d	2007-present	11 310	100.0

^aPercent of current forest area of 11 310 ha.

^bEstimates (Domínguez Cristóbal 1997a).

^cU.S. Department of Agriculture, Forest Service (1995), see endnotes.

^dFrom 1935 to 1970, the designation Caribbean included land located outside of the Luquillo Mountains. Caribbean National Forest and Luquillo Experimental Forest are coterminous, the second name recognizes research activities. Caribbean changed to El Yunque, which is the current name.

^eProposed expansion of 1835 ha will bring the Baño de Oro to a total 2580 ha (U.S. Department of Agriculture, Forest Service 1997a).

^fAreas according to dates listed. Currently, both are 11 310 ha.

^gLong-term monitoring areas: LTER = Long Term Ecological Research; LFDP = Luquillo Forest Dynamics Plot.

^hEstimate of 525 ha includes wild and scenic river corridors and adjacent recreation areas (U.S. Department of Agriculture, Forest Service 1997a). Linear corridor totals for the 3 rivers: Río Icacos (scenic) = 3.7 km; Río Mameyes (scenic) = 1.6 km and (wild) = 3.4 km; Río de la Mina (scenic) = 1.9 km. Corridor areas are arbitrarily estimated at 100 m on each side of the respective rivers.

and practices governing surveys, titles, registration, and reservations. And it has been under more administrative directions regionally, is the smallest separately administrated area, and the closest tied to Forest Research, of any Forest in the entire National Forest system.”

Management of national forests involves livestock grazing, timber harvest, mining, water resources, wildlife, and recreation. All received attention at some time during the forest’s first 50 years (U.S. Department of Agriculture Forest Service 1997a, 1997b; Wadsworth 1951, 1952a, 1952b, 1970). Nearly a century of research in the Luquillo Mountains provided much information on tree species composition,

tree size, growth, regeneration, and ecology (Britton and Wilson 1923, 1930, Little and Wadsworth 1964, Little and Woodbury 1976, Little and others 1974, Odum and Pigeon 1970, Wadsworth 1951) as well as hurricane impacts and subsequent recovery (Walker and others 1991, 1996). Human settlement, including past agriculture and tree planting at lower elevations, has imposed changes on the landscape since the early 1800s (Aide and others 1996, Marrero 1948, Scatena 1989, Wadsworth 1970, Weaver 1989a, Weaver and Bauer 1986, Zimmerman and others 1995). Terrain above 600 m in elevation largely escaped human intervention because of the inaccessible steep slopes and heavy rainfalls (Lugo 1994; Wadsworth 1949, 1950; Weaver 1972).

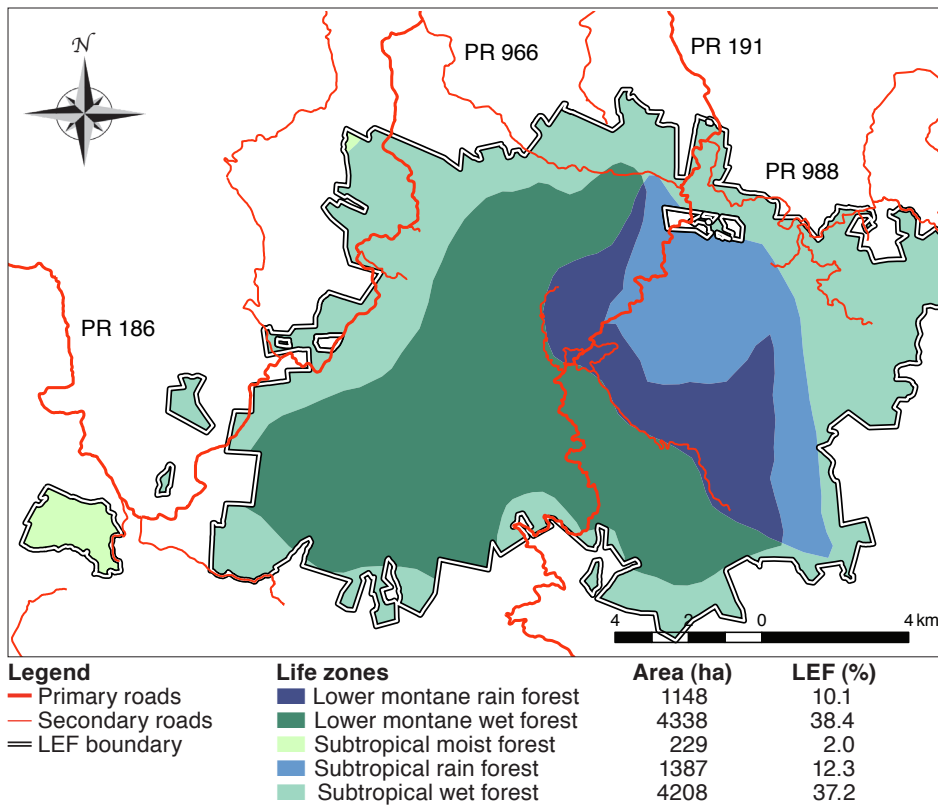


Figure 2—Ecological Life Zones within the Luquillo Experimental Forest.

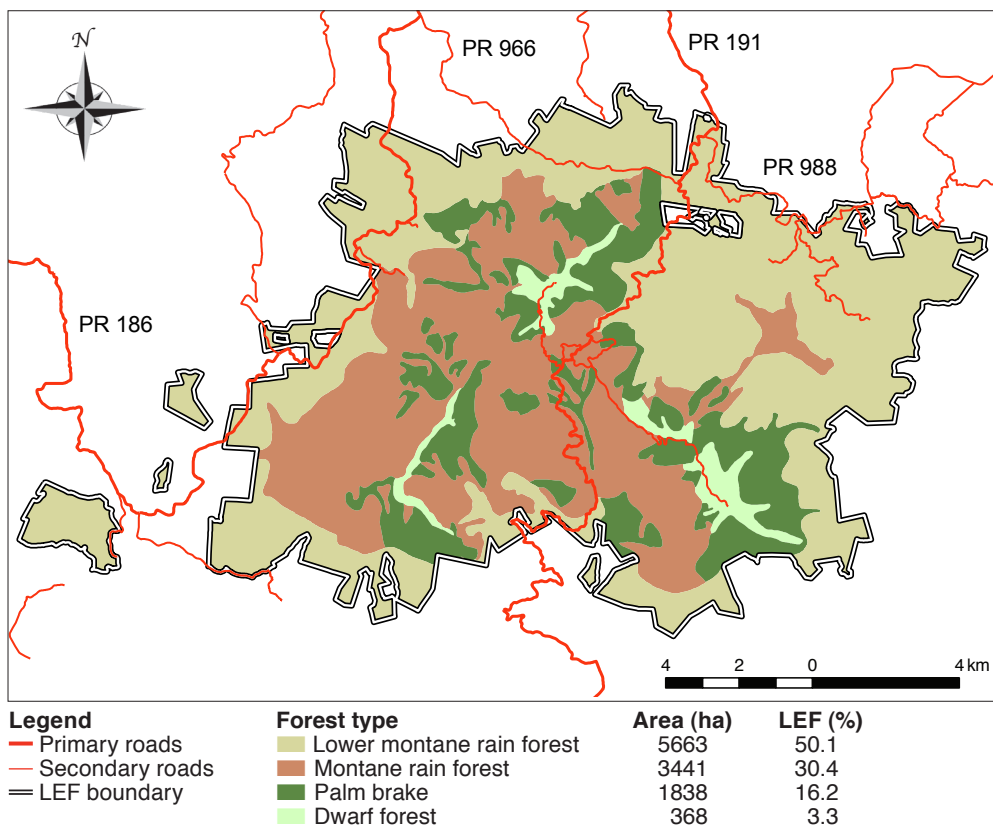


Figure 3—Forest types within the Luquillo Experimental Forest.

OBJECTIVES

One of the first observations made by foresters at the new Tropical Forest Experiment Station in 1941 was that “study of the existing literature showed that no works on forestry in Puerto Rico had been published, but a few good botanical works are available” (Anon. 1941, page 4, see endnotes). Since then, a considerable amount of forestry and ecological research has been carried out. However, the highlights of those efforts have never been conveniently summarized into a reference document. The purpose of this report is to provide an overview of the LEF’s resources and an orientation to research and management activities carried out on the forest, especially with regard to forestry:

- A chronology of major past activities or events which had an impact on the forest environment since European discovery.
- Background information on geology, physiography, soils, climate (hurricanes and recovery), water resources, flora, vertebrate fauna, classified plants and animals, scenery, recreation, roads, and trails.
- Detail on tree species composition, growth by forest type, and silvicultural activities, with special interest in permanent plot monitoring.
- A description of environmental gradients within the Luquillo Mountains along with the results of recent sampling of tree species by elevation and topography within different forest types.
- Information on plantings of native and exotic tree species for different purposes.
- General information on major research projects carried out at particular locations such as the Baño de Oro Research Natural Area, Bisley watersheds, the El Toro Wilderness Area, the El Verde field station, Pico del Este, Pico del Oeste, and scattered permanent and temporary plots.
- A concise summary of current planning and management issues on the forest.
- Maps showing the location of places mentioned in text.
- Some little known observations and facts about the LEF.

Much of the information regarding tree distributions and forest types was derived from a system of permanent plots established throughout the forest from 1943 to 1956. Figures, tables, and photographs illustrate much of this material. General ecological observations have also been incorporated into the text; however, detailed studies about watersheds and aquatic invertebrates, other fauna (i.e., bats, birds, lizards, frogs, and fishes), soils, and nutrient cycling are outside of the scope of this review. Plant nomenclature is based on relatively recent work (Liogier 1985, 1997). Authorities for plant species not listed in appendices appear in text.

Chapter 1. HISTORICAL PERSPECTIVE

The Luquillo Mountains have a long history that involves pre-Columbian cultures, Spanish colonization, gold mining and timber exploitation, the construction of access roads and facilities, and ultimately forest management and research. Details and most citations for the following historical section appear in the chronology (appendix A).

Pre-Colonial Era

Archaeological finds confirm the presence of pre-Columbian cultures in Puerto Rico around 300 B.C. and new discoveries possibly date to 2,000 years B.C. or earlier. During the pre-colonial era, the forests on the lower slopes of the Luquillo Mountains provided indigenous cultures with a source of food and materials for the construction of shelters and boats. However, the impact of these groups on forest resources was minimal. Archaeological discoveries—including petroglyphs near and within the forest—and pre-Columbian names for different sites (e.g., El Cacique, El Yunque, and Cubuy) indicate that native peoples were familiar with the mountains. The Luquillo Mountain summits, visible for about 100 km offshore, were likely used as a geographical reference by indigenous sailors; moreover, the mountaintops were probably the first lands sighted by Spaniards as they approached the island from the southeast.

Spanish Arrival, Exploration, and Settlement

Europeans made contact in Puerto Rico during the 1490s and by the early 1500s colonization had begun in the river valleys flowing out of the Luquillo Mountains. At that time, the island's indigenous peoples were in conflict. Soon, gold was found in the sands of Río Blanco, Río Canóvanas, Río Espíritu Santo, Río Fajardo, Río Grande, Río Mameyes, Río de la Mina, Río Prieto, and Río Sabana. The first discovery was in 1509, and placer mining was underway in the Río Fajardo and Río Blanco around 1513. Mining was the island's most important economic activity during the early 16th century, including the eastern mountains. The period of greatest mining activity ended around 1530 when the houses of miners were attacked and burned. Forced labor, introduced diseases, confrontations, and migrations elsewhere devastated the island's indigenous population by the mid-1500s. As late as 1582, colonists reported the mountains as unsafe because they were still occupied by hostile groups. Mining continued into the 20th century along several streams, including the Río Mameyes where gold was sought in the upper watershed



TOP: Petroglyphs are found within the Luquillo Experimental Forest (LEF), including sites in the Quebrada Jiménez, La Coca, Río Cubuy, Río Icacos, Río Comándulas, and Río Sabana watersheds, and near La Mina peak. (Photo from IITF files) BOTTOM: A pre-Columbian stone ax probably used between 600 and 1500 A.D. was found during survey activities within the LEF. (Photo by Iván Vicéns)



TOP: Gold placer mining was common along prominent Luquillo Mountain streams. Surnames of past miners such as Guzmán, Jiménez, and Toro survive on maps of the forest and surrounding areas as do the names of streams such as Río de la Mina and Quebrada Baño de Oro. (Photo from IITF files) BOTTOM: An olive jar, possibly used during exploration for gold during the Spanish colonial period between 1500 and 1700 A.D. was found at high elevation in the Luquillo Experimental Forest. (Photo by Iván Vicéns)

until 1870 and below the bridge referred to as Puente Roto until 1946. Locally, mining had an impact in the mountains. Mining camps depended on felled trees for the construction of tunnels, dikes, canals, shacks for protection, corrals for livestock, fuelwood, and the transport of equipment (Anderson-Córdova 2005). Throughout this period, the Spanish used the resin from *Dacryodes excelsa* to caulk their ship timbers.

During the 1600s, Puerto Rico remained isolated with only three populated areas and residents lived through contraband. In the 1730s, coffee was introduced and planted on the lower slopes of the Luquillo Mountains. Settlement in eight towns surrounding the Luquillo Mountains took place between 1772 and 1890, with the greatest influx after 1820. In 1815, the Cédula de Gracias conceded Crown Lands on the island for agricultural development, stimulating the local economy through new farms and businesses. During the 1830s, some of the lands made available were situated in the Luquillo Mountains. Between the mid-1830s and the mid-1890s, timbers were cut on the lower slopes of the mountains, including the Bisley, Jiménez, and Mameyes watersheds, and exported through the coastal town of Luquillo. Subsistence crops were planted as Spanish Crown lands decreased in area. As early as 1839, however, the Spanish expressed concern regarding the protection of forests, fish, and wildlife within the mountains. In 1853, two Spanish foresters were sent to survey and manage Crown Lands, including those of the



Timber cutting occurred in the lower montane rain forest and the montane rain forest from the time of initial settlement through the early 1950s. (Photo from IITF files)

Luquillo Mountains. The 19th century in Puerto Rico was characterized by a rapid increase in population, an increased demand for agricultural land, poor farming practices, constant political disturbances, a lack of communication between metropolitan centers and the rural population, and a scarcity of personnel and budget for forestry activities—all of which led to the dramatic decline of the island's forest cover (Domínguez Cristóbal 1989).

Forest Proclamation and Land Acquisition

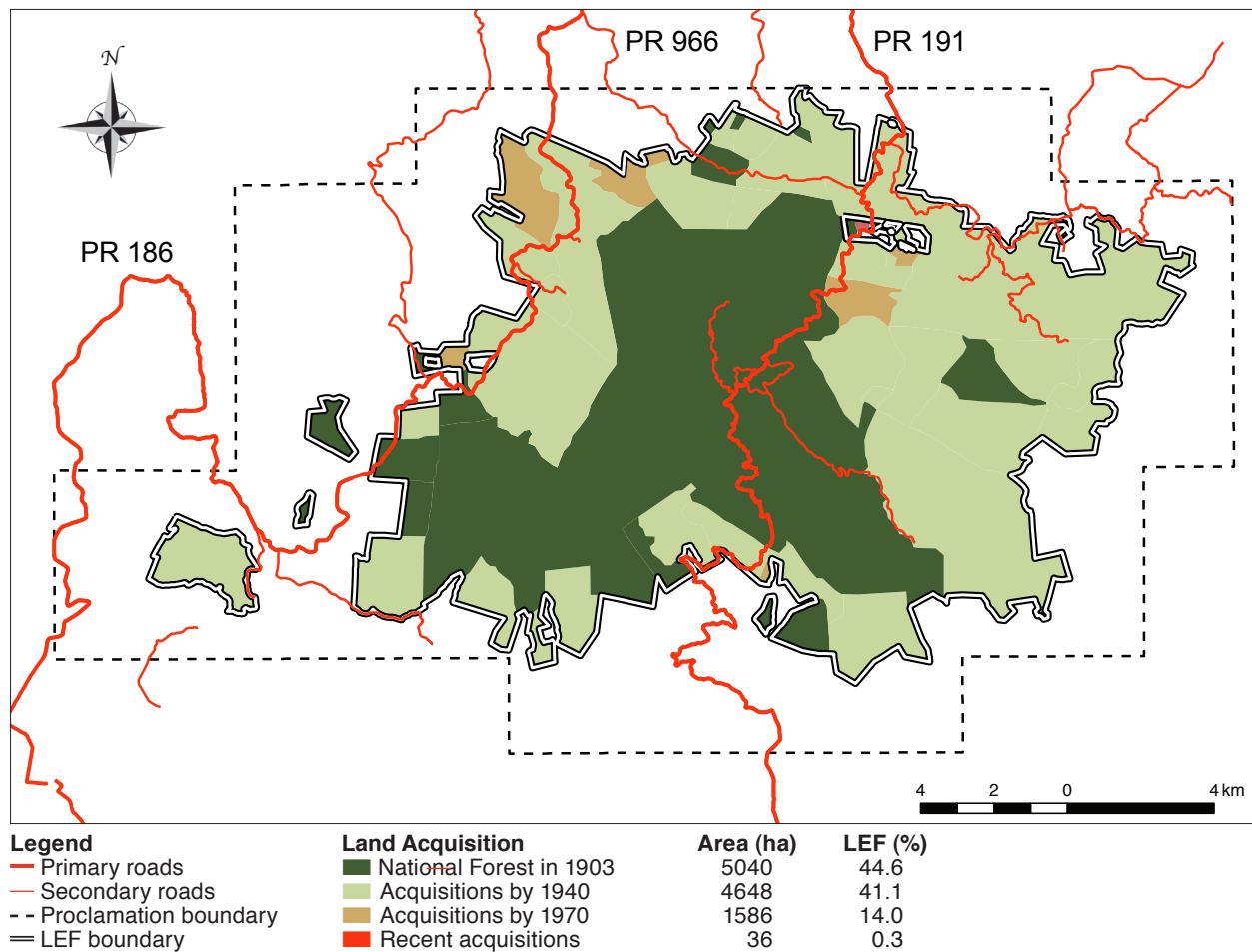
In 1876, Spanish King Alphonso XII proclaimed forest reserves in Puerto Rico, including the 10 000 ha Luquillo forest reserve. In 1885, a forest guard was assigned to patrol the Luquillo Mountains. At that time, transportation problems were a major deterrent to timber exploitation. In 1898, the Spanish Crown ceded Puerto Rico to the United States in the Treaty of Paris. By then, most of the island's original forests had been cut over. However, the Luquillo Mountains still protected about 16 000 ha of forest and shrub land, including nearly 2300 ha of virgin forest at higher elevations. In July 1898, Puerto Rico was renamed Porto Rico, a Federal designation that would remain until May 1932.

Between 1891 and 1897, two acts (i.e., Land Revision Act and Organic Administrative Act) passed by the U.S. Government allowed the President to set aside forest lands; subsequently in 1903, President Theodore Roosevelt proclaimed the transferred Crown lands as the Luquillo Forest Reserve. The original proclamation boundary encompassed about 25 650 ha classified as public forest as soon as the government might acquire the lands; later, the boundary was modified. About 1200 ha remained as property of the people of Puerto Rico until 1916 when the land was legally turned over to the Federal government by the local legislative assembly. Between 1903 and the early 1930s, the national forest contained 21 parcels of land totaling 44 percent of today's LEF (fig. 4). Between 1933 and 1949, an additional 48 parcels totaling 5625 ha, or nearly 50 percent of the current land area, were acquired or purchased by the Federal government and added to the national forest. In 1970, another 19 parcels amounting to about 635 ha, or < 6 percent of the total area, were attained through exchange. Toro Negro and St. Just, previously Forest Service, U.S. Department of Agriculture, properties in other parts of the island, were exchanged for tracts in the Luquillo Mountains and added to the forest. Finally, in the early 1990s, four more parcels with about 37 ha, or about 0.3 percent, were purchased, bringing the grand total to about 11 310 ha.

The Luquillo Mountains total about 19 660 ha and are administratively located within eight municipalities: Ceiba (5.4 percent), Fajardo (5 percent), Juncos (4.1 percent), Las Piedras (5.6 percent), Loíza (11.5 percent), Luquillo (10.8 percent), Naguabo (22.6 percent), and Río Grande (35 percent) (Wadsworth 1949). Today, the LEF is comprised of one major block of forest of about 11 000 ha and several small, isolated parcels: three in the southwest (i.e., Arroyo with 60.3 ha, La Condesa with 219.7 ha, and Sandoval with 12.6 ha), one to the south (15.7 ha), and other smaller tracts near the northeastern and southeastern borders. Moreover, one major inholding, Barrio Mameyes Segundo, occupies 54 ha and is situated east and west of PR route 191 at km 7.0 (U.S. Department of Agriculture, Forest Service 1997a) (fig. 1). Three other smaller inholdings are located in the same vicinity, and two others are situated along PR route 186. The total area of inholdings is about 70 ha.

Opening of the Forest

From 1903 until 1918, the U.S. Government was not able to dedicate much attention to the newly acquired national forest. Other challenging overseas commitments, including the construction of the Panama Canal (1903-14), negotiations for the purchase of the U.S. Virgin Islands (pre-1917), and World War I (1914-18) assumed center stage. During this period, several activities like placer gold mining, timber extraction, and charcoal production continued in the mountains. In



Land acquisition

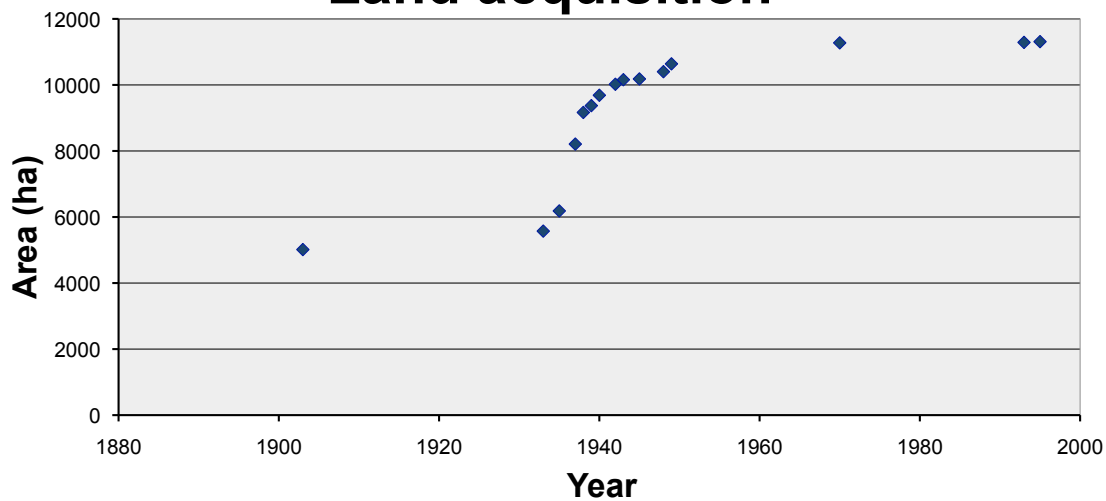


Figure 4—Acquisition of properties (tracts) in the Luquillo Experimental Forest.

1905, narrow trails existed to El Yunque, sites across the mountains to the south, and into the Espiritu Santo and Jiménez watersheds. In 1910, a visiting U.S. Department of Agriculture official found property ownership records in the mountains to be in a state of chaos. Between 1912 and 1916, the national forest was surveyed, mapped, and the boundaries were monumented. Those farming within the boundaries were allowed to continue by permit.

Between 1912 and 1926, water was diverted from the forest borders to supply the needs of communities and towns surrounding the Luquillo Mountains. In 1928, construction began on the Río Blanco Hydroelectric plant with intakes on the Río Cubuy, Río Icacos, Río Prieto, and Río Sabana. During the 1970s, the same system supplied water to the Roosevelt Roads Navy Base near Ceiba and the island of Vieques. In 1950, San Juan began to receive water via the reservoir on the Río Grande de Loíza watershed. Today, two new reservoirs are planned or under construction; one on the Río Blanco south of the forest and the other near the town of Juncos.

From 1919 to 1926, about 60 km of horse trails were laid out to patrol forest boundaries. Several construction projects began in the mountains in the 1920s and their development continues to the present, with the major efforts taking place in the 1930s. Between 1926 and 1929, the first section of PR route 191 was built between Palmer and Catalina (fig. 1). In 1933, the Emergency Conservation Program began extensive reforestation, road construction, and recreational

improvements within the mountains. Moreover, in 1928, a narrow gage cable railway was built in the Río Blanco watershed just below the southern boundary of the forest to develop water control structures on the Río Icacos and nearby streams originating in the Luquillo Mountains.

U.S. military involvement in the Luquillo Mountains began in 1933 when U.S. Army reserve officers briefly supervised Puerto Rico's Emergency Conservation Program; later cooperation continued with the Forest Service in Civilian Conservation Corps (CCC) projects. In 1942, preparations for World War II in the Caribbean basin were initiated by army engineers who built a road and laid a telephone line to El Yunque peak where the U.S. Army Signal Corps operated an early warning radar system to detect enemy aircraft. In the 1960s under Forest Service permits, the Atomic Energy Commission, as part of the "Atoms for Peace" program, initiated the gamma radiation project near El Verde to determine the ramifications of using nuclear devices to excavate a proposed sea level canal in Panama. In 1963, the U.S. Army carried out a 0.4 ha defoliation experiment testing the herbicide Agent White (2, 4-D, and Picloram without dioxin). In the same year, the U.S. Navy used the electronic site at Pico del Este to trace missiles on a target range in nearby Vieques. Later in the 1960s, surveillance radar was installed for different agencies, among them the Federal Aviation Administration (FAA), which monitored flights approaching the San Juan airport. In 2003, the U.S. Navy departed from the Roosevelt Roads Naval Station and discontinued its use of the Pico del Este electronics site.



Construction of PR route 191 from Palmer to Naguabo started in 1926 and was completed in 1942. The road traversed the Luquillo Mountains and later provided access via tributary roads to the summits of El Yunque, Pico de Este, and Pico del Oeste. (Photo from IITF files)

From 1935 to 1943, the CCC implemented its work program in cooperation with the Forest Service, building 100 km of roads and 80 km of trails to open the forest for human use. At La Mina, CCC workers built two picnic areas, 18 stone cabins that were later converted to picnic shelters, two bathing pools (i.e., Baño de Oro and Baño Grande), a fish hatchery, and the El Yunque pavilion, which later became the Rain Forest restaurant. Also built on nearby summits were the Mt. Britton tower and El Yunque radar post, and at lower elevations barracks and overnight shelters on the El Toro and El Yunque trails. Opened to the public in 1934, the La Mina recreation area was immediately popular among islanders. The recreation area and subsequent improvements remain today. However, an attempt to introduce rainbow trout into the LEF's streams failed. In 1935, applications were accepted for the construction of eight summer cottages near La Mina. Soon after, two spur roads, PR routes 930 and 9938 were built to accommodate about 20 additional cottages. Later, all but three of the cottages were removed.

In 1937, the Puerto Rico Reconstruction Administration built the El Verde field station, which has served as a major research site since the early 1960s. In 1949, construction of the El



TOP LEFT: Completed in 1982, the Catalina Service Center houses the administrative offices of Forest Service specialists in wildlife, water resources, and forest management. (Photo by Peter L. Weaver) BOTTOM LEFT: Rainbow trout eggs imported from the United States during the mid-1930s were introduced into this circular pool along one of the trails within the Luquillo Experimental Forest. (Photo by Iván Vicéns) TOP RIGHT: Mt. Britton tower was built in 1938 to commemorate Nathaniel Britton, a New York Botanical Garden botanist, who collected plants during expeditions to El Yunque from 1913 to 1917. (Photo by Iván Vicéns) BOTTOM RIGHT: El Yunque observation tower and storage buildings were constructed in 1938 as defense measures. (Photo by Peter L. Weaver)

Yunque Peak Electronics Communication Center began, and between 1974 and 1995, the facilities were consolidated. In 1950, the Eliza Colberg Girl Scout Camp was dedicated near El Verde. In 1963, the radar facilities at Pico del Este and the Yokahú tower along PR route 191 were both opened. In 1976, the Youth Conservation Corps (YCC) program began operating and in 1982 the Catalina Service Center opened as the new Forest Service office complex.

PR route 191, the principal forest road, was completed in 1942 and served the public until 1970 when it was covered by major landslides in the Río Icacos watershed. Repairs were attempted in the mid-1970s but reconstruction plans were abandoned in 1992. Another 16 roads still present today were constructed within or along forest borders at different times (fig. 5) (table 3). These may be conveniently divided into three major groups:

1. Tributary roads to PR route 191 (Mameyes-Río Blanco road), which include the PR route 930 (Molindero road), PR route 9938 (Mt. Britton road), and FS-10 (El Yunque road) were built in the late 1930s. FS-27 (Pico del Este road)

was built from 1958 to 1962. These roads served to access recreation areas or Federal Government observation points.

2. PR route 186 (El Verde Road) was built in stages between 1945-48 and 1955-57. Its major tributary roads, PR route 946 (Cubuy road), PR route 956 (Guzmán Arriba road), and PR route 9948 (no local name) were constructed between 1935 and the 1970s to serve settlements within the respective areas. The PR 911 (Sonadora link), PR 903 (El Verde station link), and PR 963 (Eliza Colberg link) connections with PR route 186 were built between the late 1930s and late 1940s to access Forest Service facilities along the western boundary of the LEF. The Youth Conservation Corps link was built in 1973.

3. The last group of roads was located within or near the northern boundary of the LEF. PR route 966 (Jiménez road), PR route 983 (Sabana-Pitahaya road), and PR route 988 (Sabana-Catalina road) connected major highways and settlements. These roads could also serve for timber extraction that was being contemplated along the northern boundary of the LEF. Two smaller roads, PR 9915 (Bisley road) and PR 915

Table 3—Major roads and connecting roads within or bordering the Luquillo Experimental Forest

Date(s) ^a	Route No. length (km) ^a	Road name	Brief comments: road purpose and notes
PR route 191 and tributary roads			
1926-42	PR 191 (18.6)	Mameyes-Río Blanco	Forest highway dissected the LEF until 1970 landslide blocked road at km 13 ^b
late 1930s	PR 930 (1.3)	Molindero	Summer cottages near the La Mina Recreation Area.
late 1930s	PR 9938 (0.8)	Mt. Britton	Summer cottages; also serves as access to Mt. Britton trail.
late 1930s	FS 10 (2.0)	El Yunque	Military observation post before and during World War II; paved in 1943.
1958-62	FS 27 (5.0)	Pico de Este	Access to Pico del Este radar dome used by the Federal Aviation Administration; also for U.S. Navy maneuvers off Roosevelt Roads and Vieques until 2003.
PR route 186 and tributary roads			
1943-57	PR 186 (8.0)	El Verde	Built in stages to serve the public and access the western part of the forest; rock surfaced by 1943; later construction carried out in 1945-48 and 1955-57.
1934-47	PR 956 (0.6)	Guzmán Arriba	Built in stages to serve the Guzmán Arriba area.
late 1930s	PR 911 (0.1)	Sonadora link	Access to a water station on LEF land.
~1938	PR 903 (0.3)	El Verde link	Access to the El Verde Field Station; later improved.
~1948	PR 963 (0.5)	Scout camp link	Access to Eliza Colberg Girl Scout Camp.
~1955	PR 946 (0.7)	Cubuy	To serve the public near isolated LEF outlier property called La Condesa.
~1973	PR 9948 (1.0)	None	To serve public living near isolated southwestern corner of the LEF.
~1973	Link (0.2)	Job Corps link	Access to Youth Conservation Corps (Job Corps) Camp
Routes along or near northern or northwest forest border			
late 1960s	PR 966 (3.4)	Jiménez	Originally to export timber from the proposed Jiménez working area.
late 1960s	PR 9966	Jiménez (extension)	Connect PR 186 and PR 191.
~1962	PR 983 (0.5)	Sabana-Pitahaya	Serve Sabana and vicinity; later extends south to northeastern forest corner.
1965-72	PR 988 (4.5)	Sabana-Catalina	Connect highways PR 191 and PR 983 near Sabana.
1942	PR 915 (1.0)	Cristal	Access timber in upper Cristal valley; never completed; today, a hiking trail.
1943	PR 9915 (1.3)	Bisley	Originally to export timber; since 1985 to carry out LTER research. ^c

^aDates and road lengths (km) are best estimates based on approved plans or purported construction dates (El Yunque Forest 2009, see endnotes).

^bLEF = Luquillo Experimental Forest; Source: U.S. Department of Agriculture, Forest Service (2009), see endnotes.

^cLTER = Long term Ecological Research.

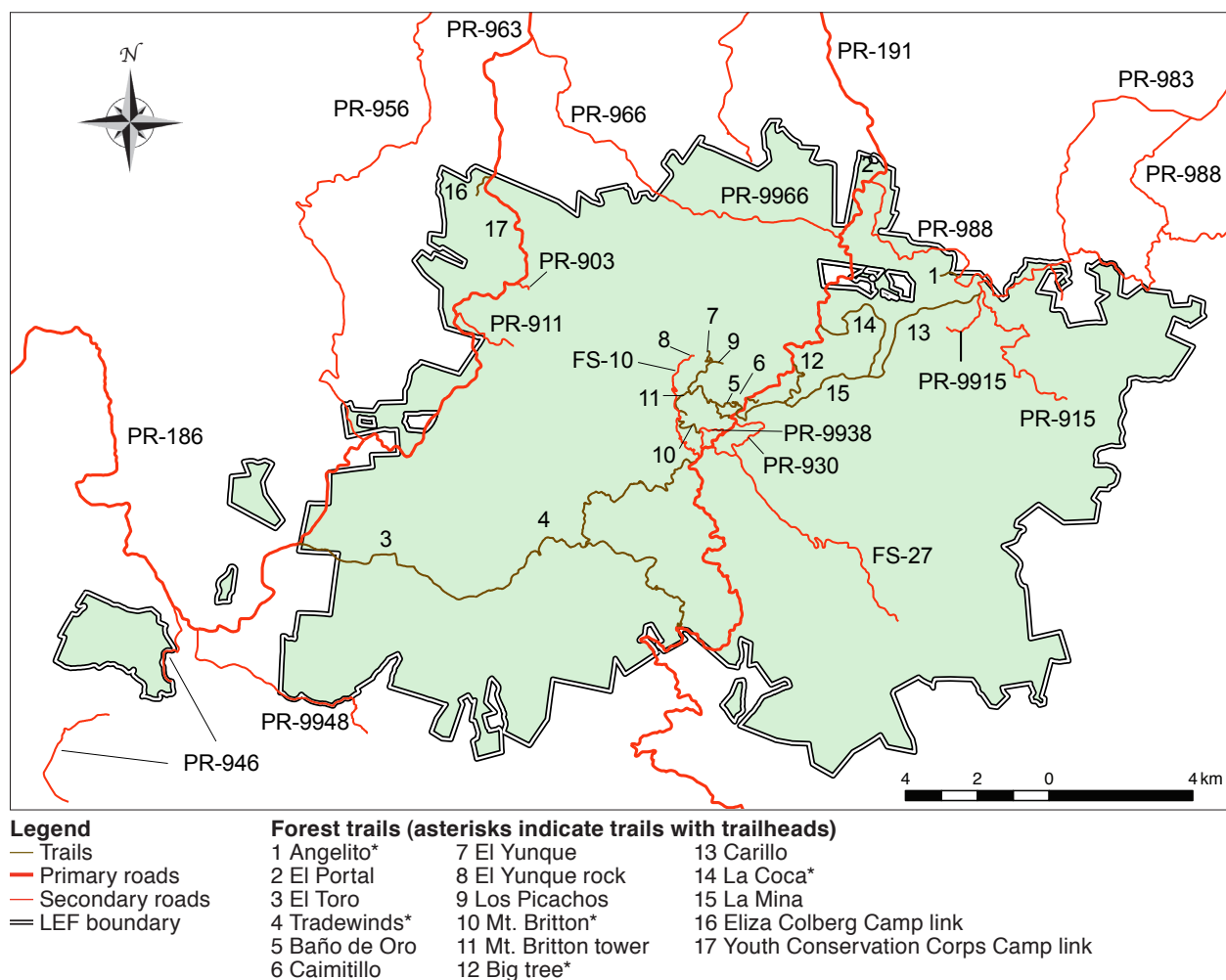


Figure 5—Roads and hiking trails in the Luquillo Experimental Forest.

(Cristal road), which served communities in the vicinity, were improved in anticipation of logging planned for the late 1950s.

In 1996, the El Portal Rain Forest Center opened to the public. More than 60 years had elapsed since the first recreation area had been opened at La Mina and about 35 years since the first small visitor information center served the public at that site.

Management of the Forest

For nearly a century, island foresters have been involved in forest planning and management. In the 1920s, sawmills began to operate at low elevations near the forest boundary. The most valuable timbers for furniture were *Dacryodes excelsa*, *Magnolia splendens*, *Manilkara bidentata*, and *Ocotea moschata*. In 1931, the first mahogany plantations were established within the forest and by 1949 all tree plantings totaled >1500 ha (fig. 6).

In 1932, the forest supervisor (appendix B) completed a policy statement which outlined forest protection and timber production. Before 1932, no timber was sold in the national forest but the Forest Service allowed the removal of trees damaged by Hurricane San Felipe in 1928. Between 1932 and 1962, four systematic forest surveys were implemented, including a timber cruise on 6900 ha, to determine stocking, sawtimber, and regeneration. Also, between 1932 and 1949, timber sales were carried out on 2150 ha yielding >293 000 m³, including sawtimber (11 percent), pole wood (6 percent), and fuelwood (83 percent). From 1937 to 1943, a sawmill located in Sabana cut lumber for the use of temporary residents (i.e., “parceleros” in Spanish) living within the forest. The number of parceleros increased from one person in 1919 to about 220 families by 1940; by 1953, all of the parceleros had departed from the forest. Parceleros had a house, cistern, and access to land for a period of time. They occupied tracts where they were allowed to intercrop foodstuffs with trees (i.e., a system called taungya or agroforestry), gradually reforesting Federal lands.

In 1945, timber stand improvement was carried out to alleviate a post-war energy crisis and provide jobs. Also in 1945, exotic bamboo was first introduced to help stabilize soils. In 1949, kerosene stoves eliminated the charcoal market but logging for furniture quality *Magnolia splendens* continued into the early 1950s, reaching lower elevations of montane forest in a couple of areas.

In 1950, the Puerto Rico Department of Agriculture set up a tree nursery along the northern forest border at Catalina where it operated until 1974 (fig. 6). In the early 1950s, a multiple use and timber management plan was devised for the forest. Among the topics considered were timber production, watershed conservation, research, protection of high elevation forests, and parrot habitat. Timber production areas were divided into working areas (i.e., about 20 percent of the forest) based on previous forest inventories (table 4). Tree species were classified according to their value based on wood properties, size, resistance to pathogens, and availability (table 5). In 1955, logging within the forest finally ceased when imported mahogany depressed the demand for local timber. However, in 1956 the Forest Service began building timber access roads to the Bisley, Espíritu Santo, Jiménez, and Sabana working areas along the northern and western LEF boundaries (fig. 5) (table 4). The roads were in anticipation of future forest harvests in areas designated for timber management (fig. 7).

Between 1956 and 1978, pilot forest management was initiated on >2800 ha of lands designated for timber production. Field activities included the liberation of crop trees and the establishment of plantations. In 1961, an arboretum was set up at Caracoles along PR route 186 in the driest part of the forest. Line planting of mahogany was started in 1963 on the lower northern slopes near Sabana and by the mid-1970s plantings covered about 1275 ha. In 1965, the Forest Service drafted a timber management plan. The plan was based on past inventory information and growth data that allowed estimates of timber volumes for sustainable harvest. In 1986, the Agency developed a more elaborate plan for land use and resource management, this time with invited comments from the public. The 1986 plan was accompanied by several management alternatives, including timber production. There was also a record of decision and an environmental impact



ABOVE: A plantation of *Cordia alliodora* planted in the early 1930s at Del Valle averaged 3 m in height after 1.3 years. ABOVE RIGHT: From the 1920s to the 1940s, three sawmills operated in the lower Espíritu Santo and Sabana watersheds supplying lumber from the lower montane rain forest. (Photos from IITF files)

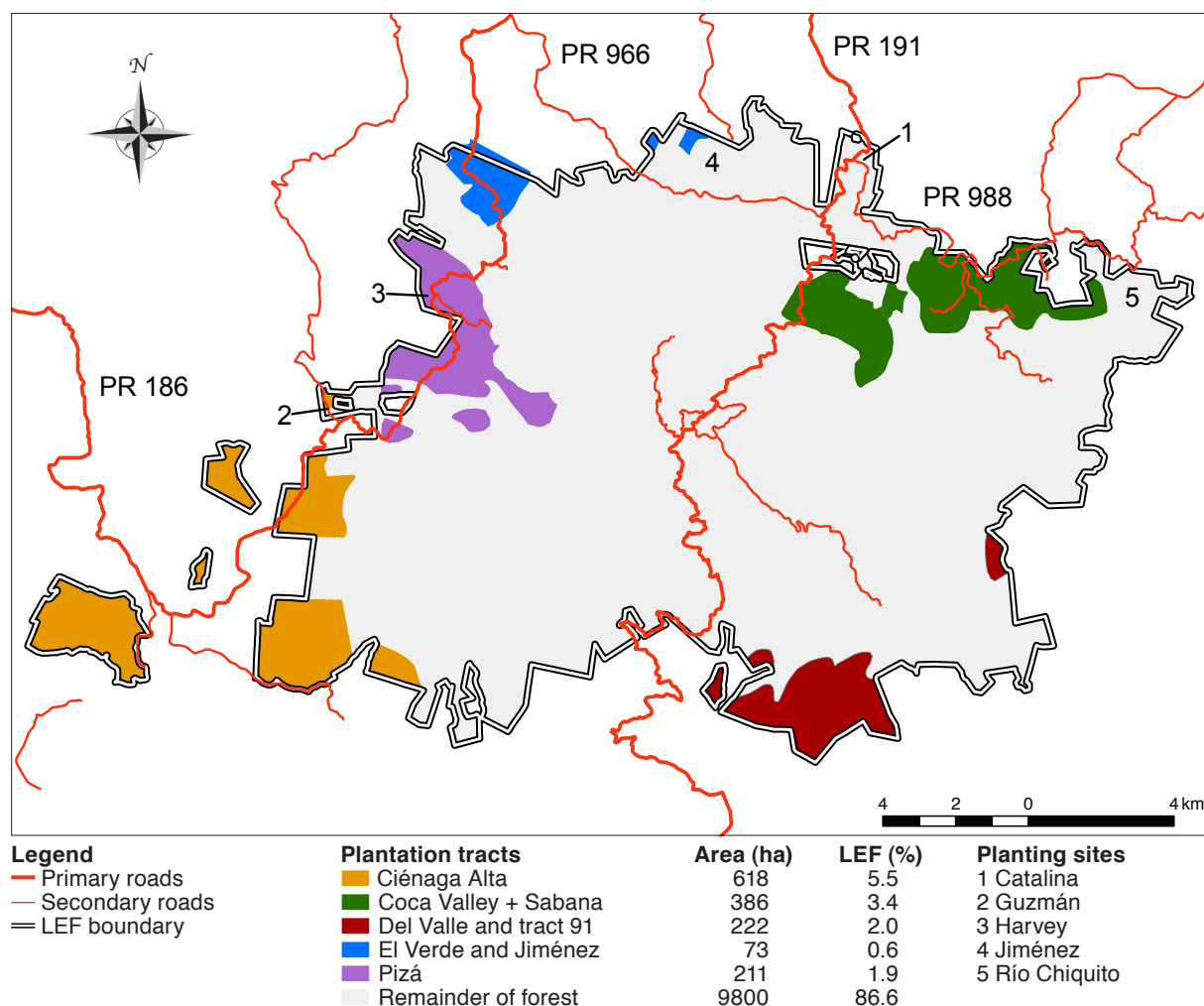


Figure 6—Plantation sites in the Luquillo Experimental Forest in 1947.

statement. By the late 1980s, however, the public no longer considered logging to be appropriate within the LEF. The plan was revised and adopted in 1997 without timber management.

In 1992, the first interpretative plan for public education was completed for the forest. This plan was later revised and updated into a more comprehensive interpretative and conservation education master plan. In 1999, an environmental education program for teachers was developed to complement tours within the forest; moreover, in 2002, interpretative guides were published in English and Spanish. A severe drought in the mid-1990s and increased use of the national forest resulted in additional concerns. An emergency plan was devised in 1994 to supply water from forest streams during periods of prolonged drought. Moreover, a forest transportation study completed in 2002 concluded that a mass transit system should be implemented for PR route 191 to alleviate congestion during holidays and other periods of heavy use.

The entire LEF was proclaimed as a Biosphere Reserve in 1976 (table 2). Other separate designations within the forest include: the Baño de Oro Natural Area in 1949, a long-term ecological research (LTER) site in 1985, and a long-term ecological grid site (i.e., the Luquillo Forest Dynamics Plot or LFDP) in 1990. Also designated were three stretches of rivers as scenic and one stretch as a wild river in 2002, and the El Toro Wilderness area in 2005. All of the separately designated areas total about 70 percent of the forest.

Research and Training in the Forest

Research began with the earliest field biologists and continues today with various ongoing projects. In 1797, Pierre Ledru explored northeastern Puerto Rico and collected plant specimens. During the 19th and 20th centuries, several botanists including the Swiss Heinrich Wydler (1797-98), Danish Henrick F.A. von Eggers (1883), German Paul Ernst



TOP LEFT: Typical forest home. Between 1919 and 1953, forest residents (i.e., *parceleros* in Spanish) occupied tracts where they were allowed to intercrop foodstuffs with trees (i.e., a system called *taungya* or agroforestry), gradually reforesting parts of the Luquillo Experimental Forest. TOP RIGHT: Charcoal production, common in several areas within the Luquillo Mountains, was permitted after hurricanes and during silvicultural operations. The practice survived until the introduction of kerosene stoves in 1949. ABOVE: Located along the Luquillo Experimental Forest border, the Catalina nursery produced seedlings for reforestation projects between 1950 and 1974. (Photos from IITF files)

Emil Sintenis (1885), and Puerto Rican Augustin Stahl (1898) visited the Luquillo Mountains and collected plants. Americans Percy Wilson (1902) and W.A. Evans (1902) also collected plants in the mountains, ascending to El Yunque. Although the German Ignatz Urban (1903-11) never visited the island, he collected plants from the West Indies, including Puerto Rico, and later published *Flora Portoricensis*. Between 1913 and 1917, Nathaniel Britton and coworkers Henry A. Gleason and Melville T. Cook of the New York Botanical Garden contributed to the scientific survey of Puerto Rico and the U.S. Virgin Islands, publishing their detailed observations between 1923 and 1930. Between 1905 and 1932, several other visiting U.S. scientists provided information regarding the mountains, including: John C. Gifford, Louis Murphy, and E. Murray Bruner on forest resources; Alexander Wetmore on birds; H.E. Anthony on native bats; and W.P. Kramer on forest policy. In 1933, Leslie R. Holdridge began a Forest Service herbarium, contributing numerous specimens collected from the Luquillo Mountains. Also in 1933, Howard Augustus Meyerhoff described the geologic resources of the island, including those of the Luquillo Mountains. The history of mining and the mineral prospects within the mountains were summarized 50 years later. Other well-known botanists and foresters working in the field from the early 1940s until the 1990s included Elbert L. Little, Jr., Frank H. Wadsworth, and Roy O. Woodbury. They published texts and numerous research papers on forest resources, including the trees of Puerto Rico. Henri A. Liogier, Luis F. Martorell, and Richard A. Howard, all prominent taxonomists active at the same time, published texts on the flora of Puerto Rico and the West Indies.

Between 1935 and 1939, small scale timber stand improvement was carried out in forests of the Espíritu Santo and Mameyes Valleys. In 1938, study plots were set up on 55 ha to evaluate the results. In 1939, the Tropical Forestry Experiment Station, now the International Institute of Tropical Forestry (IITF), was established under the McSweeney-McNary Act to implement forestry research in Puerto Rico. Prior to 1939, field experience guided forestry practices. During the Institute's 70 years, the staff published a forestry journal from 1939 until 1964, carried out about 2,600 research studies, tested >100 native and 350 introduced tree species, and established one of the best libraries on tropical forestry in the hemisphere. Many of the research documents and journal articles were based work in the Luquillo Mountains.

In 1943, long-term research began on a 0.72 ha permanent plot located at El Verde, and at the end of the decade local scientists summarized research on forest resources and plantations, producing a forest type map for the forest. By 1956, >400 permanent plots, including the pilot management study, had been established in three different forest types to determine species composition, stand characteristics, and timber production potential.

Table 4—Proposed working areas for timber harvest in the Luquillo Experimental Forest

Working areas ^a	Area ha
Cacique	502
Ciénega Alta	808
Cristal	499
Cubuy	289
Espíritu Santo	789
Fajardo	665
Gurabo	510
Icaco	1173
Jiménez	763
La Mina	732
Total	6730

^aSource: Wadsworth (1949).

Other resource studies were also undertaken over the years. In 1942, stream gaging stations were first monitored on the Río Espíritu Santo and the Río Icacos. In 1943, topographic maps were developed for the mountains, and in 1952 they were revised. During the early 1960s, the University of Puerto Rico began ecological studies in lower montane forest near El Verde and in 1990 the long-term ecological grid was established nearby. Dwarf forest research began at Pico del Oeste and Pico del Este during the mid-1960s and long-term ecological research started at Bisley in 1986. After the mid-1960s, scientific publications increased substantially appearing as journal articles, books, and Forest Service technical reports. Most of these publications concerned work carried out at the aforementioned sites.

After 1960, continued wildlife research in the Luquillo Mountains documented gains, losses, and changes in some animal populations. In 1963, *Eleuthrodactylus hedricki* (tree-hole coqui) was discovered and *Corvus leucognaphallus* (white-necked crow) was last recorded. In 1968, the study of the rare and endangered *Amazona vittata* (Puerto Rican parrot) was undertaken. Its population had declined from 200 to just 13 birds between the mid-1950s and the early 1970s. In 1968, the parrot recovery program was implemented through the cooperation of Federal and Commonwealth of Puerto Rico government agencies. In 1975, eight captive birds were placed in the La Mina barracks which was converted to a parrot aviary. In 1971, at a time when it was believed that all of the island's bird species were known, *Dendroica angelae* (elfin-woods warbler) was discovered in the LEF's dwarf forest.

Table 5—The classification of timber species in the Luquillo Experimental Forest^a

Forest type Scientific name ^b	Ranking ^c	Uses ^d	Wood ^e	Termites ^f	Mean annual increment cm yr ⁻¹ (no.) ^g	Mean annual increment cm yr ⁻¹ (no.) ^h
Lower montane rain forest						
<i>Alchornea latifolia</i> Sw.	37	P	L	21	0.21 (6)	0.38 (225)
<i>Alchorneopsis portoricensis</i> Urban	41	P			0.45 (4)	
<i>Andira inermis</i> (W. Wright) DC.	24	P	L	46		
<i>Beilschmiedia pendula</i> (Sw.) Hemsl.	17	C	L			
<i>Buchanania tetraphylla</i> (Aublet) R. Howard	4	F	L	69	0.19 (7)	0.69 (41)
<i>Byrsonima spicata</i> (Cav.) HBK	26	P	L	39	0.17 (9)	0.48 (61)
<i>Chrysophyllum oliviforme</i> L.	18	C				
<i>Cinnamomum elongatum</i> (Nees) Kostermans	16	C				
<i>Cordia alliodora</i> (Ruiz & Pav.) Oken	7	F	L	60		
<i>Cupania americana</i> L.	31	P				
<i>Dacryodes excelsa</i> Vahl	2	F	L	31	0.16 (167)	0.36 (207)
<i>Genipa americana</i> L.	21	C	L	34		
<i>Guarea guidonia</i> (L.) Slumer	1	F	L	70		0.81 (18)
<i>Guazuma ulmifolia</i> Lam.	36	P		33		
<i>Hernandia sonora</i> L.	23	C	L			
<i>Homalium racemosum</i> Jacq.	9	C	L	71	0.19 (4)	0.50 (36)
<i>Hymenaea courbaril</i> L.	13	C	L	88		
<i>Inga laurina</i> (Sw.) Willd.	29	P	L		0.14 (6)	0.46 (150)
<i>Laetia procera</i> (Poeppig) Eichler	38	P				
<i>Laplacea portoricensis</i> (Krug and Urban) Dyer	28	P			0.11 (5)	
<i>Linociera domingensis</i> Lam.	27	P		46		0.37 (20)
<i>Mammea americana</i> L.	15	C	L	30		
<i>Manilkara bidentata</i> (A. DC.) Chev.	8	C	L	58	0.12 (15)	0.55 (49)
<i>Matayba domingensis</i> (DC.) Radlk.	30	P	L		0.26 (33)	0.44 (96)
<i>Meliosma herbertii</i> Rolfe	20	C	L		0.07 (11)	
<i>Ocotea coriacea</i> (Sw.) Britton	40	P	L	53?		
<i>Ocotea globosa</i> (Aubl.) Schlect & Cham.	19	C		53?		
<i>Ocotea leucoxydon</i> (Sw.) Mez.	25	P	L	48		0.35 (128)
<i>Ocotea membranaceae</i> (Sw.) Howard	34	P	L	53?		
<i>Ocotea moschata</i> (Meisn.) Mez.	5	F	L	36	0.07 (23)	
<i>Ocotea nemodaphne</i> Mez.	22	C				
<i>Ocotea patens</i> (Sw.) Nees.	39	P				
<i>Ormosia krugii</i> Urban	32	P	L		0.37 (21)	0.48 (77)
<i>Petitia domingensis</i> Jacq.	6	F	L	51		
<i>Phoebe elongata</i> (Vahl) Nees	33	P				
<i>Pouteria multiflora</i> (A. DC.) Eyma	10	C	L			
<i>Schefflera morototoni</i> (Aubl.) McGuire	42	P	L		0.23 (36)	0.35 (193)
<i>Sloanea berteriana</i> Choisy	11	C	L	53	0.09 (31)	0.46 (66)
<i>Tabebuia heterophylla</i> (DC.) Britton	14	C	L	34	0.19 (10)	0.29 (514)
<i>Tetragastris balsamifera</i> (Sw.) Kuntze	3	F	L	45		
<i>Vitex divaricata</i> Sw.	12	C	L	42		
<i>Zanthoxylum martinicense</i> (Lam.) DC.	35	P	L			0.39 (5)
Means					0.18 (388)	0.46 (1559)

(table continued on following page)

Table 5 (continued)—The classification of timber species in the Luquillo Experimental Forest^a

Forest type Scientific name ^b	Ranking ^c	Uses ^d	Wood ^e	Termites ^f	Mean annual increment cm yr ⁻¹ (no.) ^g	Mean annual increment cm yr ⁻¹ (no.) ^h
Montane rain forest						
<i>Clusia clusioides</i> (Griseb.) D'Arcy	8	P			0.35 (5)	0.96 (2)
<i>Eugenia stahlii</i> (Kiaersk.) Krug & Urban	6	P	L			
<i>Henriettea squamulosa</i> (Cogn.) Judd.	10	P	L		0.08 (74)	0.09 (19)
<i>Homalium racemosum</i> Jacq.	2	C	L	71		
<i>Magnolia splendens</i> Urban	1	F	L	40	0.09 (32)	0.24 (1)
<i>Matayba domingensis</i> (DC.) Radlk.	9	P	L			
<i>Micropholis garciniifolia</i> Pierre	4	C	L		0.07 (144)	0.07 (226)
<i>Micropholis guyanensis</i> (A. DC.) Pierre	3	C	L	48	0.12 (170)	0.10 (12)
<i>Ocotea spathulata</i> Mez.	7	P	L		0.06 (45)	0.06 (7)
<i>Ternstroemia luquillensis</i> Krug & Urban	5	C				
<i>Weinmannia pinnata</i> L.	11	P				
Means					0.09 (470)	0.08 (267)

^aSource: Wadsworth (1952b).

^bNomenclature: Liogier (1985-97).

^cTentative ranking by forest type: Lower montane rain forest, 1 = best and 42 poorest (i.e., 1 to 7, furniture woods from most to least valuable; 8 to 23, construction woods most the least valuable; and 24 to 42, post woods from most to least valuable. Montane rain forest, 1 = best and 11 = poorest (1, furniture wood; 2 to 5, construction woods from most to least valuable; and 6 to 11, post woods from most to least valuable).

^dUse: F = furniture; C = construction; P = large post. Uses determined to some extent by availability of large diameter specimens (Wadsworth 1952b). See also: Little and Wadsworth 1964; Little and others 1974.

^eL = description of wood characteristics available (Longwood 1955, 1961).

^fTermite resistance index: low = 20, high = 100; *Nectandra* (*Ocotea*) spp. = 53? classed as a group (Wolcott 1946, 1950).

^gSource: Weaver 1983 (i.e., Tabonuco ridge (TR-1), Tabonuco slope (TS-3), Colorado valley (CV-1), Colorado slope (CS-2). Tabonuco is Lower montane rain forest and Colorado is Montane rain forest.

^hSource: Crow and Weaver (1977). Lower montane rain forest plots (i.e., Río Grande, Sabana 4, Sabana 8). Montane rain forest plot (i.e., Cutover Colorado (CCU)).

Training activities in the Luquillo Mountains have been a part of the Forest Service program for nearly 60 years. In 1953, the Institute held the first of 16 international tropical forestry short courses, which included excursions to the Luquillo Mountains. The earliest programs were designed for visiting foresters from tropical countries throughout the world and included instruction and field training in dendrology, ecology, surveying, inventory, aerial photo interpretation, silviculture, and forest management, protection, and utilization. In addition, exposure to environmental and conservation issues was provided through activities at the Eliza Colberg Girl Scouts camp starting in 1950, and the Youth Conservation Corps camp beginning in 1976.

In the early 1960s, students from U.S. universities were introduced to tropical forestry and silviculture through National Science Foundation sponsored programs that had field activities in the LEF. Since the mid-1980s, students from universities in Puerto Rico and elsewhere have pursued undergraduate and graduate programs based on ecological studies carried out within the forest. Several major publications, some dating back nearly a century, contain

valuable information on the flora, fauna, related resources and management in the Luquillo Mountains, including:

- The scientific survey of Porto Rico and the Virgin Islands (Anthony 1925, 1926; Britton and Wilson 1923, 1930; Gleason and Cook 1927). These documents plus others from the New York Botanical expeditions in Puerto Rico provide some of the earliest observations regarding flora, fauna, geology, paleobotany, and archaeology. The survey series contains 18 volumes between 1919 and 1953.
- The 24 volumes of the Caribbean Forester. This journal, published between 1939 and 1963, contains a wealth of information on tree species, forest types, stand conditions, silvicultural research, nursery practices, reforestation and forest plantations, herbicides, forest policy and legislation, forest insects, wood resistance to termites, wood preservation and utilization, climate and hurricane impacts, soils, training courses, and annual summaries of work. Contributions from elsewhere in the tropics, mainly the Caribbean and Latin America, were also included. English and Spanish were the principal languages, but articles also appeared in French and Portuguese.

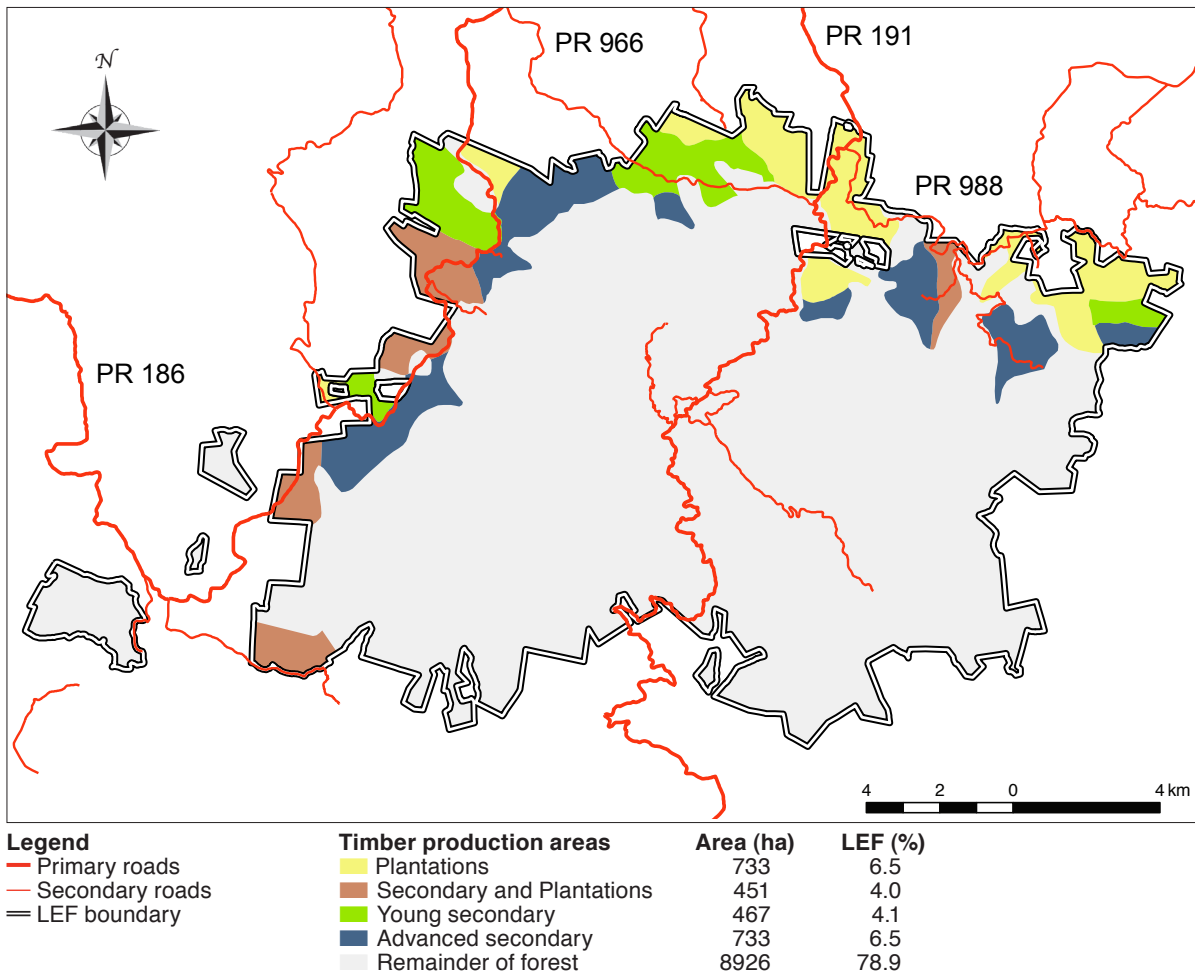


Figure 7—Proposed timber production areas within the Luquillo Experimental Forest in 1950.

- The Caribbean Forest atlas (Upson 1949, see endnotes). The atlas contains a chronology of legislation and events relating to the creation, enlargement, improvement, and management of the national forest between December 10, 1899 and June 30, 1949.
- Puerto Rican woods: their machining, seasoning and related characteristics of Puerto Rican woods (Longwood 1961). This publication describes the wood properties 60 native and introduced tree species.
- Trees of Puerto Rico and the Virgin Islands, Volumes I and II (Little and Wadsworth 1964, Little and others 1974). These two tomes on dendrology describe the island's 547 known native trees and 200 introduced species.
- A tropical rain forest: a study of irradiation and ecology at El Verde (Odum and Pigeon 1970). This 1,600 page compendium contains 9 chapters and 111 research papers on tropical flora, fauna, and ecology.
- A descriptive flora of Puerto Rico, Volumes I-V (Liogier 1985, 1997), Los bejucos de Puerto Rico, Volumen I (Acevedo-Rodríguez and Woodbury 1985), and Vines

and climbing plants of Puerto Rico and the Virgin Islands (Acevedo-Rodríguez 2005). These documents contain relatively recent taxonomic updates of the island's flora.

- History and conservation of the Puerto Rican Parrot (Snyder and others 1987). This book summarizes 20 years of work and includes the history, ecology, and current efforts to save the rare and endangered Puerto Rican parrot.
- Biotropica special issues: (1) Ecosystem, plant, and animal responses to hurricanes in the Caribbean; and (2) Long term responses of Caribbean ecosystems to disturbance (Walker and others 1991, 1996). Most of the post-hurricane studies described were carried out within the forest.
- Tropical forests: management and ecology (Lugo and Lowe 1995). This book commemorates the 50th anniversary of the IITF and contains several review chapters on ecological research.
- The food web of a tropical rain forest (Reagan and Waide 1996). This work summarizes past studies of fauna, including information on their abundance, food habits, and ecological roles in the ecosystem.

- The revised land and resource management plan for the Luquillo Forest and the final environmental impact statement (U.S. Department of Agriculture, Forest Service 1997a, 1997b). These documents consider forest resources, recreation, access, and research in a proposed 10-year management plan.
- Forest biodiversity in North, Central and South America, and the Caribbean: research and monitoring (Dallmeier and Comiskey 1998). This tome on the neotropics contains five chapters on the flora and fauna of the LEF.
- Producción forestal para América Tropical (Wadsworth 2000). This major effort contains > 600 pages that describe forest management practices throughout the tropics with some experiences derived from years of research within the LEF.
- The bioecology of native and exotic tree species in Puerto Rico (Francis and Lowe 2000). This summary of tree life histories contains information on 102 species, including many native and introduced trees.
- Geology, geochemistry, geophysics, mineral occurrences and mineral resource assessment for the Commonwealth of Puerto Rico (Bawiec 2001). This compendium includes information for all of Puerto Rico, with nine geologic formations found in the LEF.
- The soil survey of the Luquillo Experimental Forest (U.S. Department of Agriculture, Natural Resources Conservation Service 2002). This volume updates five general and 20 detailed soil map units within the LEF, and describes their soil classification, potential use, and management.
- Distribution, ecology, and life history of *Margarops fuscatus* (Pearly-eyed thrasher) (Arendt 2006). This book summarizes observations on an avian supertramp and major competitor of the Puerto Rican parrot, a species well adapted to the LEF where many of the observations were made.

Chapter 2. ENVIRONMENTAL SETTING

Puerto Rico was heavily deforested during the past three centuries leaving only 3500 ha (i.e., about 0.4 percent) of the island completely undisturbed by human activities (Wadsworth 1949, 1950). Today, the forests of the LEF survive like a large central park surrounded by San Juan, Fajardo, Naguabo, Humacao, Caguas, and other northeastern towns where about 40 percent of the island's population resides (CEEPUR 2009, Watlington 2008) (fig. 1). The LEF represents about 1.3 percent of Puerto Rico and nearly 15 percent of the island's protected areas held by commonwealth, Federal, and nongovernmental agencies (Gould and others 2008).

Geology

Island chains may form through compression, the subduction of one oceanic crustal plate under another, causing magma generation beneath the upper plate and volcanism on the surface of that plate (Donnelly 1996). Before the Cretaceous (a period from 145 to 65 million years ago), the geographic site that Puerto Rico currently occupies was a deep ocean (Meyerhoff 1933, Picó 1974). In the early Cretaceous, the site was characterized by submarine volcanic eruptions and the gradual appearance of transitory islands. In the Late Cretaceous, a chain of islands appeared, growing into a large volcanic island that extended from the Dominican Republic to the Virgin Islands. Puerto Rico, situated on the northern edge of the Caribbean plate, is part of this island arc complex (Bawiec 2001).

The Luquillo Mountains were first described as monadnocks (i.e., residual isolated peaks or mountains) not because of structural resistance or lack of stream erosion but rather due to uparching and faulting (Beinroth 1969, Mitchell 1954). The mountains are part of a volcanic-plutonic province that is underlain by rocks ranging in age from early Cretaceous to mid-Eocene (i.e., about 45 million years ago). Marine volcanoclastics (i.e., breccia, conglomerate, mudstone, and sandstone) underlie about 80 percent of the LEF and intrusive rocks (i.e., the quartz-diorite Río Blanco stock) most of the remainder (Cox and Briggs 1973, Seiders 1971). A contact metamorphic zone surrounds the Río Blanco stock.

A recent geologic summary for Puerto Rico outlined the following sequences, four of which account for 96 percent of the LEF (Bawiec 2001, Seiders 1971) (fig. 8).

- Augite andesite porphyry (TKap)—Intrusive rocks of the late Cretaceous.
- Dagua formation (Kd)—Massive andesitic breccia, hyaloclastic breccia, and fine grained volcanoclastic rocks. Dagua, the oldest mapped sequence, is assumed to be early Cretaceous.
- Figuera lava (Kf)—Pillowed andesitic lava flows. Figuera is also assumed to be early Cretaceous.
- Fajardo formation (Kfa)—Tuffaceous sandstone-siltstone, and tuff breccia of Albian age (i.e., Cretaceous, about 100 to 110 million years ago).
- Hato Puerco formation (Kh)—Andesitic to basaltic volcanic sandstone, breccia, conglomerate, and basaltic lava flow of middle Cenomanian age (i.e., late Cretaceous, about 85 to 100 million years ago).
- Lomas formation (Klo)—Basaltic to andesitic lava, volcanic breccia, and sandstone. Age has not been established.
- Quaternary alluvium (Qa)—Sand deposits and quaternary alluvium. The alluvium is found in mountainous river valleys and the surrounding lowlands.
- Río Blanco unit (TKh)—A highly magnetic pluton that dates to 46 million years ago. The stock intrudes the Fajardo, Hato Puerco, Lomas, and Tabonuco formations.
- Tabonuco formation (Kta)—Calcareous and tuffaceous sandstone-siltstone and volcanic breccia of Albian age.

Tuffaceous sandstone, siltstone, breccia, conglomerate, and quartz diorite parent materials underlie the lower montane and montane forests in the LEF (Bogart and others 1964). Surveys carried out by forest researchers indicated that tree species composition did not change across a line that separated parent materials within montane forest (Wadsworth and Bonnet 1951).

Two zones of mineral occurrence are found within the Luquillo Mountains—a northern zone with gold deposits and a southern zone with copper and related iron oxides, sulfur, and traces of mercury. A review of early Spanish mining documents indicates at least 23 sites associated mainly with gold placer mining operations were set up along prominent Luquillo Mountain streams (Cardona 1984). Today, the surnames of past miners such as Guzmán, Jiménez, and Toro survive on U.S. Geological Survey quadrangle maps as part of the forest's legacy (figs. 5 and 6). Gold also played a role in the naming of streams such as Río de la Mina and Quebrada Baño de Oro.

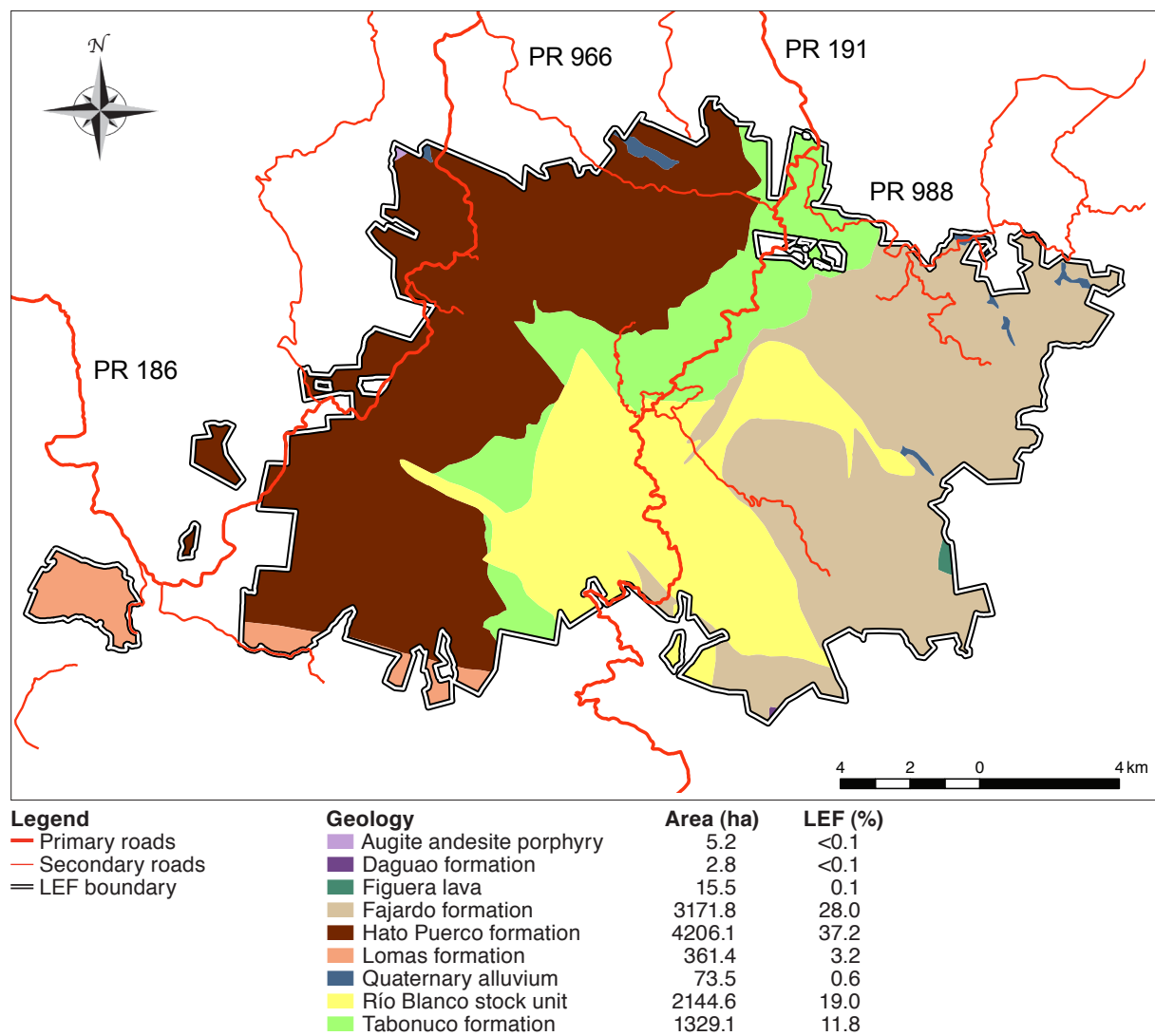


Figure 8—Geology of the Luquillo Experimental Forest.



Not too distant from the La Mina Recreation Area, a few quartz boulders and numerous quartz fragments are exposed on the soil surface. (Photo by Peter L. Weaver)

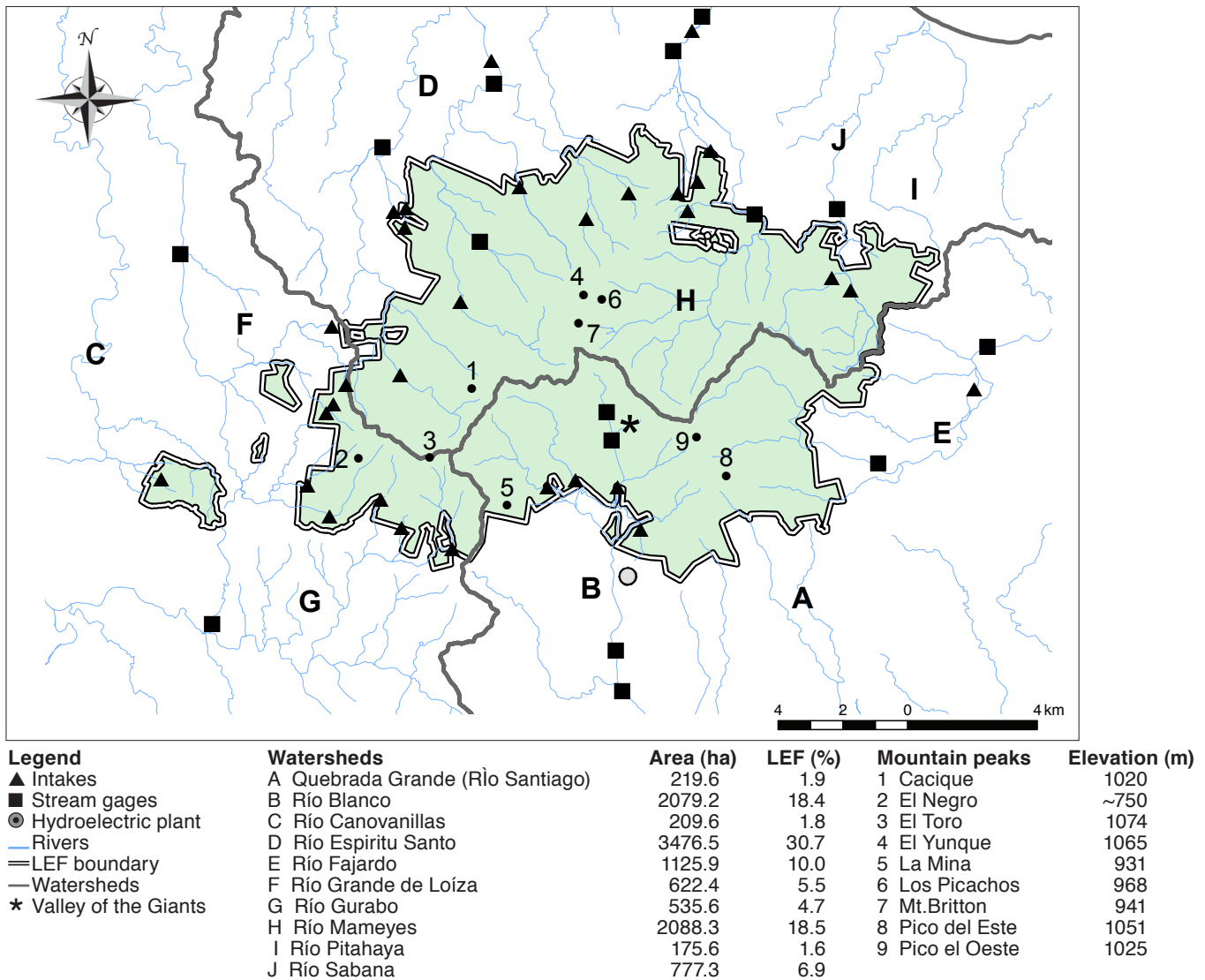


Figure 9—Major peaks, rivers, watersheds, flow gages, and water intakes in and around the Luquillo Experimental Forest.

Physiography and Hydrology

The topography of the Luquillo Mountains is rugged with cliffs and exposed rocks at high elevations (Wadsworth 1951). One-quarter of the LEF lies between 120 and 400 m in elevation; nearly one-half between 400 and 600 m; another one-quarter between 600 and 900 m; and about 3 percent lies above 900 m in elevation (Wadsworth 1951). The lowest point is along the northeastern boundary near the town of Sabana. Five peaks in the LEF exceed 1000 m in elevation: El Toro (1074), El Yunque (1065), Pico del Este (1051), Pico del Oeste (1025), and El Cacique (1020). For many years El Yunque was thought to be the highest peak but subsequent surveys proved otherwise (Wadsworth 1970).

Ten rivers, some with numerous tributaries within the forest, arise at some point within the LEF. Four, the Río Blanco, Río Espíritu Santo, the Río Grande de Loíza (with its tributaries), and the Río Mameyes drain nearly 80 percent of the forest (fig. 9):

- **Quebrada Grande**—flows southeast from the forest and ultimately into the Río Santiago at Naguabo.
- **Río Blanco**—flows south with LEF tributaries Río Cubuy, Quebrada Maizales, Río Icacos, Río Prieto, and Río Sabana.
- **Río Canovanillas**—flows northwest from the outlying La Condesa property, becoming a tributary to the Río Grande de Loíza outside of the LEF.
- **Río Espíritu Santo**—flows northwest with LEF tributaries Quebrada Grande, Quebrada Jiménez, and Quebrada Sonadora.

- **Río Fajardo**—flows east with LEF tributaries Quebrada Grande and Quebrada Sonadora.
- **Río Grande de Loíza**—flows west with LEF tributaries Río Cubuy, Río Gurabo, Quebrada Grande, and Río Canovanillas (confined to the La Condesa tract).
- **Río Gurabo**—flows initially south out of the forest, becoming a tributary of the Río Grande de Loíza outside of the LEF.
- **Río Mameyes**—flows north with LEF tributaries Quebrada La Coca and Quebrada Juan Diego, Quebrada La Máquina, Quebrada Linguete, Quebrada Tabonuco, and Río de la Mina.
- **Río Pitahaya**—flows north without tributaries in the LEF.
- **Río Sabana**—flows north with LEF tributaries Río Camándulas and Río del Cristal.

On the northern slope, rivers descend rapidly at high elevation and more gradually below (Wadsworth 1951). The reverse happens on the southern exposure where basin-like valleys occur at relatively high elevations. Several of the streams and rivers have waterfalls and cascades.

One study of the LEF's water budget shows that rainfall averages about 3600 mm yr⁻¹ of which 63 percent is runoff and the remainder is evapotranspiration (Crook 2005, Crook and others 2007). An earlier study placed the same estimates at 60 percent for runoff and 40 percent for evapotranspiration (Naumann 1994). The average volume of water extracted from forest streams is about 250 mm yr⁻¹, which equals 7 percent of the annual rainfall and 11 percent of the annual runoff. Although little groundwater exists at high elevations within the watersheds, it may become important at lower levels (Larsen 1997).

Hydrograph data show that heavy rainfalls cause rapid runoff from the LEF landscape (Bogart and others 1964, Larsen and Torres Sánchez 1992). Water infiltrates vertically but relatively low soil permeability limits the amount that permeates to greater depths (Jordan 1970). When denser soil is encountered, water flows laterally down slope. Stream hydrographs show rapid peaks within a few minutes to hours after rainfalls lasting <24 hours. Return to baseflow takes 5 to 10 hours (Larsen and Torres Sánchez 1992).

Streamflow in the LEF (e.g., Río Icacos) varies considerably due to scattered showers of different intensity (Bogart and others 1964). Sediment levels in streams will likely be minimal during periods of low flow, but much greater during floods. Low flow, derived from ground water, produces a greater proportion of dissolved materials. Chemical concentrations, however, vary and may remain low if the flow is caused largely by storm runoff. In addition, the pH, color, temperature, odor, and taste of water may change with the amount of flow.

Stream gage records within the Río Icacos watershed “show more runoff produced than rainfall” (Crook and others 2007). This phenomenon was first observed during the 1940s after the installation of a weir on the Río Icacos (Wadsworth 2009). The anomaly was explained as a possible non-linear relationship between basin size and runoff (Crook and others 2007). Other factors, however, may be important. The upper reaches of the Río Icacos watershed contain dwarf forest between Pico del Este and Pico del Oeste. Previous monitoring of rainfall and cloud moisture interception on both Pico del Este and Pico del Oeste showed that intercepted fog increased the amount of water received at ground level by 10 percent (Baynton 1969, Weaver 1972)—a fact that might explain some of the missing rainfall input. Also, rainfall records for Pico del Este showed that the amount of rainfall just to the leeward of the peak surpassed the amount measured to the windward, an orographic phenomenon called spillover effect (Linsley and others 1949, Weaver 1972). The Icacos watershed lies to the leeward of the northeast-facing saddle (<750 m in elevation), which is situated between Pico del Oeste and a string of peaks to the west, including El Yunque, El Toro, and La Mina (fig. 9). The ridge that extends from Pico del Oeste to the PR route 930 gate, or the upper boundary of the Mameyes watershed, is occupied by montane forest and is the wettest area within the LEF (Ewel and Whitmore 1973). Spillover could funnel through the mountain pass adding rainfall to the Icacos watershed, particularly during periods of high winds and heavy cloud cover.

Soils

The warm climate and heavy rainfalls in the LEF cause deep weathering and produce a saprolite (i.e., residual soil zone with boulders of parent rock) that averages 11 m deep on slopes. This zone is underlain by weathered bedrock, which in turn is underlain by bedrock lower in the profile (Simon and others 1990). Mass wasting (i.e., downhill movement of soil and rock induced by gravity) appears to be the principal process responsible for erosion in the Luquillo Mountains.

LEF soils are highly leached inceptisols and ultisols comprised of silty clay loams, silty clays, and clays in different horizons. Twelve types of soils were recognized during early surveys: Los Guineos clay, Rough stony land, Catalina stony clay, Catalina clay, Catalina clay (steep phase), Lares silty clay loam, Múcara silty clay loam (steep phase), Pandura sandy clay loam, Picacho stony clay loam, Sabana silt loam, Sabana silty clay loam, and Via silty clay (broken phase) (Roberts 1942). The first three types were estimated to cover about 60 percent of the mountains, mainly in the interior (Wadsworth 1951). Later, the Los Guineos-Guayabota Rock land association and the Los Guineos-Humatas-Lirios association were described (Boccheciamp 1977).

Recently the forest's soils were surveyed again. Five general map units (or associations) and 18 detailed map units were located and described (U.S. Department of Agriculture, Natural Resources Conservation Service 2002). Three of the units cover nearly 50 percent of the land area (fig. 10). The general and detailed map units are:

Zarzal-Cristal-Humatas Association—This association contains very deep, well drained and somewhat poorly drained clayey soils that formed in residuum that weathered from volcanic sandstone and mudstone of the Fajardo, Hato Puerco, and Tabonuco formations.

- Cristal Zarzal complex (5 to 50 percent slopes)—very deep, somewhat poorly drained Cristal soil and very deep, well drained Zarzal soil found on mountain side slopes at elevations <600 m. Depth to bedrock is >150 cm. The soils have medium organic matter content, slow permeability, and medium natural fertility.
- Humatas Zarzal complex (5 to 30 percent slopes)—very deep, well drained Humatas soil and very deep, well drained Zarzal soil. They are found on hill summits, ridge tops, and mountain footslopes at elevations <450 m. Depth to bedrock is >150 cm. The soils have medium organic matter content, moderately slow permeability, and medium natural fertility.
- Zarzal Cristal complex (20 to 60 percent slopes)—very deep, well drained Zarzal soil and very deep, somewhat poorly drained Cristal soil. They are found on mountain slide slopes at elevations <600 m. Depth to bedrock is >150 cm. The soils have medium organic matter content, moderately slow permeability, and medium natural fertility.
- Zarzal very cobbly clay (40 to 60 percent slopes)—very deep, well drained soil found mainly on convex mountain side slopes at lower elevations <550 m. Depth to bedrock is >150 cm. The soil has medium organic matter content, moderately slow permeability, and medium natural fertility.

Sonadora-Caguabo-Prieto Association—This association is composed of moderately deep and poorly drained clayey soils that formed in residuum that weathered from volcanic mudstones and conglomerates of the Fajardo, Hato Puerco, and Tabonuco, formations.

- Caguabo gravelly clay loam (8 to 15 percent slopes)—shallow, well drained soil at lower elevations <550 m on side slopes and footslopes of lower hills, and on strongly dissected uplands. Depth to bedrock is between 25 and 50 cm. The soil has low organic matter content, moderate permeability, low natural fertility, and is one of the least productive soils in the lower montane forest zone.
- Coloso silty clay loam (occasionally flooded)—very deep, somewhat poorly drained soil at lower elevations <400 m on flood plains and low terraces along mountain streams. Depth to bedrock is >150 cm. The soil has medium organic matter

content, slow permeability, and medium natural fertility.

- Luquillo stony clay loam (occasionally flooded)—very deep, well drained soil on flood plains and low stream terraces at elevations <400 m. Depth to bedrock is >150 cm. The soil has medium organic matter content, moderately slow permeability, and medium natural fertility.
- Prieto very cobbly clay loam (25 to 50 percent slopes)—moderately deep, poorly drained soil in concave positions on side slopes and in drainages at elevations <600 m. Depth to bedrock is 50 to 100 cm. The soil has medium organic matter content, moderate slow permeability, and medium natural fertility.
- Sonadora Caguabo complex (25 to 40 percent slopes)—moderately deep, well drained Sonadora soil and the shallow, well drained Caguabo soil situated on mountain side slopes at lower elevations <500 m. Depth to bedrock is 50 to 100 cm. The soils have medium organic matter content, very slow permeability, and medium natural fertility.

Yunque-Los Guineos-Moteado Association—This association is composed of very deep and deep, moderately well drained and poorly drained clayey soils that formed in residuum that weathered from volcanic sandstone and mudstone of the Fajardo, Hato Puerco, and Tabonuco formations.

- Palm Yunque complex (35 to 85 percent slopes, extremely stony)—very deep, poorly drained Palm soil and very deep, moderately well drained Yunque soil located on mountain side slopes at upper elevations (750 to 900 m). Depth to bedrock is >150 cm. The soils have high organic matter content, moderately slow permeability, and high natural fertility.
- Yunque cobbly clay (40 to 80 percent slopes, extremely stony)—very deep, moderately well drained soil found in canyons and on side slopes at elevations between 600 and 900 m. Depth to bedrock is >150 cm. The soil has high organic matter content, moderate permeability, and medium natural fertility.
- Yunque-Los Guineos-Moteado complex (5 to 30 percent slopes)—very deep, moderately well drained Yunque soil and the very, deep well drained Los Guineos soil, and deep, poorly drained Moteado soil. The soils occur on summits, ridge tops, and mountain side slopes at elevations from 600 to 900 m. Depth to bedrock is >150 cm. They have high organic matter content, moderate permeability, and medium natural fertility.
- Yunque Moteado complex (20 to 65 percent slopes)—very deep, moderately well drained Yunque soil and deep, poorly drained Moteado soil. They are found on mountain side slopes at elevations between 600 and 900 m. Depth to bedrock is >150 cm. The soils have medium organic matter content, moderate permeability, and medium natural fertility.

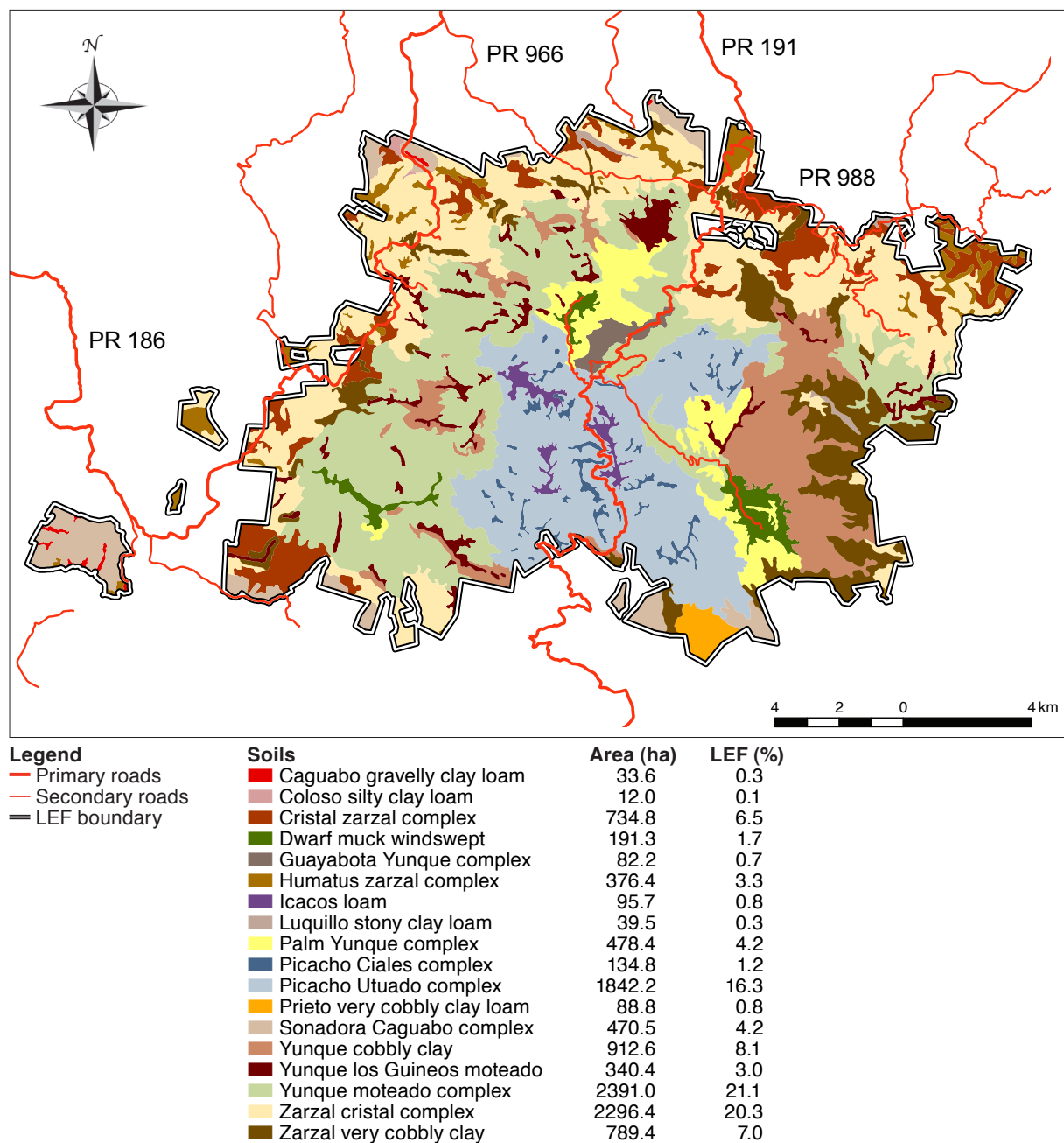


Figure 10—Soils of the Luquillo Experimental Forest.

Picacho-Utuado-Ciales Association—This association is composed of very deep, somewhat poorly drained and poorly drained loamy soils underlain by granitic saprolite and formed in residuum weathering from intrusive rocks of the Río Blanco formation in the plutonic uplands.

- Guayabota Yunque complex (30 to 60 percent slopes)—shallow, poorly drained Guayabota soil and very deep, moderately well drained Yunque soil found on mountain side slopes at elevations from 600 to 750 m. Depth to bedrock is 25 to 50 cm. The soils have medium organic matter content, slow permeability, and low natural fertility.
- Icosos loam (occasionally flooded)—very deep, somewhat poorly drained soil found on flood plains and low terraces along perennial stream valleys at elevations between 600 and 750 m. Depth to bedrock is >150 cm. The soil has high organic matter content, moderate permeability, and high natural fertility.
- Picacho Ciales complex (5 to 30 percent slopes)—very deep, somewhat poorly drained Picacho soil and very deep, poorly drained Ciales soil found on ridge tops and mountain side slopes at elevations from 600 to 800 m. Depth to bedrock is >150 cm. The soils have low organic matter content, moderate permeability, and low natural fertility.
- Picacho Utuado complex (5 to 35 percent slopes)—very deep, somewhat poorly drained Picacho and Utuado soils found on hills and footslopes in mountain stream valleys at elevations from 600 to 850 m. Depth to bedrock is >150 cm. The soils have low organic matter content, moderate permeability, and low natural fertility.

Dwarf—This association is very deep, poorly drained clayey soils that have an organic surface layer, are on summits and ridges of mountains, and formed in residuum that weathered from metamorphosed andesitic to basaltic, marine-deposited, volcanic sandstone of the Hato Puerco, Fajardo, and Tabonuco formations.

- Dwarf muck (10 to 65 percent slopes, windswept)—very deep, poorly drained soil on both convex and concave slopes at elevations >800 m. Depth to bedrock is >150 cm. The soil has very high organic matter content, moderately slow permeability, and high natural fertility.

Mean surface soil properties within the LEF differ significantly among forest types, topographic positions, and seasons (Cox and others 2002). Soil differences among forest types include those associated with biological processes and water inputs such as bulk density, soil moisture, and the nutrients Na, P, C, and S. In contrast, differences among topographic positions are typically related to geochemical processes and involve Ca, Mg, K, and Al.

Soil erosion varies by topographical position (Basnet 1992a). Slopes have the highest rates of erosion because of their steepness. In contrast, ridges are more stable because they are densely covered with trees and are underlain by stable geologic substrates. Sedimentation is highest in ravines, which receive runoff from other topographic positions and have lower tree densities. Also, ravines typically descend at lower slope angles.

The status of soils is also affected by past agricultural activities and climatic events. Cultivation began on the lower slopes of the mountains in the 16th century, with most concessions continuing until the 19th century (Wadsworth 1951). In 1899, Hurricane San Ciriaco heavily impacted the forest and caused a subsequent decline in coffee plantings. Other storms have similarly affected the forest causing landslides (Larson and Torres-Sánchez 1992). By 1943, land used for cultivation and livestock grazing had decreased to only 160 ha. Soil erosion and degradation from these events not only influenced forest recovery and natural succession but also subsequent efforts to restore the landscape by tree planting (Marrero 1948).

Climate

Puerto Rico, lying in the path of the easterly trade winds, has a tropical maritime climate influenced by the surrounding ocean. During the year, the island is affected by tropical waves, depressions, storms, and hurricanes that normally occur from May to October as well as by northerly cold fronts during the winter months (Calvesbert 1970, Daly and others 2003, Larsen 2000, Larsen and Torres-Sánchez 1998, Scatena 1998a). The elevational gradient within the LEF produces differences in rainfall, relative humidity, wind velocity, cloud cover, temperature, atmospheric saturation deficit, and solar radiation. The first four parameters increase with ascent and the last three decrease. Seasonal differences in climate are evident during the year. For example, seasonality at El Verde on the lower northwestern slopes was generalized as follows (Odum and others 1970): “A winter season, December through March, could be differentiated from the remainder of the year by small average differences: temperature, 2° C less; relative humidity, 5 to 10 percent less; 5 to 18 percent of the days with westerly and northwesterly winds; 66 percent as much rain per month (January to March); 25 percent less insolation (November to February); and a higher frequency of almost clear days (15 percent).”

Precipitation—Several studies of rainfall have been carried out (Lugo 1986, Odum and others 1970, Wadsworth 1970), each varying slightly in its estimates. According to one study, the entire LEF receives an average of 3860 mm yr⁻¹ during a typical year (García-Martín and others 1996). Rainfall

estimates by forest type averaged 3540 mm yr⁻¹ in lower montane forest, 4190 in montane forest, 4170 in palm brake, and 4850 mm yr⁻¹ in dwarf forest. The average number of days with rainfall and the amount of stream runoff increased with elevation. Heavier rainfalls occurred during the last 8 months of the year, notably in May and from September to November (fig. 11).

Mean annual rainfall averaged from 2475 to 4650 mm yr⁻¹ at six different sites on the LEF's northern slopes between 150 and 1065 m in elevation (Briscoe 1966, Heartsill Scalley 2006, National Oceanic and Atmospheric Administration 2002, Ramírez and others 2005, Scatena 1998a, Wadsworth 1948) (fig. 11). Because the records represent different periods and vary considerably in duration, valid comparisons among sites are impossible. Mean annual rainfall averaged >4000 mm yr⁻¹ at El Yunque, La Mina, Pico del Este, and Pico del Oeste, sites between 715 and 1065 m in elevation (Baynton 1968, Briscoe 1966, National Oceanic and Atmospheric Administration 2002, Wadsworth 1948). The highest daily rainfall of 485 mm was recorded at Pico del Este on May 20, 1969 (Weaver 1972).

The 9-year period of rainfall observations carried out at La Mina beginning in 1935 is of special interest. The mean of 4650 mm yr⁻¹, with an annual range of values between 3725 and 6450 mm yr⁻¹ (Wadsworth 1948), is the highest multiyear record for the mountains. Rainfall was detected on nearly 75 percent of the days and averaged 19 minutes in duration. Rainfall intensity was nearly 8 mm hr⁻¹ for the 1,625 showers recorded annually.

Rainfall that arrives on the forest canopy is distributed to the ground by throughfall (i.e., water falling from leaf surfaces through the canopy to the ground) or stemflow (i.e., water moving via tree branches and trunks to the ground). Throughfall estimates for the lower montane forest average about 60 percent of the annual rainfall (Odum and others 1970, Scatena 1998a). These estimates are typically 20 to 30 percent lower than for many other montane and lowland tropical forests (Scatena 1990). The differences are due to a high frequency, low intensity rainfall regime rather than characteristics of the forest itself.

Despite the heavy rainfall associated with the LEF, droughts occur occasionally and their effects are noteworthy. Puerto Rico experienced regional droughts from 1966 to 1968, 1971 to 1974, 1976 to 1978, and from 1993 to 1995. All had a profound impact on streamflow and reservoir storage in watersheds that supply the island's major towns (Larsen 2000), and all resulted in agricultural losses and water rationing in metropolitan areas.

One other climatic phenomenon merits reporting. During January 1969, hail fell in the vicinity of Pico del Este, and

possibly elsewhere in the forest, for about 10 minutes at about 10 a.m.¹ Hail is rare in the LEF and other occurrences have not been noted.

Temperature—Temperature varies from about 24 to 27 °C at the base of the LEF to 17 to 20 °C at the summits (Baynton 1968, Briscoe 1966, Brown and others 1983) (fig. 11). Diurnal temperature variation and temperature range in any particular month are greater at lower elevations than at higher elevations. Reported minimum and maximum temperatures were 11 and 32 °C, respectively. The dew point temperature varies little over Puerto Rico, indicating that the overlying air mass is relatively constant with regard to moisture content during the year (Calvesbert 1970).

Wind chill would seem inappropriate to mention with regard to the LEF. However, a notable chilling is felt at the summits, especially during the cool winter months when wind-driven fog is deposited onto surfaces, including humans. One memorable experience was the penetrating cold that researchers felt while removing epiphytes from trees near Pico del Este during January and February of 1991 and 1997.

Relative humidity and evapotranspiration—Relative humidity at El Verde, about 350 m in elevation facing northwest, was above 95 percent except during a few hours on sunny days, or when air trajectories were unusual (Odum and others 1970). At Catalina located at 150 m, it averaged 88 percent, with regular descents into the high 60s and 70s at midday (Briscoe 1966). At the summits of Pico del Este, Pico del Oeste, and El Yunque, relative humidity was at or near 100 percent most of the time, with the lowest recordings between 12:00 noon and 2:00 p.m. (Baynton 1968, Briscoe 1966, Weaver 1972). Prevailing climatic conditions reduce transpiration rates but occasional clear days allow stomates to regulate water losses from tree species (Gates 1969, Medina and others 1981, Weaver and others 1986).

In the Bisley watersheds at 350 m elevation, evapotranspiration estimated by hydrological and micrometeorological techniques ranged between 2180 and 2420 mm yr⁻¹ during 1996 and 1997 (Schellekens and others 2000). The values were considered high for lowland tropical areas and were partially attributed to frequent, low intensity rainstorms. Other possible influencing factors were also suggested. These were an effective net upward transport of evaporated moisture, proximity to the warm waters of the Atlantic providing advected energy, an irregular canopy due to the recent passage of Hurricane Hugo, and the watershed's location in dissected terrain.

¹ Personal observation. 1969, P.L. Weaver, Research Forester, U.S. Department of Agriculture Forest Service, International Institute of Tropical Forestry, Jardín Botánico Sur, 1201 Calle Ceiba, Río Piedras, PR 00926-1119.

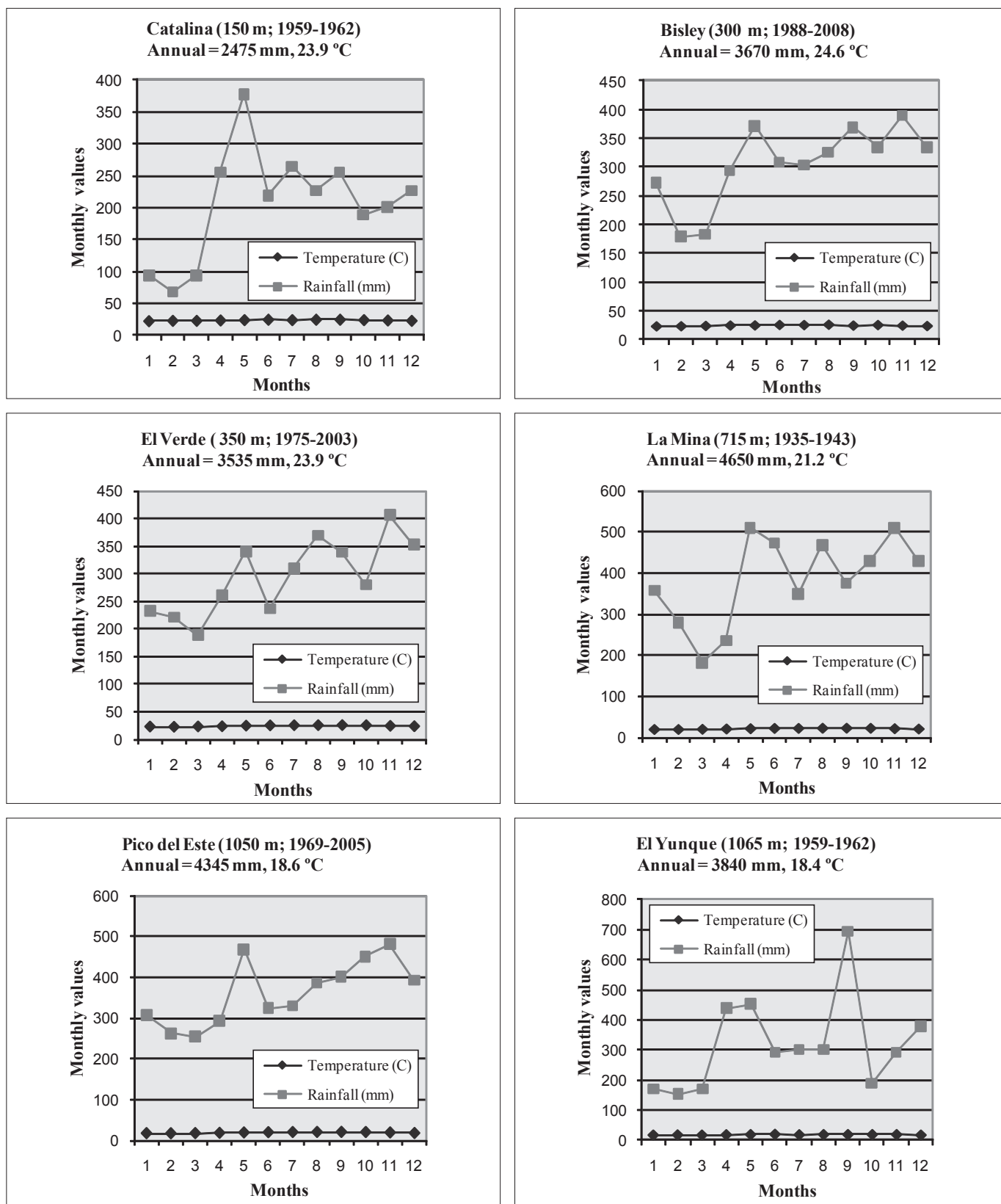


Figure 11—Climatic diagrams for sites within the Luquillo Experimental Forest.

Wind velocity and direction—Consistent trade winds, blowing mostly from an easterly direction, are the outstanding feature of climate in Puerto Rico (Calvesbert 1970). Wind velocity at El Verde averaged about 2 to 6 km hr⁻¹ just above the forest, diminishing downward into the canopy (Odum and others 1970); similar velocity estimates were recorded at Catalina (Brown and others 1983). Wind velocities on the summits, strongest at night and weakest during the afternoon, averaged from 8 to 18 km hr⁻¹ in any month (Baynton 1968, Briscoe 1966), but gusts of 100 km hr⁻¹ were recorded during periods of normal winds elsewhere (Wadsworth 1948).

Winds may be tied to aberrant occurrences of insects within the forest. One incident involved *Polistes americanus* (Paper wasp) described as follows: “enormous numbers of these wasps have been observed on El Yunque rock (April 5, 1939), so abundant that one could not approach in safety” (Wolcott 1948). Updrafts were suggested for the phenomenon. During October of 1968, a similar swarm of unidentified wasps was observed on the crowns of dwarf forest trees (see footnote 1). The swarm completely surrounded Mt. Britton tower, which lies 1 km south of El Yunque (fig. 9). Indeed, these occurrences may be more common than is realized yet go unreported. In both cases, observers were able to look down on the swarms. The wasps, however, may have gone unnoticed by people walking on trails below the canopy.

Cloud cover and solar insolation—Cloud cover increases with elevation in the LEF where the summits are frequently bathed in clouds while the surrounding lowlands remain clear. Above 600 m, the base of trade wind cumulus clouds passes through the forest, depositing condensed cloud moisture on vegetative surfaces. Cloud moisture deposition adds 10 percent more water to the annual moisture balance than would result from rainfall alone (Baynton 1969, Weaver 1972). Runoff from the summits of the dwarf forest is estimated to be virtually all of the ~5000 mm of combined rainfall and intercepted cloud moisture received by the soil surface during the year.

February and March are the months when the peaks are most likely to be free of clouds. Cloud cover also affects solar radiation. Mean annual solar radiation on El Yunque and Pico del Oeste averages about 60 percent of that received on the northeastern coast of Puerto Rico (Baynton 1968, Briscoe 1966).

Hurricanes—Hurricanes that traverse Puerto Rico typically originate off the coast of Africa and come from the southeast; occasionally, other storms originate in the Gulf of Mexico and may move northeast towards the Bahamas and Florida. Based on existing data, hurricanes may be expected to pass directly over the LEF once every 62 years and within 60 km once every 22 years (Scatena 1989). Since 1738, at least 33 hurricanes of varying intensity have passed over or near

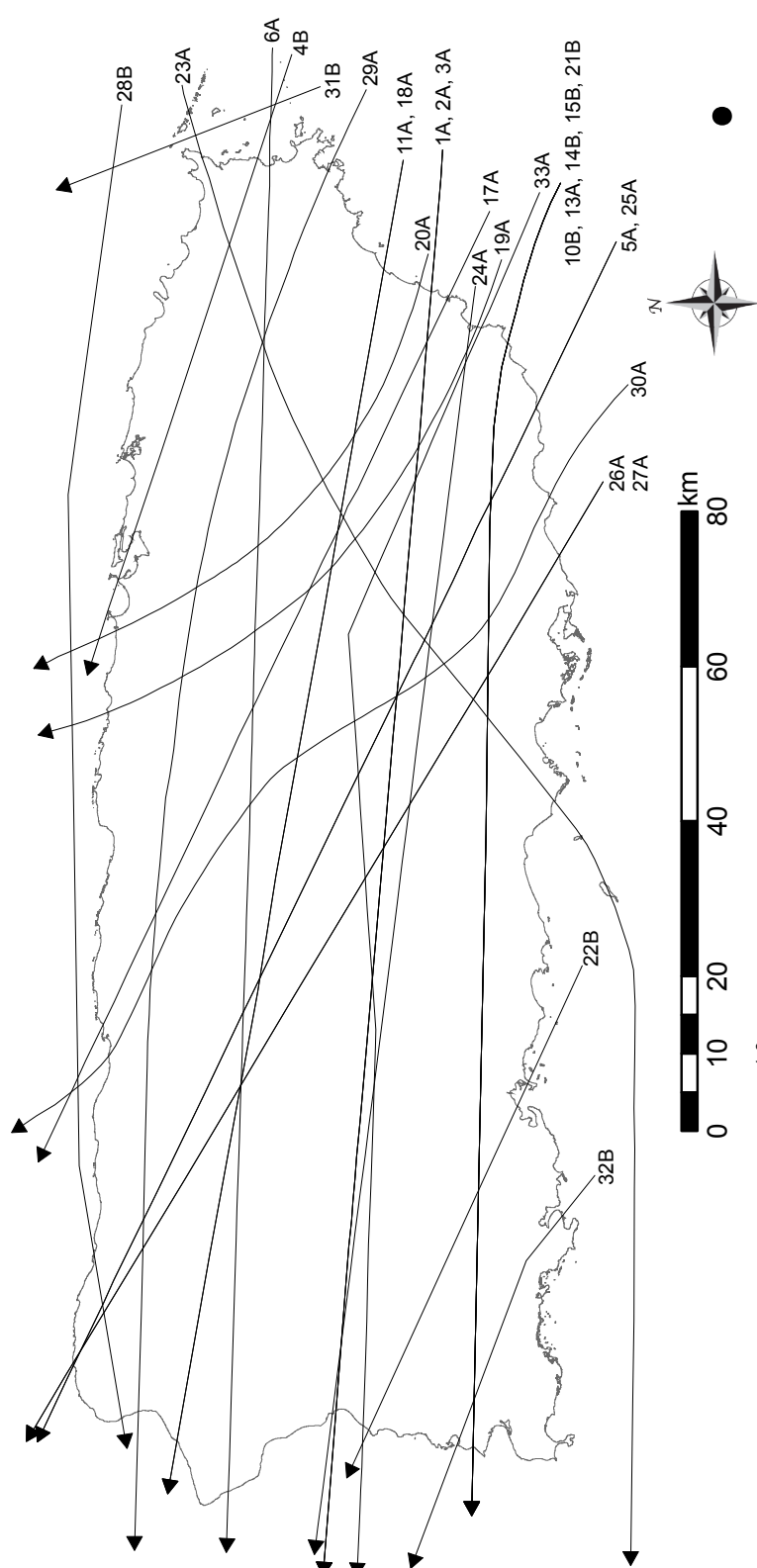
Puerto Rico, virtually all of them with trajectories sufficiently close to the Luquillo Mountains to have caused some impact within the LEF (Neumann and others 1988; Salivia 1972; Weaver 1986a, 1989b) (fig. 12).

Hurricane nomenclature in Puerto Rico, borrowing from different traditions, has varied over time. The Spanish explorers and early settlers named hurricanes according to saint's days on the church calendar (Salivia 1972). In 1941, the fictitious “incipient little whorl” —a wind called “Maria” in the novel “Storm”—led to a revolution in hurricane nomenclature (Stewart 1941, page 18). Apparently, U.S. Navy meteorologists adopted Stewart's innovation during World War II, remembering girlfriends back home by giving their names to tropical cyclones. It was certainly easier to personalize the storms than try to recall their degrees of latitude and longitude. In the early 1950s, Atlantic cyclones were labeled according to the phonetic alphabet, but in 1953, the U.S. Weather Bureau switched to female names. That tradition continued until 1979 when male and female names were alternated during the year. It is interesting to note that the 1956 Hurricane labeled as Betsy by the U.S. Weather Bureau was called “Santa Clara” when it traversed Puerto Rico (fig. 12). Today, the World Meteorological Organization has a procedure to designate the names of tropical storms and hurricanes in different regions of the world.

San Janero (1766) and San Agustín (1772) were the only recorded 18th century hurricanes that traversed the Luquillo mountains. San Jacinto I (1807), a slow moving storm, passed just south of the Luquillo Mountains, spending 50 hours over some part of Puerto Rico (Salivia 1972). Santa Ana (1825), San Jacinto II (1827), and Nuestra Señora de los Angeles (1837) all passed a short distance to the south of the Luquillo Mountains. In 1867, the island experienced Hurricane Narciso, which traversed directly over the Luquillo Mountains; moreover, only 3 weeks later, a major earthquake shook the island (Salivia 1972).

At least six hurricanes during the 20th century passed over Puerto Rico and had varying effects on the forests of the LEF (table 6):

- San Felipe (1928), with maximum winds of 240 km hr⁻¹ and 735 mm of rain, the “the largest, most violent, and most destructive” of hurricanes (Salivia 1972), or the island's legendary storm, passed west of the Luquillo Mountains and spent 36 hours over the island.
- San Nicolas (1931), with winds of 145 km hr⁻¹ and 125 mm of rain, traversed the island's north coast for 40 hours (Salivia 1972).
- San Cipriano (1932), with 200 km hr⁻¹ winds and 430 mm of rain, passed directly over the LEF and spent 18 hours over the island (Crow 1980).



Legend for major hurricanes in Puerto Rico since 1700^{1,2}

Key	Year	Name	Key	Year	Name	Key	Year	Name
1-A	1738	Santa Rosa II	10-B	1805	San Vicente II	18-A	1827	San Jacinto II
2-A	1738	San Leoncio III	11-A	1807	San Jacinto	19-A	1835	San Hipólito
3-A	1751	San Agapito	12-B/?	1809	San Esteban III	20-A	1837	N.S. de los Angeles
4-B	1766	San Jenaro	13-A	1813	San Liborio II	21-B	1851	San Agapito II
5-A	1766	San Marcus	14-B	1814	San Liborio III	22-B	1852	San Llorenzo
6-A	1772	San Agustín	15-B	1816	San José de Cupertino	23-A	1867	San Narciso
7-B/?	1772	San Ramón II	16-A/?	1819	San Mateo III	24-A	1876	San Felipe I
8-B/?	1780	San Antonio	17-A	1825	Santa Ana	25-A	1893	San Roque III
9-B/?	1785	San Lupo						

¹Key: A = hurricane vortex passed over island with hurricane force winds; B = hurricane vortex passed over part of the island or offshore, with hurricane force winds on part of the island; A/? and B/? = uncertain trajectory (i.e., San Ramón II in 1772 passed northeast of the island). Trajectories in 1899 and later are known; pre-1899 trajectories were sketched from descriptions except those classed as A/? or B/?.

²Sources: Neumann et al. 1988, Salvia 1972.

Figure 12—Hurricane trajectories over Puerto Rico since 1700.

Table 6—Impacts of 20th century hurricanes on vegetation in the Luquillo Mountains, mainly the Luquillo Experimental Forest

Names and dates of hurricanes

Forest type or area, and brief summary of storm impacts and recovery in the LEF (source)

San Felipe (9/13/28)

Luquillo District: Field surveys showed defoliation, and snapping and uprooting of trunks. Post-storm seed production was abnormally high for some species. The time elapsed before recovery varied by species, mainly from 4 to 6 months (Bates 1929).

San Felipe (9/13/28), San Nicolás (9/10/31), and San Cipriano (9/26/32)^a

Lower montane rain forest: The 1943-76 record for the El Verde III plot showed two distinct phases in post-hurricane forest structure and species composition: in early 1940s, secondary species were common, and stem numbers and biomass increased rapidly; in the mid-1970s, fewer stems and species were present, and biomass accumulation slowed. The percentage loss of secondary tree species was greater than for primary species (Crow 1980). Also, a 1946-88 record for permanent plot TR-1 showed stem density, species numbers, and the rate of biomass accumulation at a maximum 14 years after the last hurricane. Secondary species declined in numbers over time and *Dacryodes excelsa* dominated in stems and biomass throughout the post-hurricane recovery period (Weaver 2002b).

Montane rain forest: The 1946-81 combined record for seven stands showed positive changes in diameter and height class distributions. Secondary species present initially declined more rapidly in numbers than primary species. The mean specific gravity of the forest (i.e., weighted by tree volumes) increased during 30 years by 1.9 percent including palms, and 3.9 percent for broadleaf species alone. Both tree diameter growth rates and species diversity (i.e., mixture of secondary and primary species) were greatest a few years after the hurricane, declining over time. Stand volumes and biomass increased during the recovery period (Weaver 1989b).

Santa Clara or Betsy (8/13/56)

LEF: Defoliation, breakage, and uprooting did not appear to increase with elevation. Impacts on ridges were limited to defoliation whereas windthrow within the Mameyes Valley was locally severe. More defoliation occurred on east-facing slopes than on west-facing slopes. Breakage was most common on shallow soils whereas uprooting was most pronounced on deep soils. Dominant trees in stands suffered more damage than subordinate trees. Forest plantations suffered heavy losses in certain areas. Younger plantations survived better than older (i.e., larger trees) plantations. Some tree species were more susceptible to breakage or windthrow than others (Wadsworth and Englerth 1959).

Hugo (9/18/89)

Lower rain montane forest: In Bisley, Sabana 4, and Río Grande, large trees were damaged with greater effects closer to the trajectory (Parresol and Alemañy 1998). More trees were more severely defoliated at Bisley (closer to Hurricane Hugo trajectory) than at El Verde. The proportion of uprooted or snapped stems between sites was not significantly different. Buttressing was not a deterrent to uprooting. Specific gravity of snapped trees was significantly negatively correlated with damage at Bisley but not at El Verde (Walker and others 1992). Severe defoliation occurred on 56 percent of the trees, with 11 percent of the trees snapped, 9 percent uprooted, and 7 percent killed. Most damage occurred on north-facing sites. Tall trees with large diameters were the most likely to be uprooted (Walker 1991). At Bisley, all trees were defoliated, and 35 percent had broken branches, 5 percent had broken trunks, and 48 percent were uprooted and broken. The rate of recovery (resprouting, regeneration, and growth) was high. *Dacryodes excelsa* showed the most resistance to hurricane damage and recovered quickly from injury. The most severe impacts were in valleys rather than ridges or slopes. Most introduced tree species, planted in ravines, were severely affected. All palms were defoliated, but 46 percent remained standing. Large trees were highly susceptible to damage. No clear pattern of damage was evident for tree size classes <50 cm in diameter (Basnet 1993a; Basnet and others 1992). Continued measurement of permanent plot TR-1 stand showed an immediate post-hurricane decline in species numbers and biomass along with an explosion of *Cecropia schreberiana* ingrowth (Weaver 2002b). On the Bisley biodiversity plot, species composition was relatively constant before and after Hugo except that *Cecropia schreberiana* replaced *Prestoea montana* as the most common species. Live standing trees decreased by 61 percent and basal area by 64 percent 5 months after the storm (Dallmeier and others 1998). In the Bisley watersheds, total vegetative biomass declined by 62 percent from 301 to 113 t ha⁻¹, reducing aboveground nutrient content of the forest by 45 to 48 percent (Scatena and others 1993). Deposition of fine litterfall (leaves, and small woody and miscellaneous debris) varied from 420 to 450 times the mean daily pre-storm input (Lodge and others 1991). Litter accumulation inhibited the establishment of seedlings, with variability in species responses likely to change tree composition in the forest (Guzmán-Grajales and Walker 1991). At El Verde, about 25 percent of the trees suffered impacts and 9 percent died. Pioneer species suffered high breakage and mortality, and had low capacity to sprout whereas nonpioneers suffered moderate damage and resprouted. Stem breakage was related to wood density and branch damage increased with tree size (Zimmerman and others 1994). Light increased in the post-hurricane understory (Fernández and Fetcher 1991). Post-hurricane treefall pits altered the recruitment and mortality of understory species but did not change species richness; moreover pit sizes did not affect species seedling or sapling densities (Walker 2000).

(table continued on following page)

Table 6 (continued)—Impacts of 20th century hurricanes on vegetation in the Luquillo Mountains, mainly the Luquillo Experimental Forest

Names and dates of hurricanes

Forest type or area, and brief summary of storm impacts and recovery in the LEF (source)

Growth rates of *Manilkara bidentata* seedlings increased in response to light available at the forest floor (You and Petty 1991). Post-hurricane seed rain, coinciding with periods of high seed production, was dominated by shrubs that colonized landslides (Walker and Neris 1993). Live fine roots ≤ 10 cm in depth disappeared 3 months after the storm (Parrotta and Lodge 1991). Herbaceous cover was at 55 percent 1 year after the storm when vine cover was at a maximum. The cover and species richness of herbs and vines, but not ferns, were significantly reduced after 4 years (Chinea 1999). At El Verde, eight understory tree species showed an increase in leaf numbers and a more even seasonal production of leaves than in pre-hurricane conditions; also, herbivory levels declined from 16 to 2 percent (Angulo-Sandoval 2004). The reorganization of aboveground biomass was characterized by an initial period of foliage and canopy recovery, followed by a peak of aboveground productivity as successional species grew as saplings and pole-size stems. Within stands, nutrient-use-efficiency was very low and aboveground productivity (e.g., $21.6 \text{ t ha}^{-1} \text{ yr}^{-1}$) was very high (Scatena and others 1995). A summary of recovery at Bisley showed an immediate post-hurricane loss of 50 percent of the biomass, and a loss in stem density and species richness followed by a 15-year period when biomass recovered to pre-hurricane levels, and tree numbers and species richness exceeded pre-hurricane levels (Heartsill and others 2010).

Montane rain forest: Fine litterfall deposition was 680 times the pre-storm mean daily input (Lodge and others 1991). Rainfall caused >400 landslides ranging in size from 18 m^2 to 4500 m^2 in an area of 6475 ha , or 0.11 percent of the forest area sampled (Larsen and Torres-Sanchez 1992).

Palm brake: Thirty percent of the trees suffered impacts with 84 percent of the damage in the canopy. Tree mortality was only 1 percent of the stems. Recovery was characterized by rapid refoliation, epicormic branching, adventitious root production, sprouting, and regeneration from seed in open areas (Frangi and Lugo 1991). Five year post-hurricane stem density, basal area, and biomass exceeded pre-hurricane values with 76 percent of the biomass accumulation between 1990 and 1995 due to palms. Litter on the forest floor decreased immediately after the hurricane to pre-hurricane values by 1995. Delayed tree mortality between 1990 and 1995 was twice the instantaneous tree mortality immediately after the hurricane. The regeneration of palms, trees, and tree ferns was dependent on a combination of factors, including hydroperiod, light, and space (Frangi and Lugo 1998).

Dwarf forest: The 1990-95 record for six small plots showed that post-hurricane mortality (i.e., delayed mortality) accounted for a loss of 20 percent of the stems, notably in the smallest diameter and height classes. Mortality rates varied considerably by tree species. Pre- and post-hurricane total litterfall were virtually the same, but the leafy fraction decreased and the woody fraction increased. Post-hurricane primary productivity (1991) exceeded pre-hurricane (1981) values when post-hurricane coarse woody debris was included (Weaver 1999b, Weaver and Murphy 1990). Stripping of epiphytes from trees was widespread, and varied by topography (i.e., exposure to wind) (Weaver, pers. obs.). About one-third of the biomass recovered in 16 months and >40 percent in 8 years (Weaver 1999).

Forests of the LEF: Profiles of the percent of foliage at different heights above the ground changed dramatically, with upper levels decreasing and the ground levels increasing after the storm (Brokaw and Gear 1991). The establishment of woody species by seeds is more important to post-hurricane regeneration in Lower montane forest than in Dwarf forest. The recovery of forest productivity is less responsive to nutrient availability in Dwarf forest than Lower montane forest. Opportunistic, rapid responses to nutrient additions (*Cecropia schreberiana* and graminoids in Lower montane forest, and graminoids in Dwarf forest) contrast with the slow responses of mature trees (Walker and others 1996).

Georges (9/21/98)

Lower montane rain forest: Continued measurement of permanent plot TR-1 stand revealed a continual decline in species numbers along with a proportionately greater dominance of *Dacryodes excelsa* in both residual stems and biomass (Weaver 2002b). Basal area explains 61 percent of the post-hurricane mound volume of uprooted trees; also, soil turnover rates based on uprooted trees during hurricanes is between 1,600 and 4,800 years, and exceeds turnover rates caused by either background treefall or landslides (Lenart and others 2010).

Dwarf forest: Continued measurement of the six small permanent plots on Pico del Este showed that stem numbers and biomass declined slightly (Weaver 2008).

Forests of the LEF: Post-hurricane litterfall deposits for six different forests ranged from 0.55 to 0.93 times the annual rates and their decomposition rates varied from 0.74 to 1.09 years. Subsequent decomposition returned litter levels to normal within ≤ 1.1 years at all sites (Ostertag and others 2003).

^aLong-term data analyses included the combined effects of all three hurricanes (Crow 1980, Weaver 1989b).

- Santa Clara (1956), with maximum of 145 km hr⁻¹ and 230 mm of rainfall, crossed the center of the island and caused localized damage in the Luquillo Mountains (Wadsworth and Englerth 1959).
- Hugo (1989), with maximum sustained winds of 165 km hr⁻¹ and gusts to 194 km hr⁻¹, and >200 mm of rainfall, passed 15 km northeast of the LEF but lasted only 4 hours (Brennan 1991, Scatena and Larsen 1991).
- Georges (1998), with maximum sustained winds of 185 km hr⁻¹ (gusts to 240 km hr⁻¹) and rainfall between 125 and 150 mm, passed about 15 km south of the LEF, spending 6 hours over the island (Ostertag and others 2003, U.S. Geological Survey 1999).

A monthly classification of 102 past hurricanes between 1500 and 1970 revealed: July with 12; August with 35; September with 41; and June, October, and November together with 14 (Salivia 1972). An oft repeated rhyme of uncertain origin conveniently generalizes these results: “June, too soon; July, stand by; August, don’t trust; September, to remember; October, it’s over.”

Queries are sometimes made regarding the most damaging hurricane or the most frequently hit location on the island. Hurricane impacts at any site are influenced by numerous factors, for example:

- Trajectory: Twenty of the 33 hurricanes that crossed all or a part of Puerto Rico entered in the southeastern corner of the island and departed in the west or northwest (fig. 12). From the standpoint of the Luquillo Mountains, San Janero, San Agustín, San Narciso, and San Cipriano were powerful storms whose trajectories actually crossed over the mountains.
- Intensity: San Felipe II (1928) had violent winds with a trajectory through the middle of the island causing considerable damage to homes, crops, and forests (Salivia 1970).
- Duration: San Jacinto I (1807), a slow moving storm, battered different parts of Puerto Rico for 50 hours (Salivia 1970).
- Concurrent events: San Narciso (1867) was followed within 20 days by a major earthquake that shook Puerto Rico and the Virgin Islands, causing tidal waves (Lewisohn 1964).
- Human lives: Although its winds over Puerto Rico were barely hurricane force and its trajectory was largely south of the island, the heavy rainfall that accompanied Hortense (1996) killed about 20 persons (Bennett 1996). Hortense also caused several landslides within the LEF and closed PR route 191 for about 1 month.

- Economic: Georges (1998), the most recent, traversed the entire island and caused \$1.9 billion in damages to a modern Puerto Rico (U.S. Geological Survey 1999).

Hurricanes have other effects as well. After defoliation, breakage, and windthrow caused by Hurricane Hugo, clouds appeared to be positioned higher on or above the mountains, sometimes leaving the summits clear for extended periods (Scatena and Larsen 1991). A decrease in the number of brief episodes of orographic rainfall at lower elevations was also noted. Many factors could contribute to such a phenomenon. Forest openings and loss of leaves at lower elevations could lead to a temporary increase in heating at ground level (Van der Molen and others 2006) and a reduction in transpiration rates. Also, runoff could be temporarily increased because more rainfall reaches the ground in the absence of intercepting leaf surfaces. In comparison, a temporary loss of leaves and epiphytes on the summits could reduce the amount of cloud moisture interception (Weaver 1999).

Widespread effects on vegetation also influenced the LEF’s wildlife populations—birds, reptiles, amphibians, bats, and invertebrates. Some birds are killed and others are forced to either adapt to new environmental conditions or temporarily migrate to new surroundings (Wiley and Wunderle 1993, Wunderle 1995). Adult populations of *Eleutherodactylus coqui*, the island’s best known frog, increased sixfold as a result of the deposition of canopy branches on the ground (Woolbright 1996). Juvenile frogs also increased 1 year later. Both hurricanes and droughts also influence the abundances and distributions of freshwater shrimp in headwater streams by modifying channels and substrates, or temporary drying out waterways (Covich and others 1996, 2006).

An attempt was made to associate either distant or short-term climatic events (e.g., six hurricanes and five droughts of varying intensity between 1989 and 1998) with field observations in the LEF (Beard and others 2005). Litterfall was heavily impacted by the major hurricanes of 1989 and 1998 (table 6) and fine root biomass by the intense 1994–95 prolonged drought. The remaining phenomena caused minor structural and functional forest responses and could be considered as background variation.

Chapter 3. TREE DISTRIBUTIONS AND MAJOR FOREST TYPES

Tree distributions and major forest types are a product of climate, recurrent disturbances, and human activities. With reference to the LEF, some have noted that the “ubiquitous human activity across this mountainous landscape mandates that all research, management decisions, and ecological interpretations incorporate an awareness of land use history.” They also cautioned that “Despite compelling field and historical evidence of land use, there has been tendency to interpret forest structure and dynamics largely in natural terms” (Foster and others 1999).

Tree Species Affinities and Geographic Distribution

The Luquillo Mountains have at least 830 native species of plants, including >250 species of trees, and are one of the centers of high species richness and endemism in Puerto Rico (Figueroa Colón 1996). The LEF, occupying 58 percent of the Luquillo Mountains (table 2), has at least 225 species of native trees in 144 genera and 59 plant families with the following regional distributions: 41 percent are also found in continental areas (i.e., South and Central America, Mexico, and Florida); 28 percent grow elsewhere in the West Indies, but not on the continent; and 31 percent are endemic to Puerto Rico and the Virgin Islands (Little 1970; Little and Woodbury 1976, 1980). Of the 88 tree species classified as either endemic or rare in the LEF, 16 were classed as endemic only to the LEF, 52 as endemic to Puerto Rico and also found in the LEF, and 20 species as rare in Puerto Rico but also native to areas outside of the island. Recent work has reduced the number of LEF endemics to 8, which means that 60 species are currently classed as endemic to Puerto Rico and also found in the LEF (Axelrod 2011).

The results of several surveys and studies provide other estimates of tree species by forest type (tables 7 and 8):

- **Lower montane**, 73 tallied on 4 ha and 168 noted during excursions to several sites (Little 1970); also, 69 tallied on 0.9 ha during gradient sampling (Weaver 2010a).
- **Montane**, 51 tallied on 4 ha (Little 1970) and 73 on 3.75 ha during past sampling (Weaver 1989b).
- **Palm brake**, 63 recorded on 4 ha (Little 1970) and 36 tallied on 0.6 ha in gradient sampling (Weaver, 2012).
- **Dwarf**, 54 observed on 0.82 ha during gradient sampling (Weaver 2008, 2010b).

Although some areas within the LEF have never been sampled, it seems improbable that additional surveys could add more than a few rare tree species for the forest.

Field Sampling and Permanent Plot Monitoring

The Forest Service and collaborators have carried out surveys in the Luquillo Mountains for nearly a century and have monitored primary and secondary forest plots for nearly 70 years. Since 1943, at least 618 demarcated plots with >134,000 trees have been established on 66.75 ha located between 210 and 1,025 m in elevation (Lugo and Brown 1981, Wadsworth 1970) (fig. 13) (table 7). Although receiving less attention than better known research sites, plot monitoring has contributed background information on tree species and forest types, and remains an integral part of the Institute’s research program. Ideally, sampling would have included more plots near the forest border. However, most of those areas were heavily impacted by human activities such as agriculture, timber harvest, charcoal production, road and trail construction, forest plantations, and timber stand improvement (Crow 1980, García-Montiel and Scatena 1994, Scatena 1989, Thompson and others 2002, Wadsworth 1950, Weaver and Bauer 1986).

The results of plot studies and monitoring reflect study objectives, sampling design and replication, and the period of time when measurements were carried out, especially with regard to previous hurricanes or land use. Many of the studies emphasized tree species, timber volumes, or other aspects of the vegetation, as follows:

- **Timber surveys**—Temporary plots were used to: survey the stocking of sawtimber species in lower montane forest in 1905; estimate standing timber volume in 1918; carry out strip surveys of forest stocking in 1930; and conduct linear strip timber surveys in areas scheduled for future harvest in 1937 and 1948. The data was for used for planning and management purposes (Wadsworth 1970) (appendix A).
- **Isolated permanent plots**—Trees on 24 plots of variable size located within representative forest cover were permanently tagged and measured (fig. 13) (table 7): in 1943, a lower montane plot near El Verde; in 1946 and 1951, five plots in lower montane forest, nine in montane forest, and two in palm brake; in 1980, another palm plot; in 1990, six small dwarf forest plots. All trees above a specified diameter at breast height (d.b.h.) were identified and measured, and height was omitted, measured, or estimated. Ingrowth (i.e., recruitment of trees attaining the minimum d.b.h. size) and mortality were tallied. All plots were re-measured periodically. The information was initially used to determine tree species’ compositions and distributions, typical tree sizes, stem densities, basal areas, locally derived volume tables, and d.b.h. growth rates by tree species and

Table 7—Permanent and temporary tree monitoring plots established in the Luquillo Experimental Forest^a

Location Plot name	Dates established	Plots no.	Total area ha	Elevation m	Stems no.	Species no.
Long-term tree species monitoring plots						
Lower montane rain forest ^b						
El Verde III	1943	1	0.72	380	955	46
Tabonuco ridge 1 (TR-1)	1946	1	0.40	400	713	48
Tabonuco slope 2 (TS-2)	1946	1	0.40	500	827	46
Tabonuco slope 3 (TS-3) ^c	1946	1	0.40	570	949	48
Tabonuco cutover 1 (TCU-1)	1947	1	0.20	470	402	47
Tabonuco cutover 2 (TCU-2)	1947	1	0.20	470	493	42
Montane rain forest ^d						
Colorado slope 1 (CS-1)	1946	1	0.40	700	905	35
Colorado slope 2 (CS-2)	1946	1	0.40	700	725	47
Colorado slope 3 (CS-3) ^c	1946	1	0.40	880	676	40
Colorado slope 4 (CS-4) ^c	1946	1	0.40	880	733	33
Colorado valley 1 (CV-1) ^c	1946	1	0.40	750	662	37
Colorado valley 2 (CV-2) ^c	1946	1	0.40	740	588	27
Colorado valley 3 (CV-3) ^c	1946	1	0.40	650	785	58
Colorado valley 4 (CV-4) ^c	1946	1	0.40	650	805	49
Colorado cut over (CCU)	1947	1	0.40	670	794	24
Palm brake ^e						
Palm slope 1 ^c	1946	1	0.40	500	705	26
Palm slope 2	1946	1	0.40	570	703	33
Riparian palm brake	1980	1	0.25	750	765	27
Dwarf forest ^f						
East Peak (near road)						
Ridge	1990	1	0.025	1000	101	6
Slope	1990	1	0.025	970	48	6
Ravine	1990	1	0.025	970	49	7
East Peak (near wreck)						
Ridge	1990	1	0.025	900	78	9
Slope	1990	1	0.025	900	89	7
Ravine	1990	1	0.025	900	81	7
Subtotal (long-term plots)	1943-90	24	7.12	380-1000	13,631	NA

(table continued on following page)

Table 7 (continued)—Permanent and temporary tree monitoring plots established in the Luquillo Experimental Forest^a

Location Plot name	Dates established	Plots no.	Total area ha	Elevation m	Stems no.	Species no.
Special research monitoring plots						
Lower montane rain forest						
Pilot management plots ^a						
Cubuy	1957	100	8.00	350-550	799	29
Río Grande	1957	104	8.32	420-600	404	14
Sabana 4	1957	106	8.48	210-600	273	8
Sabana 8	1957	107	8.56	180-360	1,332	17
Luquillo Forest dynamics plot ^h	1990	1	16.00	333-428	86,788	145
Montane rain forest						
FIA inventory plots ⁱ	2000	6	0.40	608-808	229	27
Subtotal (special plots)	1957-2000	424	49.76	210-808	89,825	NA
Gradient sampling plots						
Lower montane rain forest ^l	2000-02	18	0.90	380-550	3,619	42
Montane rain forest ^k	1980-81	69	3.75	600-900	8,183	87
Palm brake ^j	2000-02	12	0.60	550-850	1,122	35
Dwarf forest ^m	2000-02	33	0.82	900-1025	3,621	42
Northeastern island gradient ⁿ	2001-02	12	1.20	380-1000	1,764	71
Metacommunity study ^o	2001-02	26	2.60	300-1000	12,361	99
Subtotal (gradient plots)	1980-2002	170	9.87	300-1025	30,670	NA
Total	1943-2002	618	66.75	210-1025	134,126	NA

^aOther small plots were established early within the LEF but not maintained. Minimum d.b.h. for all plots is ≥ 4 cm unless otherwise indicated. Stem and species numbers are from the first tallies made on each plot. NA = Not available.

^bSources: Crow (1980); Drew and others (2009); Johnston (1990); Weaver (1983, 1998, 2002b).

^cPermanent plots within the El Toro Wilderness Area.

^dSources: Weaver (1983, 1986, 1987a, 1987b, 1989b, 2000a).

^eSources: Frangi and Lugo (1985, 1991, 1998); Lugo and Frangi (1993); Weaver (1983).

^fSources: Weaver (1999, 2008).

^gSources: Anonymous (1958); Crow and Grigal (1980); Crow and Weaver (1977). Each area contained selected crop trees ≥ 10 cm.

^hSource: Thompson and others (2002). Minimum d.b.h. is ≥ 1 cm.

ⁱSource: Brandeis and others (2007). Minimum d.b.h. is ≥ 12.5 cm.

^jSource: Weaver (2010a) (18 plots 50x10 m in size).

^kSource: Weaver (1991, 2000, 2001). Also, gradient study (69 plots 50x10 m in size).

^lSource: Weaver (XXX) (12 plots 50x10 m in size).

^mSource: Weaver (2010b) (33 plots 25x10 m in size).

ⁿSource: Gould and others (2006) (12 plots 10x10 m in size). Minimum d.b.h. is ≥ 2 cm.

^oSource: Barone and others (2008) (26 plots 50x20 m in size). Minimum d.b.h. is ≥ 1 cm.

Table 8—Comparison of forest structure and dynamics data for the Luquillo Experimental Forest gradient

Feature	Forest type			
	Lower montane rain forest	Montane rain forest	Palm brake	Dwarf forest
Forest type boundaries, elevation (m)	120-600	600-900	>450	>900
Total tree species per type ^a	168	88	63	54
Tree species (no. ha ⁻¹) ^b	40-50	35-40	25-30	15-20
Species in gradient sample (no.) ^c	69	84	36	42
Single most abundant species (%) ^d	20	19	57	23
Five most abundant species (%) ^d	47	52	84	72
Ten most abundant species (%) ^d	65	71	90	91
Structural characteristics^e				
Mean density (trees ha ⁻¹)	1,557 ± 100	2059 ± 72	1892 ± 93	3,328 ± 242
Ridge topography	1677 ± 144	2385 ± 130	2165 ± 50	3878 ± 386
Slope topography	1623 ± 200	2164 ± 98	1820 ± 225	3843 ± 460
Ravine topography	1370 ± 174	1627 ± 84	1690 ± 31	2263 ± 173
Total range of density values	680-2380	1060-3840	1160-2300	1320-4660
Mean canopy tree height (m)	19.4 ± 0.1	13.0 ± 0.3	12.5 ± 0.5	8.8 ± 0.4
Ridge topography	21.1 ± 1.9	12.4 ± 0.5	11.2 ± 0.6	7.4 ± 0.7
Slope topography	19.3 ± 1.2	12.5 ± 0.4	13.5 ± 0.8	8.3 ± 0.7
Ravine topography	17.9 ± 1.2	14.1 ± 0.5	12.8 ± 0.9	10.7 ± 0.5
Total range of tree height values	14.2-25.9	7.3-17.9	9.9-15.3	4.0-13.5
Mean aboveground woody biomass (t ha ⁻¹)	244 ± 28	190 ± 11	105 ± 14	172 ± 12
Ridge topography	361 ± 38	243 ± 23	146 ± 36	181 ± 25
Slope topography	229 ± 29	198 ± 13	90 ± 5	178 ± 17
Ravine topography	142 ± 20	129 ± 11	78 ± 10	148 ± 17
Total range of biomass values	95-512	77-519	59-249	76-356
Additional structural characteristics^b				
Typical d.b.h. range; maximum d.b.h. (cm) ^b	4-50; 120	4-30; 250	4-30; 50	4-15; 40
Typical basal area range (m ² ha ⁻¹) ^b	35-45	35-45	30-35	30-45
Typical mean plot specific gravity (g cm ⁻³) ^e	0.49 (0.60)	0.56 (0.66)	0.35 (0.52)	0.63 (0.64)
Leaf biomass (t ha ⁻¹) ^b	7.9	5.8	25.1	2.9
Leaf area index (m ² m ⁻²) ^b	67	35	3.3	33.5
Mean specific leaf area (cm ² g ⁻¹) ^b	127	91	NA ^f	47
Soil organic matter (t ha ⁻¹) ^{b g}	420	330	320	550

(table continued on following page)

Table 8 (continued)—Comparison of forest structure and dynamics data for the Luquillo Experimental Forest gradient

Feature	Forest type			
	Lower montane rain forest	Montane rain forest	Palm brake	Dwarf forest
Dynamic characteristics^b				
Ingrowth (stems ha ⁻¹ yr ⁻¹) ^{h,i}	13	23	12	32
Mortality (stems ha ⁻¹ yr ⁻¹) ^{h,i}	28	18	22	75
Litterfall (t ha ⁻¹ yr ⁻¹)	8.6	6.8	8.8	3.1
Leaf	4.94	5.05	6.26	2.45
Wood	1.38	1.22	0.86	0.28
Fruit/Flower	0.51	0.23	0.56–1.32	0.07
Miscellaneous	1.78	0.3	0.36	0.37
Loose litter (t ha ⁻¹)	6.0	8.76	5.4	4.34
Standing herbivory (%)	7.0	NA	5.0	NA
Herbivory rate (t ha ⁻¹ yr ⁻¹)	0.38	0.25	NA	0.13
Litterfall/loose litter	1.2	0.78	1.62	0.7
Mean d.b.h. growth (cm yr ⁻¹)	0.09–0.14	0.10	0.23	0.03
Woody biomass increment (t ha ⁻¹ yr ⁻¹)	2.50	0.57	3.30	0.45
Total aboveground NPP (t ha ⁻¹ yr ⁻¹)	10.5	7.6	19.5	3.7

^aSources: Lower montane (Little 1979), Montane (Weaver 1989b), Palm (Little 1970), and Dwarf (Weaver 2008). The entire LEF has 225 tree species (Little 1970, Little and Woodbury 1976).

^bSources: Lugo and Frangi 1993; Weaver 1983, 1999, 2008; Weaver and Murphy 1990.

^cSource: Species, mean stem density, canopy height, biomass, and values by topography (gradient sampling). All plots had closed canopies and measured 500 m² except for the Dwarf forest plots with 250 m². All stems >4.0 cm were tallied.

^d% = percent of total stems.

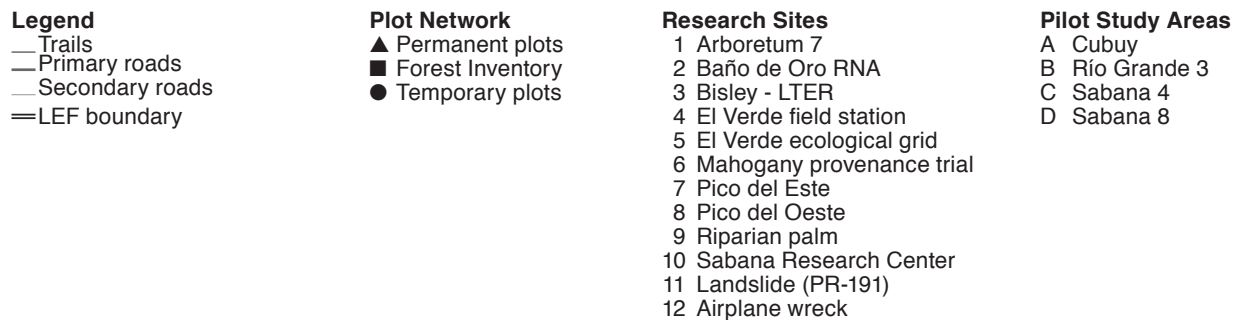
^eSpecific gravities were estimated as the mean of available values weighted by number of stems by forest type. The first estimate includes *Prestoea montata* and the second estimate only broadleaf species (Chudnoff 1981, see endnotes; Little and Wadsworth 1964; Little and others 1974; Reyes and others 1992; Smith 1970; Weaver 1992; appendix F). Mean values were based on most common species weighted according to their numerical abundance (Table 9).

^fNA = not available.

^gSoil depths: Lower montane, 25 cm; Montane and dwarf, 50 cm; Palm, 100 cm.

^hLower montane (2), Montane (2), and Palm (1) plots 0.4 ha in size measured for 30 years (Weaver 1983).

ⁱDwarf forest plots 0.025 ha in size measured for 15 years, post-hurricanes Hugo and Georges (Weaver 2008).



forest type (Wadsworth 1947, 1951, 1953, Weaver 1983) (table 8). Later, the datasets were used to determine biomass, evaluate hurricane impacts, and to derive estimates of net primary productivity, nutrient fluxes, tree ages, and to help characterize tree life cycles.

- **Pilot management plots**—In 1957, the pilot management study employed a grid of plots in four areas—in the secondary lower montane forests in Cubuy, Río Grande, and Sabana 8, and in the mature lower montane forest at Sabana 4 (figs. 3 and 13) (table 7). Thinnings were carried out within the secondary forests and the d.b.h. growth rates of 2,060 trees were determined.
- **Gradient sampling**—After 1980, a systematic series of temporary closed forest plots (i.e., untagged trees on plots marked with corner stakes) was set up along elevational gradients throughout the LEF (Weaver 1987a, 1991, 2000b, 2010a, 2010b) (fig. 13) (table 7) (appendix C). The plots were stratified in groups of three by topography (i.e., ridge, slope, and ravine). Plot sizes were relatively small yet provided good estimates of variation in forest structure and species composition (figs. 14, 15, 16, 17, and 18) (tables 9, 10, 11, and 12) (appendix C). The total number of species tallied was relatively high because the sample plots were limited to closed forest conditions and encompassed considerable environmental variation.
- **Vegetation surveys**—After Hurricane Hugo, surveys were carried out on disturbed sites (i.e., landslides, areas heavily impacted by hurricanes, or roadsides). Sampling usually involved relatively small areas with temporary plots (appendix D). In these instances, survey results may be influenced by local conditions.
- **El Verde Ecological Grid (forest dynamics plot)**—Starting in 1990, a complete tree census was carried out on a 16-ha permanent plot composed of a grid of subplots set up at El Verde to explore hurricane recovery and tree species dynamics (Thompson and others 2002) (fig. 13) (table 7). Large plots may subsequently be divided into subplots for particular studies (e.g., nutrient analyses, riparian zone species compositions). Their remeasurement requires considerable time.
- **Forest Inventory and Analysis (FIA) Program**—Since 1980, FIA has surveyed secondary forests throughout Puerto Rico. The FIA, first called the Forest Survey, dates to McSweeney-McNary Act that also established the research branch of the Forest Service (Shaw 2006; U.S. Department of Agriculture, Forest Service 1983). Island-wide inventories carried out in 1980 and 1990 (Birdsey and Weaver 1982, Franco and others 1997), were expanded in 2001 to include six plots within the LEF (Brandeis and others 2007) (fig. 13) (table 7). Data from the standardized LEF plots are analyzed along with other plots in the FIA network for Puerto Rico and its offshore islands.

- **Northeastern gradient**—In 2001-02, several plots were established along an elevational gradient between the coastal lowland and Pico del Oeste to determine forest structure and composition. Twelve were located in the LEF (Gould and others 2006) (figs. 1 and 13) (table 7).
- **Metacommunity structure**—In 2001-02, woody stems were sampled on 26 plots along elevational transects in the Baño de Oro and Río Sonadora watersheds (Barone and others 2008) (fig. 9) (table 7).
- **Plantations**—Since the 1950s, trees have been planted as part of species trials, provenance studies, forest plantations, or as additions to the Caracoles arboretum (figs. 6, 7, and 13). Subsequent surveys of select plots or labeled trees were used to determine survival and growth (Francis 1987, 1995) (appendix E). Study results may be influenced by tree species, their genetic attributes, site quality, or field techniques, including plot maintenance schedules.

Lower Montane Forest

The lower montane forest, the most diverse in the LEF, contains the tallest trees and has the longest history of human activity, including mining, logging, subsistence agriculture, and temporary settlement in certain areas. Research has included tree planting and experimental silviculture in secondary stands, permanent plot monitoring, gradient sampling, and numerous ecological studies carried out at two major sites—Bisley and El Verde.

Stand features and notable tree species—Mature lower montane forest contains three layers of trees, mainly evergreen. Canopy species reach 30 m in height with occasional diameters approaching 1.5 m (Wadsworth 1951). The forest type, occupying about one-half of the LEF, has the lowest average stem density, and greatest mean canopy height and biomass (fig. 3) (table 8). *Dacryodes excelsa*, *Prestoea montana*, *Sloanea berteriana*, *Cordia borinquensis*, *Manilkara bidentata*, *Schefflera morototoni*, *Cecropia schreberiana*, *Micropholis garciniifolia*, *Henriettea squamulosa*, and *Quararibea turbinata* (Sw.) Poir., as listed, were the 10 most common of > 80 species that were recorded on 4 ha of permanent plots during the 1940s (Briscoe and Wadsworth 1970). *Cecropia schreberiana* is most abundant after hurricanes when its dormant seeds germinate in response to canopy openings; however, it is uncommon in abandoned pastures at lower elevations (Brokaw 1998). During post-hurricane recovery of the forest, *Cecropia schreberiana* and *Schefflera morototoni* declined significantly in numbers. *Cecropia schreberiana* trees persist within the forest along road cuts and within riparian areas, ravines, landslides, and treefall gaps.

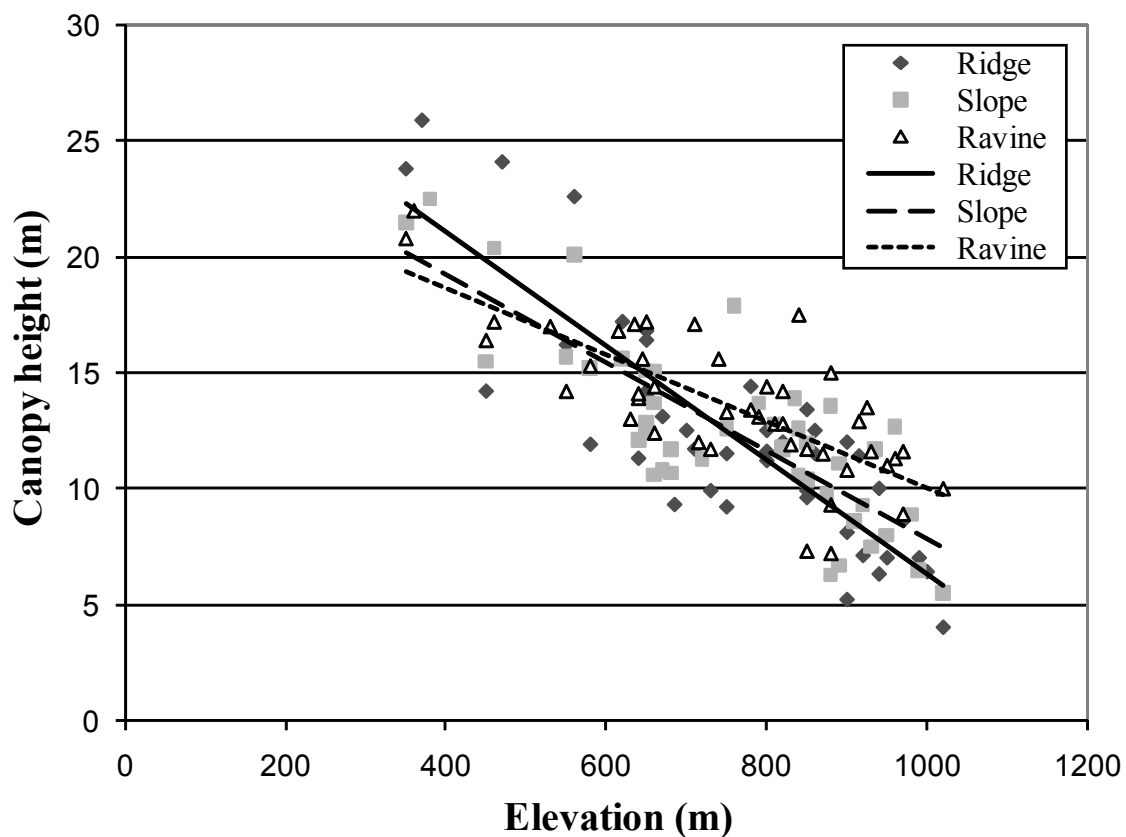


Figure 14—Mean canopy heights per plot by elevation in the Luquillo Experimental Forest (linear trends for ridge, slope, and ravine).

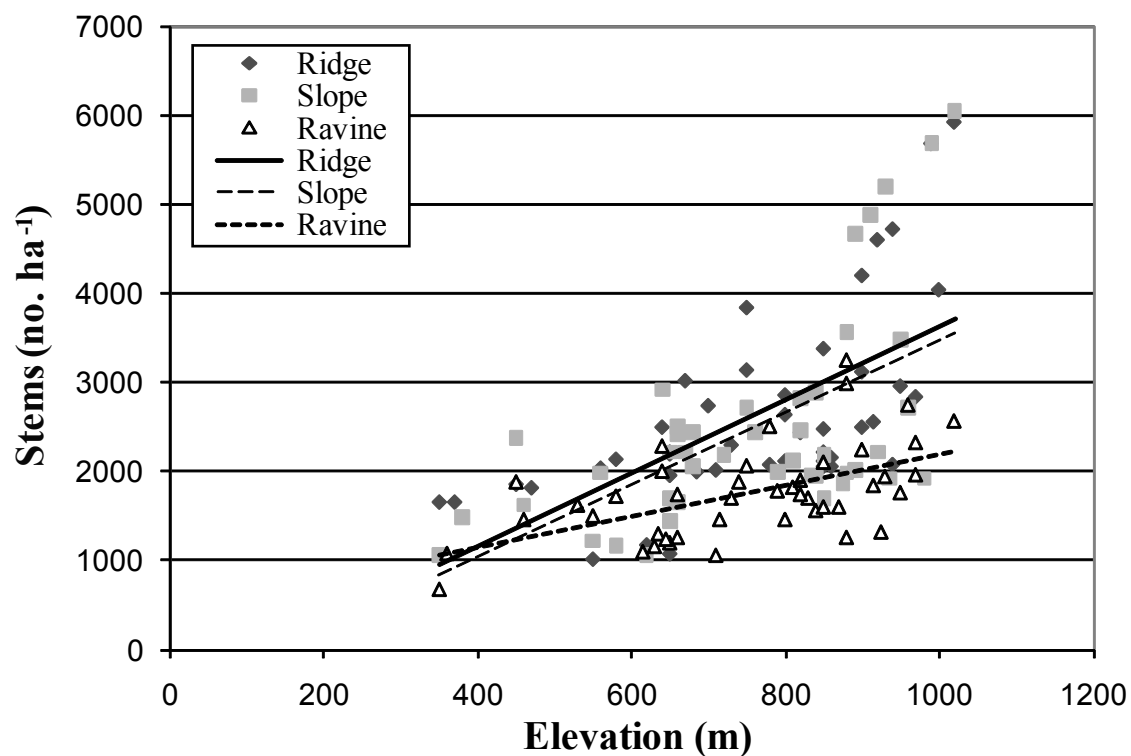


Figure 15—Mean density of stems ≥ 4 cm d.b.h. per plot by elevation in the Luquillo Experimental Forest (linear trends for ridge, slope, and ravine).

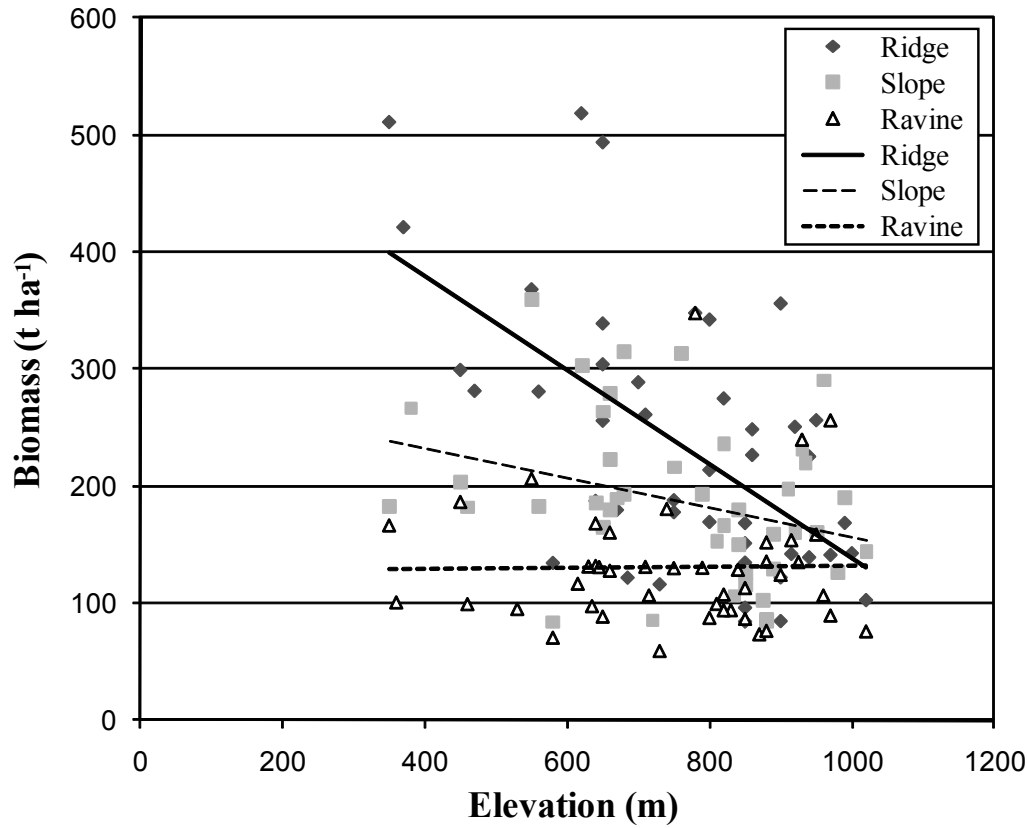


Figure 16—Aboveground dry weight biomass per plot for stems ≥ 4 cm d.b.h. by elevation within the Luquillo Experimental Forest (linear trends for ridge, slope, and ravine).

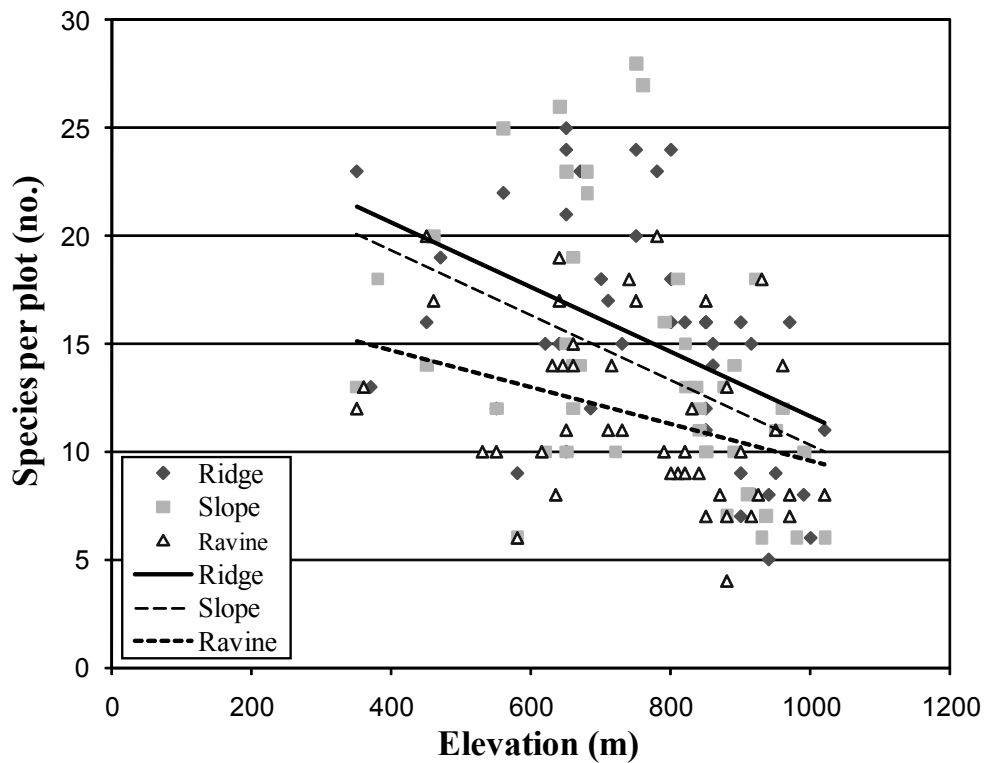


Figure 17—Number of tree species per plot for stems ≥ 4 cm d.b.h. by elevation within the Luquillo Experimental Forest (linear trends for ridge, slope, and ravine).

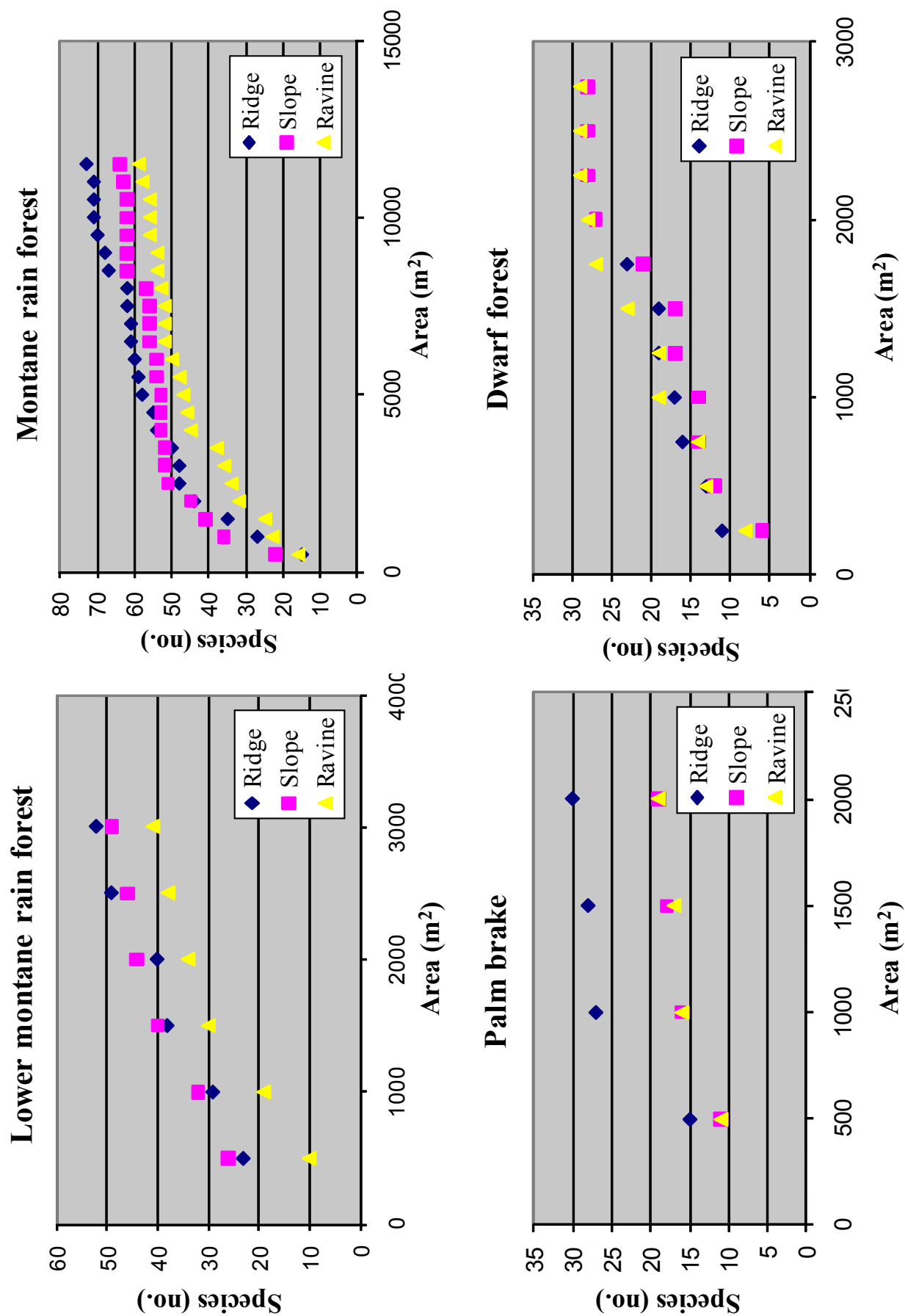
Figure 18—Species-area curves for stems ≥ 4 cm d.b.h. by forest types within the Luquillo Experimental Forest.

Table 9—Lower montane rain forest: occurrence of 31 tree species on 18 plots each 50 x 10 m in size within the Luquillo Experimental Forest^a

Species	Occurrence		Topography ^b		
	Plots	Stems	R	S	V
			Stems no.		
<i>Prestoea montana</i>	17	285	48	42	195
<i>Dacryodes excelsa</i>	9	150	83	65	2
<i>Micropholis garciniifolia</i>	9	83	31	49	3
<i>Manilkara bidentata</i>	10	80	31	38	11
<i>Sloanea berteriana</i>	12	60	19	17	24
<i>Drypetes glauca</i>	10	55	16	30	9
<i>Tetragastris balsamifera</i>	8	52	32	17	3
<i>Croton poecilanthus</i>	7	51	7	4	40
<i>Daphnopsis philippiana</i>	6	49	19	24	6
<i>Cecropia schreberiana</i>	7	48	10	14	24
<i>Cyrilla racemiflora</i>	5	36	17	18	1
<i>Henriettea squamulosa</i>	5	34	4	20	10
<i>Tabebuia rigida</i>	4	32	15	12	5
<i>Cordia borinquensis</i>	12	23	4	10	9
<i>Schefflera morototoni</i>	8	23	13	8	2
<i>Psychotria berteriana</i>	7	21	12	2	7
<i>Ocotea spathulata</i>	5	19	13	6	0
<i>Myrcia leptoclada</i>	4	19	7	12	0
<i>Micropholis guyanensis</i>	4	19	11	8	0
<i>Tetrazygia ubanii</i>	4	17	8	6	3
<i>Matayba domingensis</i>	6	14	10	4	0
<i>Ocotea leucoxylon</i>	9	13	7	2	4
<i>Meliosma herbertii</i>	5	13	5	8	0
<i>Hirtella rugosa</i>	5	13	5	7	1
<i>Guarea glabra</i>	9	12	2	3	7
<i>Inga laurina</i>	4	9	2	5	2
<i>Ormosia krugii</i>	4	9	5	4	0
<i>Alchornea latifolia</i>	5	8	4	4	0
<i>Guatteria caribaea</i>	4	8	6	2	0
<i>Miconia tetrandra</i>	4	8	1	5	2
<i>Ixora ferra</i>	4	8	4	4	0
38 other species	—	123	53	34	36
Total	18	1394	504	484	406

— = Not applicable because the number of species varies.

^aSource: Gradient study (Weaver 2010a).

^bTopography: Six plots apiece on ridge (R), slope (S), and ravine (V) topography. Listed species ≥8 stems equal 91.2 percent of all stems tallied (summarized from appendix C).

Table 10—Montane rain forest: occurrence of 26 tree species on 69 plots each 50 x 10 m in size within the Luquillo Experimental Forest^a

Species	Occurrence		Topography ^b		
	Plots	Stems	R	S	V
			Stems no.		
<i>Prestoea montana</i>	58	1309	217	254	838
<i>Henriettea squamulosa</i>	60	937	309	454	174
<i>Micropholis garciniifolia</i>	49	643	295	319	29
<i>Tabebuia rigida</i>	35	387	177	190	20
<i>Micropholis guyanensis</i>	27	349	206	122	21
<i>Cordia borinquensis</i>	57	346	135	114	97
<i>Ocotea spathulata</i>	43	337	215	105	17
<i>Croton poecilanthus</i>	36	315	22	74	219
<i>Cyrilla racemiflora</i>	33	206	113	82	11
<i>Haenianthus salicifolius</i>	32	171	82	70	19
<i>Daphnopsis philippiana</i>	37	140	48	74	18
<i>Miconia tetrandra</i>	27	138	73	26	39
<i>Clusia clusioides</i>	27	136	66	69	1
<i>Hirtella rugosa</i>	17	121	84	6	1
<i>Eugenia borinquensis</i>	23	111	63	21	27
<i>Matayba domingensis</i>	19	108	58	44	6
<i>Myrcia fallax</i>	29	97	73	21	3
<i>Cyathea arborea</i>	13	70	30	25	15
<i>Byrsonima wadsworthii</i>	25	69	44	19	6
<i>Ditta myricoides</i>	27	61	10	27	24
<i>Magnolia splendens</i>	27	59	25	28	6
<i>Psychotria berteriana</i>	22	56	27	10	19
<i>Garcinia portoricensis</i>	6	55	43	10	2
<i>Cecropia schreberiana</i>	24	53	7	9	37
<i>Drypetes glauca</i>	9	48	4	28	16
<i>Ocotea leucoxylon</i>	22	46	34	8	4
47 other species	—	662	290	178	194
Totals	69	7030	2750	2417	1863

— = Not applicable because the number of species varies.

^aSource: Gradient study (Weaver 1989b).

^bTopography: Twenty-three plots each on ridge (R), slope (S), and ravine (V) topography. Listed species ≥ 46 stems equal 90.6 percent of all stems tallied (summarized from appendix C).

Table 11—Palm brake: occurrence of 11 tree species on 18 plots each 50 x 10 m in size within the Luquillo Experimental Forest^a

Species	Occurrence		Topography ^b		
	Plots	Stems	R	S	V
			Stems no.		
<i>Prestoea montana</i>	12	637	203	202	232
<i>Cecropia schreberiana</i>	11	129	47	50	32
<i>Henriettea squamulosa</i>	9	73	34	24	15
<i>Tabebuia rigida</i>	3	40	36	4	0
<i>Cordia borinquensis</i>	9	38	14	16	8
<i>Eugenia borinquensis</i>	4	28	22	0	6
<i>Psychotria berteriana</i>	8	19	9	8	2
<i>Croton poecilanthus</i>	4	16	1	4	11
<i>Sapium laurocerasus</i>	9	14	5	6	3
<i>Clibadium erosum</i>	4	13	5	2	6
<i>Cyathea portoricensis</i>	4	13	0	8	5
25 other species	—	102	70	14	18
Total	12	1122	446	338	338

— = Not applicable because the number of species varies.

^aSource: Gradient study (Weaver 2010).

^bTopography: Four plots each on ridge (R), slope (S), and ravine (V) topography. Listed species ≥ 13 stems equal 90.9 percent of all stems tallied (summarized from appendix C).

Table 12—Dwarf forest: occurrence of 10 tree species on 33 plots each 25 x 10 m in size within the Luquillo Experimental Forest^a

Species	Occurrence		Topography ^b		
	Plots	Stems	R	S	V
			Stems no.		
<i>Tabebuia rigida</i>	27	844	378	372	94
<i>Ocotea spathulata</i>	22	566	292	215	59
<i>Eugenia borinquensis</i>	30	432	173	183	76
<i>Cyathea bryophila</i>	21	421	41	176	204
<i>Micropholis garciniifolia</i>	26	362	166	169	27
<i>Henriettea squamulosa</i>	25	357	129	96	132
<i>Prestoea montana</i>	12	135	0	5	130
<i>Clusia clusioides</i>	11	76	24	34	18
<i>Calypttranthes krugii</i>	19	61	30	21	10
<i>Haenianthus salicifolius</i>	10	48	23	12	13
32 other species	—	317	120	100	97
Total	33	3619	1376	1383	860

— = Not applicable because the number of species varies.

^aSource: Gradient study (Weaver 2008, 2010b).

^bTopography: Eleven plots apiece on ridge (R), slope (S), and ravine (V) topography. Listed species ≥ 48 stems equal 91.2 percent of all stems tallied (summarized from appendix C).

The best developed stands in lower montane forest are on low, well-drained ridges where *Dacryodes excelsa*, a species formerly valued for furniture and general construction, is abundant and grows in large sizes (Little and Wadsworth 1964). Indigenous peoples hollowed out trunks as boats and used its resin for torches, as incense in religious ceremonies, for caulking boats, and for medicinal purposes. Although *Dacryodes excelsa* is considered the dominant tree species within the type, *Sloanea berteriana* is sometimes more abundant in smaller sizes (Basnet 1992b, Lugo and Wadsworth 1990). *Manilkara bidentata*, another stand dominant, is one of Puerto Rico's most attractive commercial timbers (Little and Wadsworth 1964). The wood is strong, hard, and heavy, and was used for construction locally and for furniture and cabinets elsewhere. Two other species, *Buchenavia tetraphylla* and *Guarea guidonia*, both valued



Lower montane rain forest. *Dacryodes excelsa* (tabonuco tree) is the dominant species that grows at elevations <600 m within the Luquillo Mountains. Tabonuco favors ridge topography where it sometimes exceeds 30 m in height and 1 m in diameter. (Photo by Gerald P. Bauer)

as furniture woods, are among the fastest growing in d.b.h. (Crow and Weaver 1977, Longwood 1961).

Within the secondary stands of the Bisley watershed, *Alchorneopsis portoricensis*, *Casearia arborea*, *Dacryodes excelsa*, *Inga laurina*, and *Manilkara bidentata* were more frequent on ridges and slopes than in ravines. In contrast, *Guarea guidonia* and *Prestoea montana* were more abundant in ravines (Basnet 1992b) (appendix C). The dominance of *Dacryodes excelsa* on ridges has been attributed to better soil drainage, better anchorage among boulders, and root grafting, which make the trees more resistant to windthrow (Basnet and others 1993). Root grafting in *Dacryodes excelsa* has been known since the early 1960s when abundant, healthy, shaded saplings were observed growing in the vicinity of larger trees (Wadsworth 2009, see endnotes). Grafted trees were taller and had smaller crowns than nongrafted neighbors probably because they received additional water or nutrients (Basnet and others 1993, Wadsworth 2009, see endnotes).

Pterocarpus officinalis, with its sinuous buttresses, is a common swamp species in the neotropics. It grows in Puerto Rico's coastal fresh- and brackish-water swamps, and is also found along the Río Mameyes and its tributaries (Francis and Lowe 2000, Little and Wadsworth 1964). One site is at and above the confluence of the Río Mameyes and the Río de la Mina. The site floods frequently, a condition similar to the seasonal flooding of coastal lowlands. The occurrence of *Pterocarpus officinalis* at elevations above the coastal plain, although rare, has been documented elsewhere in the Caribbean (Francis and Lowe 2000). Probably coincidental, this species, whose buttresses were fashioned into plates for panning gold, is only 400 m from the nearest abandoned gold mine along the Río de La Mina (Cardona 1984, Weaver 1994).

In the past, *Buchenavia tetraphylla*, a deciduous species, was prevalent in lowland forests surrounding the Luquillo Mountains (Gill 1931). Other prominent or common LEF tree species found today in lowland forest remnants or abandoned pastures and recorded in the gradient sampling include *Andira inermis*, *Brysonima spicata*, *Cecropia schreberiana*, *Dacryodes excelsa*, *Guarea guidonia*, *Inga laurina*, *I. vera*, *Manilkara bidentata*, *Miconia prasina*, *Ocotea leucoxylon*, *Schefflera morototoni*, *Tabebuia heterophylla*, *Tetragastris balsamifera*, *Trichilia pallida*, and *Vitex divaricata* (Aide and others 1996, Gould and others 2006, Wadsworth 1950) (appendix C).

Past human activity—Past human involvement in the lower montane forest was extensive and has affected the structure and composition of the forest to varying degrees. Timber extraction occurred along the forest border and in river valleys and lower slopes where 42 tree species were considered satisfactory for harvest: 7 for furniture, 16 for

construction, and 19 for large posts (table 5). From the mid-1930s to the mid-1940s, about 3500 ha of open land reforested naturally, including areas with planting trials (Wadsworth 1970). In the mid-1990s, researchers studied secondary forest stands growing on the lower, northern slopes of the Luquillo Mountains (Aide and others 1996). After 40 years of recovery, these stands could not be distinguished from undisturbed sites in terms of density, basal area, species numbers, or diversity; however, centuries would be required before the species compositions were similar. Moreover, abandoned pastures ranging from about 50 to 80 years old had tree species distinct from those on old growth forest sites > 80 years old, again suggesting that considerable time would be required for the species compositions to converge (Aide and others 2000). On another site harvested for timber around 1900 and abandoned in the 1930s, the basal area and litterfall rates 50 years later were similar to undisturbed lower montane forest in the vicinity; the dominant species, however, were successional (Zou and others 1995). It appears that secondary forests recovering after disturbance on the lower slopes of the LEF will carry the signature of past land use for centuries, at least with regard to species composition.

Gradient sampling—Gradient sampling within lower montane forest was carried out in the Río Mameyes and Río Espiritu Santo watersheds. The 18-plot sample disclosed 69 trees species, 10 of which accounted for 64 percent of the total stems (tables 8 and 9). *Prestoea montana*, with 20 percent of the total, was the most common species and *Dacryodes excelsa* followed with 11 percent. Of the remaining species, the 38 least common accounted for only 9 percent of the tallied stems.

Of the 10 most frequently encountered species, *Cecropia schreberiana*, *Croton poecilanthus*, and *Prestoea montana* were more common in ravines and *Dacryodes excelsa* and *Tetragastris balsamifera* on ridges (Weaver 2010a) (table 9). Moreover, *Manilkara bidentata* favored slopes and ridges and *Sloanea berteriana* slightly favored ravines although well represented on other topographies. Less common species such as *Cyrilla racemiflora*, *Matayba domingensis*, and *Schefflera morototoni* also grew mainly on ridges and upper slopes whereas *Cordia borinquensis* was more common on slopes and ravines. Sampling also revealed differences in species composition by watershed: the Río Mameyes faces northeast and is wetter and probably cloudier than the Espiritu Santo, which faces northwest (Ewel and Whitmore 1973). Species such as *Clusia clusioides*, *Eugenia borinquensis*, *Ocotea spathulata*, and *Tabebuia rigida*, all most abundant in dwarf forest (appendix C), survive on scattered sites at mid-elevations within the Río Mameyes watershed. These sites are mainly exposed, upper slopes and ridges similar in some respects to the summit areas.

Monitoring long-term plots—Four basically undisturbed permanent plots were established on slopes and ridges in lower montane forest (Wadsworth 1947, 1949, 1952a, 1952b, 1953, 1970) (fig. 13) (table 7):

- El Verde III, a lightly thinned 0.72 ha plot, in 1943.
- TR-1 (tabonuco ridge) and TS-3 (tabonuco slope), two previously undisturbed 0.40 ha plots, both in 1946.
- TS-2 (tabonuco slope), a 0.40 ha undisturbed plot in 1946 (abandoned in the 1960s after a service road was routed through it).

Research on El Verde III plot provided a 33-year post-hurricane history for several indicator species: *Dacryodes excelsa*, *Manilkara bidentata*, and *Sloanea berteriana*, mature forest canopy species; *Cecropia schreberiana* and *Schefflera morototoni*, both common gap species regenerating after disturbance; *Prestoea montana*, the ubiquitous understory palm; and *Croton poecilanthus*, an endemic understory species (Crow 1980). The mature species *Dacryodes excelsa* and *Manilkara bidentata* along with *Prestoea montana* increased in stem numbers and basal area during the measurement period and *Sloanea berteriana* and *Croton poecilanthus*, after initial increases, later declined. Gap species were common in the stand during the 1940s, when stem numbers and biomass increased rapidly. Later, they also declined. In the 1970s, the stand approached steady-state for biomass, and had a lower stem density and fewer species than during the 1940s.

A thinning carried out at El Verde in 1937, designed to minimize impacts in the watershed, was very light and at most “extended the period in which youthful stand characteristics persisted” (Crow 1980). Another thinning in the late 1950s was also light. Virtually all of the stems removed were ≤ 16 cm, many of which would likely have succumbed naturally as the stand matured. Consequently, the activity had little impact on composition, eliminating only *Beilschmiedia pendula* and *Micropholis garciniiifolia*, both uncommon. Because no control plots were maintained nearby the effects of these thinnings on growth rates were uncertain.

Later work at El Verde III confirmed that changes in species and stem numbers varied by successional types (Johnston 1990). Moreover, *Dacryodes excelsa* grew best on well-drained sites and *Prestoea montana* was concentrated on poorly drained soils. Species diversity and evenness (i.e., as determined by the Shannon-Weiner index and Pielou’s evenness index) gradually declined from the mid-1940s through 2005 with the exception of a slight increase associated with Hurricane Hugo in 1989 (Drew and others 2009).

Post-hurricane observations on the TS-3 plot spanning 30 years showed typical patterns for long-term recovery. Between 1946 and 1976, basal area increased by 5 percent and stem numbers decreased by 14 percent (Weaver 1983). Secondary species like *Alchorneopsis portoricensis*, *Cecropia schreberiana*, and *Schefflera morototoni* all declined considerably in stem numbers whereas mature forest species like *Dacryodes excelsa*, *Manilkara bidentata*, and *Sloanea berteriana* maintained or increased their stem numbers. Growth rates in d.b.h. for surviving broadleaf species ranged between 0.03 and 0.48 cm yr⁻¹ (Weaver 1983). *Clusia rosea*, *Croton poecilanthus*, *Matayba domingensis*, and *Ormosia krugii* all grew relatively rapidly, averaging >0.25 cm yr⁻¹ in increment during the measurement period.

TR-1, a plot located on a steep, exposed ridge at 350 m in the Mameyes watershed, is notable because its composition is made up of tree species from all four forest types: *Cyrilla racemiflora*, *Magnolia splendens*, and *Matayba domingensis*, most common in montane forest but present at higher elevations in lower montane forest (Weaver 1983, 1998, 2002b); *Henriettea squamulosa* and *Micropholis garciniifolia*, more common in montane and dwarf forests but also present in lower montane forest (Wadsworth 1951); *Eugenia borinquensis* and *Ocotea spathulata*, abundant in dwarf forest and common in montane forest but rare in lower montane forest (Weaver 2010a, 2010b); and *Prestoea montana*, dominant in palm brakes above 450 m elevation. The presence tree species normally found at higher elevations appears related to the very wet and exposed nature of the site, and the magnitude of earlier hurricanes (table 6).

TR-1 plot data, spanning >60 years, provide the best long-term record in lower montane forest. Measurements encompass a complete disturbance cycle with the initial tally being made 14 years after two major hurricanes and the last tally 2 years after another pair of major hurricanes. Recovery included a prolonged period of calm from 1932 to 1989. Initial measurements showed that stem density, species numbers, and the rate of biomass accumulation were at a maximum 15 years after the 1932 hurricane. About 50 years later, most of the secondary species associated with past disturbance—*Cecropia schreberiana*, *Psychotria berteriana*, and *Schefflera morototoni*—had decreased or disappeared and the rate of biomass accumulation for the stand began to level. *Cecropia schreberiana* again regenerated abundantly after hurricanes Hugo and Georges (Weaver 2002b). Other species that regenerated well after Hugo included *Manilkara bidentata*, *Prestoea montana*, *Psychotria berteriana*, and *Sloanea berteriana*. Growth rates of broadleaf species surviving the 1946 to 1976 measurement period ranged between 0.01 and 0.51 cm yr⁻¹ (Weaver 1983). Fast growing species such as *Buchenavia tetrphylla*, *Cyrilla racemiflora*, and *Matayba domingensis* all averaged >0.25 cm yr⁻¹ in d.b.h. increment over the measurement period.

Silvicultural research in natural forest—The first silvicultural activities carried out within the lower montane forest were exploratory in nature and had a minor impact on the species composition and forest structure of relatively small areas. The earliest timber stand improvements were implemented in 1938 and 1939 on 55 ha and involved vine cutting, thinning around desirable saplings of timber species, pruning, and limited removal of tree species with no commercial value (Wadsworth 1970). These procedures, aimed at increasing growth rates of select trees in young secondary stands, would be ineffective without repeated thinning.

Additional silvicultural activities were carried out on two types of permanent plots in lower montane forest (fig. 13) (table 7):

- In 1951, two 0.20 ha cutover lower montane forest plots (tabonuco cutover plots or, as called in table 7, TCU plots) were set up to determine the effects of thinning.
- In 1957, a pilot management project was located in four research areas—Cubuy, Sabana 4, Sabana 8, and Río Grande. Each area had at least 100 circular plots measuring 0.08 ha in size. Thinnings were carried out to increase forest productivity by eliminating the poorest species and providing ample growing space for select trees (Crow and Weaver 1977).

The thinning experiment carried out on the TCU plots between 1947 and 1975 showed that basal area increased from 16 to 33 m² ha⁻¹, averaging 0.64 m² ha⁻¹ yr⁻¹. Basal area growth on similar unthinned, mature forest plots with typical basal areas >35 m² ranged from 0.06 to 0.25 m² ha⁻¹ yr⁻¹ over the same period (Weaver 1983).

By 1957, improvement cuttings had been carried out on 930 ha in the pilot management project (Anon. 1958). In addition, undesirable trees were frilled and herbicides applied. Trees were liberated if they measured ≥10 cm in d.b.h. and their crowns were in contact. Liberation provided about 2 m of crown freedom between trees. In most instances, openings on the forest floor were kept to ≤8 m. Trees scheduled for removal included: dying, diseased, or insect infested individuals; inferior species (i.e., neither pole nor sawtimber species); trees of poor form or with heavily damaged crowns; and all remaining trees in excess of desired stand density.

The pilot management project showed that d.b.h. increment on liberated timber species in young secondary forest averaged nearly 0.40 cm yr⁻¹ over 18 years, or approaching twice the average for the same species on undisturbed lower montane forest plots (Crow and Weaver 1977). The d.b.h. growth rate for six mature forest species—*Buchenavia tetrphylla*, *Dacryodes excelsa*, *Manilkara bidentata*, *Micropholis garciniifolia*, *M. guyanensis*, and *Sloanea berteriana*—nearly

doubled whereas six typical secondary species—*Byrsonima coriacea*, *Homalium racemosum*, *Inga laurina*, *Chionanthus domingensis*, *Matayba domingensis*, and *Ormosia krugii*—increased by about 50 percent. Four pioneer species—*Alchornea latifolia*, *Cecropia schreberiana*, *Schefflera morototoni*, and *Tabebuia heterophylla*—only increased by an average of 10 percent (Weaver 1983). Unfortunately, the results are not clear because growth differences between thinned and untreated secondary forest stands were never evaluated. Regardless, these studies suggest that a single liberation of crop trees in secondary lower montane forest fosters relatively rapid d.b.h. increment for a period of time. Reduction of density also stimulated the regeneration of timber species such as *Dacryodes excelsa*, *Manilkara bidentata*, *Ocotea moschata*, and *Tetragastris balsamifera*.

A recent re-evaluation of 1,425 trees of 12 timber species with at least 40 replicates within the pilot study showed that the top 25 percent, those with the highest productivity, were growing at a rate double that of the remainder (Wadsworth and others 2010). With reduced impact logging leaving many cutover forests less disturbed, greater interest is being shown in the potential of secondary stands. The presence of fast growing trees suggests that these forests could serve as an attractive start to a second timber crop.

Mean annual d.b.h. increment (MAI), frequently used by foresters to characterize tree growth, is influenced by many factors including:

- **Tree species**—Primary species usually have denser or heavier woods (i.e., a greater specific gravity) than either secondary or gap species. Denser tree species with greater investments in wood production generally grow more slowly in d.b.h. than pioneer or secondary species (Grubb 1977, Lawton 1984).
- **Stand conditions**—Tree density and stand basal areas increase several years after hurricanes and MAI tends to slow considerably due to competition among surviving stems (Weaver 1986a, 1989b). Growth studies of thinned vs. unthinned stands also show the influence of stand density or basal area on d.b.h. growth rates (Crow and Weaver 1977, Weaver 1983).
- **Site variation (site indices)**—Tree species situated on favorable sites with regard to elevation, topography, rainfall, and soil fertility are likely to grow more rapidly in MAI than those on poor sites. An example is the gradually diminishing MAI for *Micropholis garciniifolia* with ascent in the LEF. The species is found from lower montane forest to the summits, but its best d.b.h. growth is at low elevations (Weaver 1983).
- **Crown classes**—Crown size and canopy position (i.e., dominant, codominant, intermediate, and suppressed) influence MAI for all species (Baker 1950). Crown

exposure may be altered by silvicultural treatments or past disturbances. Large, well-positioned crowns produce the most rapid MAI whereas trees in suppressed conditions grow the slowest (Wadsworth 1947).

Montane Forest

The montane forest is characterized by dense stands of pole-size trees (fig. 3). Isolated by elevation and inclement climate, past human disturbance has been limited to the occasional extraction of *Magnolia splendens* near 600 m elevation, and the development of roads, trails, and recreational facilities. For nearly a century, montane forest has been the last habitat of the Puerto Rican parrot (Rodríguez Vidal 1962). Lacking the potential for major timber production, past forestry research has been limited mainly to permanent plot monitoring, gradient sampling, and one plot for experimental silviculture.

Stand features and notable tree species—The canopy of montane forest reaches 15 m in height with about two-thirds of the tree diameters ranging between 10 and 15 cm (Wadsworth 1951). *Prestoea montana*, *Micropholis garciniifolia*, *Henriettea squamulosa*, *Micropholis guyanensis*, *Croton poecilanthus*, *Cyrilla racemiflora*, *Ocotea spathulata*, *Cecropia schreberiana*, *Tabebuia rigida*, and *Magnolia splendens*, as listed, accounted for 83 percent of the stems



Dense, pole-size stems characterize typical stands of montane rain forest, which grows between 600 and 900 m elevation within the Luquillo Mountains. This stand in the upper Río Mameyes contains a blind where field observations of *Amazona vittata* (Puerto Rican parrot) were carried out for many years. (Photo by Peter L. Weaver)

recorded on 4 ha of permanent plots during the 1940s (Wadsworth 1951). Trees are typically short and crooked, and crowns consist of heavy branches that emerge low on the trunk. Grasses, sedges, and ferns characteristically grow in openings. At least 11 species within the type had timber uses: 1 for furniture, 4 for construction, and 6 for large posts (table 5).

Among the most interesting tree species are *Cyrilla racemiflora* and *Magnolia splendens*, which are both long-lived, occasionally >1 m in diameter (Weaver 1986b, 1987a). Regeneration of both occurs in openings or after disturbance, and is largely absent under closed canopy (Weaver 1992). Three other species, *Henriettea squamulosa*, *Micropholis garciniifolia*, and *M. guyanensis* may also attain large sizes (Wadsworth 1951, Weaver 1983).

Cyrilla racemiflora ranges from eastern Virginia through the Caribbean islands to the Amazon River Basin in Brazil

(Francis and Lowe 2000) (table 1); however, it attains its greatest size and longevity in Caribbean forests. Its branches and trunks commonly decompose with age creating cavities that are occupied by forest fauna. During the 20th century, the last surviving population of Puerto Rican parrots depended heavily on branch cavities in *Cyrilla racemiflora* for nesting sites (Rodríguez-Vidal 1959, 1962; Snyder and others 1987; Wunderle and others 2003).

Cyrilla racemiflora shows several adaptations to the persistently wet, montane environment. After Hurricane Hugo, *Cyrilla racemiflora* seedlings regenerated on overturned root masses (Weaver 1994) and the exposed subsoils of landslides (appendix D). Also, *Cyrilla racemiflora* saplings sometimes grow at an angle to exploit small openings in the canopy (Snyder and others 1987). On occasion, aerial roots grow out of the lower trunk into crotches of the same tree, probably helping to absorb water and nutrients (see



LEFT: *Cyrilla racemiflora* (palo colorado), often with hollow branches and trunks, is the major nesting tree of *Amazona vittata* (Puerto Rican parrot) in the Luquillo Experimental Forest. The largest known trees form by the coalescence of proximate stems RIGHT: *Cyrilla racemiflora*, measuring 2.6 m in d.b.h. Within montane forest, the species may attain ages approaching a millennium. (Photos by Peter L. Weaver)

footnote 1). Finally, uprooted *Cyrilla racemiflora* trees in both the montane and dwarf forests sprout along the fallen trunks. The sprouts ultimately develop roots and grow into the canopy where they preserve the original tree's genetic material for another generation.

Concern regarding Puerto Rico's flora led to a preliminary classification of plants considered to be rare and possibly endangered, including *Magnolia splendens* (Little and Woodbury 1976, Woodbury and others 1975). *Magnolia splendens*, popular as a cabinet wood, was logged in the forest until the early 1950s (Weaver 1987b). By the early 1970s, many accessible mature specimens of magnolia had already been removed from the lower montane forest and a few bordering areas of montane forest, thus reducing seed sources. Moreover, gradual closing of the forest after the 1928 to 1932 hurricanes had eliminated most gaps required for magnolia's regeneration (Weaver 1991, 1992). An early 1980s survey of montane forest disclosed several species considered to be rare, including the endemics *Ardisia luquillensis* and *Ilex sintenisii*, and sensitive species such as *Marlierea sintenisii*, *Maytenus elongata* (Urban) Britton, *Ternstroemia heptasephala* Krug & Urban, *T. luquillensis*, and *Xylosma schwaneckeanum* (Weaver 1989c).

"Crown shyness," which manifests itself as channel-like gaps between the crowns of adjacent canopy trees, was observed in 1981 within groups of *Henriettea squamulosa* in an area of persistent winds on the east-facing slopes of El Yunque (see footnote 1). Similar gaps elsewhere have been attributed to high winds that result in the abrasion and death of the sensitive growing tips of twigs (Walker and Whiteaker 1988).

Gradient sampling—Gradient sampling of montane forest was carried out in the upper Río Mameyes and upper Río Blanco watersheds, and to the windward and leeward of the ridge running from El Yunque to El Toro peaks. The 69-plot sample disclosed 65 tree species, 10 of which accounted for 71 percent of the total stems (tables 8 and 10). *Prestoea montana* with 17 percent of the stems and *Henriettea squamulosa* with 14 percent were the most common species.

Of the 10 most common species, *Prestoea montana* and *Croton poecilanthus* are more abundant in ravines, and *Cyrilla racemiflora*, *Haenianthus salicifolius*, *Micropholis garciniifolia*, *M. guyanensis*, *Ocotea spathulata*, and *Tabebuia rigida* favor ridges; in comparison, *Henriettea squamulosa* and *Cordia borinquensis* are better distributed topographically (table 10). Understory species such as *Daphnopsis philippiana* and *Garcinia portoricensis* were more common on ridges and upper slopes, and *Ditta myriocoides* on slopes and in ravines (table 10).

An ordination revealed that tree species sort by elevation and topography (Weaver 1991). Species commonly found

in ravines were *Citharexylum caudatum* at high elevations and *Sapium laurocerasus* at lower elevations. *Cecropia schreberiana*, *Croton poecilanthus*, and *Prestoea montana* also favored ravines but were well-distributed within the forest. In comparison, species that favored ridges were: *Calyptanthus krugii*, *Clusia clusioides*, and *Ocotea spathulata* at high elevations; *Byrsonima wadsworthii*, *Cyrilla racemiflora*, and *Haenianthus salicifolius* at midelevations; and *Dacryodes excelsa*, *Micropholis guyanensis*, and *Matayba domingensis* at lower elevations. *Cordia borinquensis* and *Henriettea squamulosa* were well distributed with regard to topography.

An evaluation of the influence of environmental gradients on forest structure showed that tree height decreased with elevation on both windward and leeward exposures in the LEF (Weaver 2000a). Also, aboveground woody biomass decreased significantly with elevation on ridges to the windward and soil organic matter with elevation to the leeward. Tree density was greatest on ridges and least in ravines. Species-area curves showed that the greatest number of species was found on ridges and slopes, and the fewest in ravines (Weaver 2000a).

Monitoring of long-term plots—The first observations of d.b.h. growth carried out on seven 0.4 ha plots between 1946 and 1951 showed that mean growth rates in closed stands were slow with considerable differences evident among tree species and crown classes (Anon. 1957; Wadsworth 1951, 1952b). Subsequently the plots, located on slopes and in valleys, were not revisited until the mid-1970s and early 1980s when observations of longer duration were summarized. Long-term observations from 1946 to 1981 showed that the plots had experienced changes in species composition, forest structure, and growth during the post-hurricane recovery period (Weaver 1986a, 1989b) (fig. 13) (table 6). Diameters and heights on surviving trees increased during the 35-year measurement period; moreover, the number of trees in the suppressed crown class increased in response to gradual canopy closure. One notable observation regarding structure was that the mean specific gravity for broadleaf species within the montane forest increased by nearly 4 percent (table 6). The change in specific gravity reflects the gradual disappearance of short-lived secondary trees characterized by low specific gravities and the gradual dominance of longer-lived, mature forest species with denser woods.

During the 35-year period of observation, small secondary species like *Hedyosmum arborescens* and *Psychotria berteriana* virtually disappeared from the plots (Weaver 1986a, 1989b). Larger secondary species, *Cecropia schreberiana*, *Schefflera morototoni*, and *Miconia laevigata* also declined considerably in stem numbers although their basal areas remained about the same because of continued growth on residual stems. *Cyrilla racemiflora* remained

constant in stem numbers but declined in basal area due to the loss of large trees. *Cordia borinquensis*, a mature forest understory tree, increased in both numbers and basal area. *Prestoea montana* remained relatively constant in stem numbers and basal area. Finally, mature forest dominants like *Micropholis garciniifolia* and *M. guyanensis* increased in stem numbers and basal areas to varying degrees. Secondary species continue to regenerate in forest gaps many years after hurricane passage but in reduced numbers. The gradual decline of secondary species combined with the gradual dominance of mature forest species are trends associated with post-hurricane recovery.

Species richness showed a couple of trends on the seven plots during the 35-year recovery period (Weaver 1986a, 1989b). First, the total number of species on all plots combined declined from 88 in 1946 to 83 in 1981. Valley plots near the transition to lower montane forest had the greatest numbers of species. Second, species numbers per plot in 1946 varied widely, ranging between 33 and 58. By 1981, they had converged, ranging from 36 to 49. Species richness on a plot basis appears to be greatest and most variable a few years after hurricane disturbance with the simultaneous occurrence of secondary and mature forest species. With post-hurricane recovery, species richness declines. It is also evident that any single plot selected to represent species richness within the forest could be seriously biased by its location and sampling date.

Mean d.b.h. growth for all stems, regardless of species, significantly declined from 0.14 cm yr⁻¹ between 1946 and 1951 to 0.09 cm yr⁻¹ between 1976 and 1981 (Weaver 1986a, 1989b). Differences in d.b.h. growth were readily apparent by crown classes, with dominant and codominant trees growing at significantly more rapid rates. D.b.h. increment on montane forest slope and ravine plots both averaged about 0.09 cm yr⁻¹, with individual broadleaf species varying considerably (Weaver 1983). The only species that averaged >0.20 cm yr⁻¹ during the measurement period were *Clusia clusioides*, *Miconia laevigata*, and *Ternstroemia luquillensis*. The mean net increase in aboveground woody biomass during the 1946 to 1981 measurement period averaged 0.67 t ha⁻¹ yr⁻¹, and woody volume increased by 1.06 m³ ha⁻¹ yr⁻¹. The decline in d.b.h. growth reflects a gradual increase in competition among surviving stems in a post-hurricane environment.

Silvicultural activities—An experimental 50 percent basal area reduction was carried out on a 0.4 ha plot called CCU within montane forest during the mid-1940s to determine the effect on residual stems (table 7). The thinning yielded no noticeable differences in d.b.h. increment after 10 years and the study was closed (Anon. 1957). Another visit to the plot 33 years later showed that the stand had experienced a massive influx of *Clusia clusioides*, *Cyrilla racemiflora*, and *Miconia tetrandra* (Weaver 2001). Moreover, *Micropholis garciniifolia*

and *Tabebuia rigida* also showed gains in stem numbers. Thinning had not stimulated an increase in the d.b.h. growth rate of the residual stems. Instead, new stems colonized the available space within the slow-growing stand.

Silvicultural experience with pines also merits mention. About 1960, a few seedlings of Mexican pines (species uncertain) were planted on an exposed ridge at 750 m near the PR 930 gate. The trees grew to about 3 or 4 m in height, remained stunted for years, and then perished in the early 1990s (see footnote 1). Also, *Pinus caribaea* planted on the large landslide at km 21 on PR route 191 during the early 1980s have survived, grown, and regenerated. The landslide, located at 600 m elevation, is at the transition between montane and lower montane forest.

Palm Brake

Palm brake, dominated by *Prestoea montana*, is relatively simple in species composition and has been less studied than other forest types in the LEF (fig. 3). Major research has included permanent plot monitoring, gradient sampling, and ecological studies on a riparian site in the upper Espíritu Santo watershed. Palm fruits are a staple in the diet of the Puerto Rican parrot (Snyder and others 1987).

Stand features and notable tree species—Palm brakes may reach 15 m in canopy height and grow mainly in ravines, and on steep, east-facing slopes above 450 m in elevation (Wadsworth 1951). Broadleaf species from either the lower montane or montane forest are present in palm brake, depending on elevation, but typically palms with a d.b.h. between 15 and 20 cm dominate the stands. The ground sometimes contains a sparse herbaceous layer and, in the case of ravines or drainages, it is covered with rocks.

Prestoea montana is ubiquitous in the LEF above 350 m, reproducing in forest gaps, on landslides, in openings, and under shade. An autecological study of the palm showed that it grew slowly, survived for long periods, adapted well to shade, and had a high moisture requirement, all suggesting that the species was adapted to closed forest (Bannister 1970). Palms appear to survive hurricanes well (Weaver 1983). Indeed, one immediate impression of post-Hurricane Hugo damage along FS-27 was the abundance of palms on slopes above 700 m (see footnote 1). This was due in part to its capacity to survive hurricanes by shedding leaves and resprouting, and in part to storm-caused defoliation and crown damage to surrounding broadleaf species.

Palm brake was previously considered as a sub-climax community on steep soils subject to landslips or soil movement (Beard 1949). The abundance of narrow-crowned



Prestoea montana (Sierra palm), common throughout the Luquillo Experimental Forest, is the dominant species within palm brakes. It grows on steep slopes and in ravines between 350 m and the mountain summits. (Photo by Peter L. Weaver)

palms and lower basal areas allow more light to reach the understory. When viewing palm brakes from a distance, two species are readily detectable in the canopy: *Prestoea montana* because of their dominance, and scattered *Cecropia schreberiana* due to their large leaves with light colored undersurfaces. *Psychotria berteriana* is common in the understory. All three regenerate in openings or gaps

Gradient sampling—Palm brakes are frequently situated on terrain with little local relief. Slight increases in topography, however, occur and support proportionately more broadleaf species. The 12-plot palm brake sample, located on steep slopes to the windward and leeward of Mt. Britton, showed that 10 species accounted for 91 percent of the total stems (tables 8 and 11). *Prestoea montana* was the most common species with 57 percent of the stems and *Cecropia schreberiana* followed with 12 percent. *Croton poecilanthus* was most common in ravines and slopes. *Eugenia borinquensis* and *Tabebuia rigida*, both abundant at higher elevations in dwarf forest, appeared to favor ridges along with *Psychotria berteriana*. *Cecropia schreberiana*, *Cordia borinquensis*, *Henriettea squamulosa*, and *Prestoea montana* were fairly well distributed, with the broadleaf species more common on ridges and slopes and the palm on ravines and slopes.

Monitoring of long-term plots—In 1947 and 1975, *Prestoea montana* accounted for 54 to 63 percent of the stems and basal area on permanent palm plot PS-2 (Weaver

1983) (table 7). In comparison, palms ranged between 6 and 23 percent of the stems and basal area on four typical lower montane and montane forest permanent plots (Weaver 1983). Typical basal areas on palm plots average less than on lower montane and montane forests plots, where the occasional occurrence of large broadleaf trees tends to inflate basal area estimates.

Long-term d.b.h. increment for broadleaf trees on palm plots averaged double the rates on either lower montane or montane forest plots (Weaver 1983). The more rapid d.b.h. growth is probably due to lower stem densities, lower basal areas, and more open canopies that characterize palm brakes (Weaver 1983). Many of the broadleaf tree species encountered within plot PS-2, such as *Alchornea latifolia*, *Cecropia schreberiana*, *Cordia sulcata*, *Croton poecilanthus*, *Henriettea squamulosa*, *Inga vera*, and *I. laurina*, are capable of regenerating in openings (appendix D). Moreover, they all grow at fairly rapid rates over long periods under the favorable light conditions found in palm brakes.

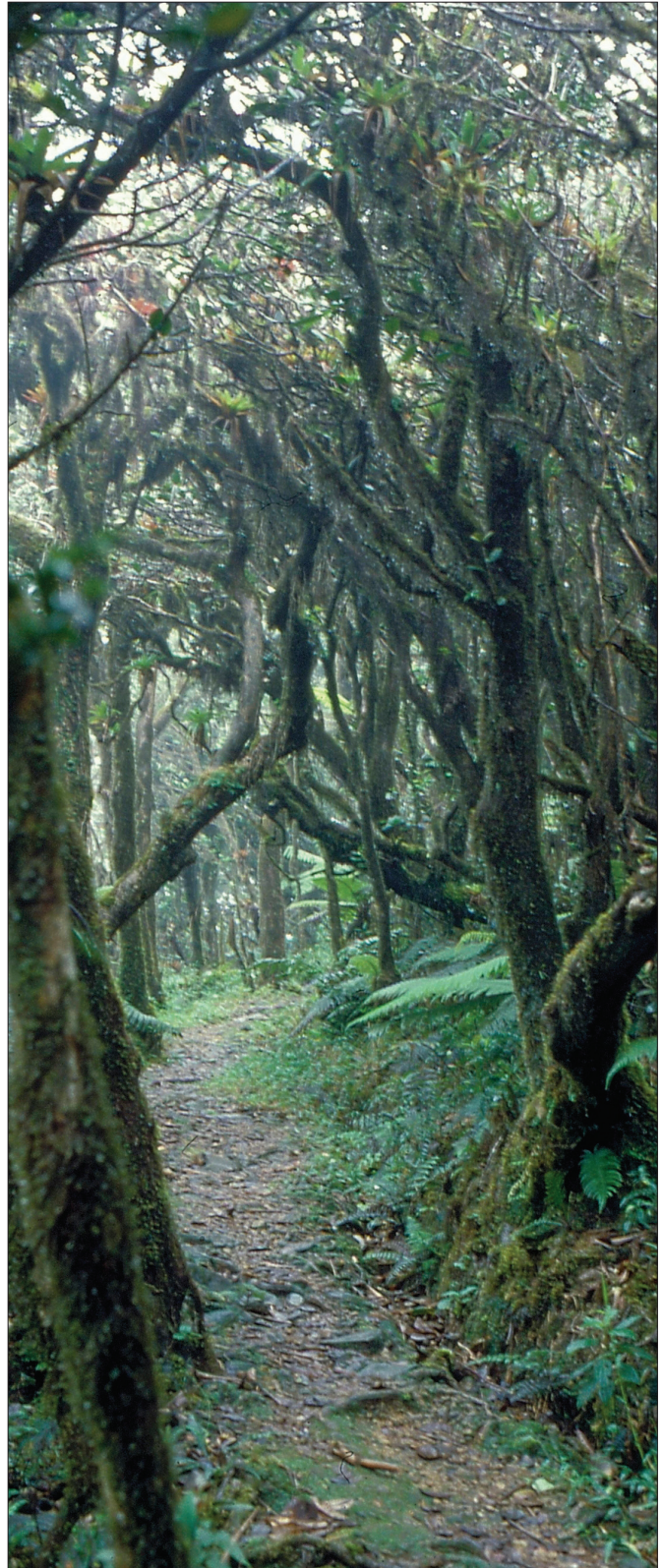
On a 0.25 ha of riparian palm brake plot established in 1980, *Prestoea montana*, *Croton poecilanthus*, and *Henriettea squamulosa*, accounted for 61 percent of the 3,060 stems ≥ 2.5 cm in d.b.h. (Frangi and Lugo 1985). The plot, surrounded by montane forest, also contained *Cyrilla racemiflora*, *Magnolia splendens*, *Micropholis garciniifolia*, and *M. guyanensis*.

Dwarf Forest

In most of the neotropics, ascent to dwarf forest is difficult because no roads and few trails exist. The earliest expeditions to the Luquillo Mountain summits were done by hiking or horseback. After the completion of PR route 191 through the forest, El Yunque peak was first made accessible by dirt road in 1938, and both Pico del Este and Pico del Oeste by paved road nearly 25 years later (figs. 3 and 5) (table 3) (appendix A). The roads presented unparalleled opportunities for studies at three major sites. Research on El Yunque dealt with climate and on Pico de Este with forest recovery after disturbance, cloud moisture interception, and permanent plot monitoring. Studies on Pico del Oeste were part of a multi-faceted project aimed at exploring the phenomenon of dwarf forest.

Dwarf forest, limited in extent, is a critical resource for Puerto Rico. It accounts for about one-sixth of the LEF's pristine forest and protects the highest slopes and summits from erosion (Murphy 1916). The forest also serves as habitat for 20 endemic tree species, 15 restricted to the island and five to the LEF (Weaver 2008). The summits offer panoramic views and runoff provides critical water supplies to growing island populations. In many areas of Middle America and the Caribbean, cloud forests are being cut for new agricultural lands, highlighting the need for their protection (LaBastille and Pool 1978, Stadtmuller 1986).

Stand features and notable tree species—Dwarf forest is characterized by a single story of trees that commonly range from 1 to 6 m or more in height, depending on exposure (Wadsworth 1951). The trees are branchy and trunks are seldom straight. The upper canopy is uniform in height, and leaves are generally small, thick, and concentrated at the ends of branches. Mosses, liverworts, and epiphylls are abundant, and cover branches, trunks, and leaves. "Nearly every species of flowering plant of the forest is found as an epiphyte" (Howard 1968, page 394). Roots are generally superficial, aerial roots are common, and grasses, sedges, and ferns grow in openings. Several genera (e.g., *Podocarpus*, *Ocotea*, *Magnolia*, and *Ilex*), the dominance of relatively few species, and the abundance of mosses are similar to temperate rain forest habitats (Dansereau 1966). Although no tree species is confined to this type, only a few are adapted to survive on the exposed summits (Nevling 1971, Wadsworth 1949). Earlier observations in the vicinity of El Yunque showed that *Weinmannia pinnata* L. along with *Eugenia borinquensis*, *Ocotea spathulata*, and *Tabebuia rigida* composed 75 percent of the dominant trees in dwarf forest (Gleason and Cook 1927). On Pico del Oeste, *Ocotea spathulata* and *Tabebuia rigida* made up 70 percent of the canopy (Howard 1968). El Yunque Rock, El Yunque peak, Los Picachos, Pico del Oeste, the area surrounding the radar dome on Pico del Este, El Toro peak, and the steep east-facing slopes below Mt.



Dwarf forest. Short, gnarled, epiphyte laden trees composed of a few species, many of them endemic to the forest, grow above 900 m in elevation in the Luquillo Experimental Forest. On rocky summits, trees may be limited to 2 or 3 m in height. (Photo by Peter L. Weaver)

Britton, where trees are 1 to 3 m in height, are among the most accessible examples of stunted, windswept vegetation in the LEF (fig. 9).

The high stem density in some areas was attributed to fallen trees from which lateral branches or adventitious shoots subsequently developed (Howard 1969). Soils on the summit are saturated and contain about 50 percent organic matter; moreover, tree stems are covered with organic matter and blanketed with epiphytes (Lyford 1969). Aerial roots, recorded for 22 species of trees and shrubs, probably help stabilize plants in an environment where the combined weight of epiphytes, water, and eroding soils could topple them (Gill 1969). They also shorten the distance that nutrients have to travel.

Dwarf forest is characterized by low tree species richness, high stem density, low canopy height, small tree diameter, low leaf area index, low specific leaf area, and low amounts of aboveground biomass compared to lower forest types (table 8). Moreover, dwarf forest dynamics are slow, including: tree growth rates (d.b.h., height, and biomass accumulation); rates of litterfall, herbivory, and litter turnover; aboveground net primary productivity; and nutrient recycling. Thick dwarf leaves and dense woods represent considerable biological investments that come at the expense of growth (Grubb 1977, Lawton 1984). Moreover, slow growth on the summits assures that post-hurricane biomass recovery would take considerable time (Weaver 2008). In summary, “Saturated soils, impeded root respiration, high winds, high soil leaching, low nutrient availability, low temperatures, high fog incidence, reduced solar insolation, high humidity, and reduced transpiration have all been suggested as causal agents in stunting, either individually or in combination” (Weaver 1995). This impoverishment of forests on small, wet, isolated, tropical mountains has been attributed to the Massenerhebung effect, or the interaction of cool temperatures, frequent fog, and heavy precipitation that serves to retard mineralization of organic matter (Grubb 1971). The combined effects of these environmental conditions may effectively lower the elevational level at which a forest composed of shorter trees, mainly controlled by temperature, would normally occur.

Numerous visits to and surveys of dwarf forest over a period of 43 years have provided a few interesting observations:

- **Standing dead trees**—Surveys in 1968 showed that 10 percent of standing stems with a measureable d.b.h. ≥ 2.5 cm near Pico del Este were dead, a phenomenon possibly associated with dense post-hurricane regeneration 35 years earlier (Weaver 1972).
- **Aerial roots**—After a rare loss of their trunks, *Clusia clusioides* and *Tabebuia rigida* may be supported solely by aerial roots (Weaver 1994).
- **Protected dwarf forest**—Surrounding topography may protect isolated patches of large trees in dwarf forest from recurrent hurricane damage (Weaver 2008). One example was a *Magnolia splendens* with a d.b.h. of 78 cm and four large *Eugenia borinquensis* growing in an east-facing El Yunque ravine at 985 m.
- **Sedges and grasses**—Sedges have survived for about 50 years along portions of the abandoned 5 km Pico del Este trail between the PR route 930 gate and the Pico del Este radar domes (see footnote 1). Their presence reflects soil compaction by past hikers about 50 years ago.
- **Cans, sheds, and decomposition**—Two #10 cans used to sample throughfall near Pico del Este in the late 1960s (Weaver 1972) were deliberately left on an exposed ridge near Pico del Este. Their decomposition was nearly complete after 35 years. Also, a wooden shed used as a shelter on Pico del Oeste in the mid-1960s (Howard 1968) had decomposed into a mound of debris by the mid-1980s.

Gradient sampling—Gradient sampling within dwarf forest was carried out near El Yunque, Pico del Este, and Pico del Oeste. The 33-plot sample showed that four species accounted for nearly 70 percent and 10 species for >93 percent of the total stems (tables 8 and 12). *Cyathea bryophila*, *Eugenia borinquensis*, *Ocotea spathulata*, and *Tabebuia rigida* were not only the most abundant species, but also those that appeared to favor windward rather than leeward exposures at high elevations (Weaver 2010b).

Stratified sampling by topography throughout dwarf forest showed that *Cyathea bryophila* and *Prestoea montana* were most common in ravines and on lower slopes whereas *Calyptranthes krugii*, *Eugenia borinquensis*, *Micropholis garciniifolia*, and *Ocotea spathulata* had the majority of their occurrences on slopes and ridges (table 12). *Clusia clusioides* and *Henriettea squamulosa* had more equitable distributions by topography. Previous stratified sampling of dwarf forest by topography near Pico del Este showed similar results (Weaver 1999).

Monitoring of long-term plots—Because dwarf forest was not considered a potential source of timber, no permanent plots were established in the 1940s and 1950s when other forest types were first investigated. Subsequently, two types of long-term monitoring plots were established in dwarf forest near Pico del Este. The first study was set up to observe forest recovery after a 1968 airplane wreck and the second to monitor growth after Hurricane Hugo of 1989.

The airplane wreck near Pico del Este created a swath about 20 x 60 m (Byer and Weaver 1977). The crash site provided a rare opportunity to study forest recovery with conditions similar to slash and burn agriculture on lowland sites. Monitoring, once per decade, showed that the recovery process passed through several stages:

- After 4 or 5 years, grass, ferns, and fern allies dominated the site, and woody seedlings were scarce (Byer and Weaver 1977).
- After 19 years, ferns and broadleaf species dominated with nearly the same biomass. Of 20 broadleaf species tallied, three were dominant—*Eugenia borinquensis*, *Henriettea squamulosa*, and *Wallenia* sp. (Weaver 1990). *Cyathea bryophila* was the abundant fern. At this time, about 90 percent of the broadleaf trees were endemics (Weaver 2000b).
- After 30 years, only 31 trees of five species were ≥ 4 m tall (Weaver 2000b). Biomass on the sample plot averaged only a third of that found in surrounding mature dwarf forest.
- After 37 years, the largest broadleaf trees were *Clusia clusioides*, *Micropholis garciniifolia*, and *Tabebuia rigida* (Weaver 2008). Recovery on the wreck site remained patchy, with small areas of grasses and ferns still evident. Time for complete biomass recovery was estimated at two centuries.

In 1990, after Hurricane Hugo, six small plots were established at two sites near Pico del Este and subsequently measured at 5-year intervals (table 7). Post-hurricane monitoring indicated that about 10 percent of the biomass was lost during the storm event and delayed mortality (i.e., subsequent mortality of impacted trees that initially survived the storm) continued for many years. Tree growth and recovery from disturbance in the dwarf forest is slow; moreover, endemic tree species are important in the forest, notably during recovery (Weaver 2000b). The alpine meadows occasionally seen near the summits (Odum and Pigeon 1970) may be caused by landslides or major hurricane disturbance, which uproot trees and expose the subsoil. Subsequently, grass and ferns invade and once established may persist for decades.

Chapter 4. ENVIRONMENTAL GRADIENTS

Early botanists in the Caribbean observed that changes in forest composition and structure correlated with environmental factors such as elevation, aspect, topography, and exposure (Beard 1944, 1949; Shreve 1914). Shreve, working in Jamaica, justified sampling by topographic features stating that “slope forests far exceed the other types, but their characteristics and vegetation are intermediate between those of the ravines and the ridges, and they do not possess the interest of either of the latter habitats” (Shreve 1914). Similarly, numerous visits to the mountainous Lesser Antilles revealed that lower montane forest grew to higher elevations on leeward aspects than to the windward (Beard 1949).

The earliest researchers studying the Luquillo Mountain summits noted that dwarf forest was exposed to “four environmental conditions which may be of considerable importance in determining the peculiar vegetation of the mossy forest, low temperature, great wind exposure, a water-soaked soil, and an atmosphere of high humidity, frequent fog and mist, and heavy precipitation” (Gleason and Cook 1926). Some considered the dwarf forest in Puerto Rico to be an impoverished “subdivision of the colorado type,” (i.e., montane forest) (Wadsworth 1951). By the same measure, palm brake could be considered an impoverished version of the lower montane or montane forests. Both the palm brake and dwarf forests are characterized by saturated soils and contain fewer tree species.

Changes in elevation affect climate and influence forest structure, species composition, and stand dynamics (Wadsworth 1948, 1951; Weaver 1991, 1999, 2000a; Weaver and Murphy 1990) (fig. 11) (table 8). Likewise, structure and composition vary by aspect, topography, and exposure at any particular elevation within the major forest types (Weaver 1999, 2000b, 2010a, 2010b). Topography influences soil formation, organic matter concentrations, soil moisture content, water movement, and erosion. It also affects the occurrence of landslides and tree species colonization after disturbance (Basnet 1992a, Guariguata 1990, Simon and others 1990). The occurrence and abundance of certain species in lower montane forest was attributed to local geologic and edaphic factors—depth to bedrock or large rocks and soil moisture—as well as recurrent disturbances (Basnet 1992a, 1993b; Crow and Grigal 1979).

The measured plot parameters—tree height, stem density, biomass, and species richness—tallied in gradient sampling were highly variable partly due to small plot size and partly to the variety of habitats sampled. Some relationships, however, were apparent. Mean canopy height decreased with an

increase in elevation, most rapidly for ridges and least rapidly for ravines (fig. 14) (table 8). In comparison, stem density for all trees >4cm in d.b.h. increased with elevation (fig. 15) (table 8). Ridges and slopes showed parallel trends whereas stem density in ravines increased at a slower rate. Noteworthy variation in stem density is evident above 900 m, where some dwarf forest sites contain thickets of small stems. Mean plot biomass on ridges and slopes also decreased with elevation but with considerable variation; biomass in ravines, in contrast, showed no elevational trends (fig. 16) (table 8). Biomass varies considerably between 350 and 650 m in lower montane forest and montane forest where a few large trees, often *Dacryodes excelsa* or *Cyrilla racemiflora*, may inflate plot values. The number of species per plot also declined with elevation on all topographic positions (fig. 17) (table 8). Again, roughly parallel trends were apparent on ridges and slopes, but species numbers in ravines declined at a slower rate. The number of species per plot also varies considerably, with the greatest values found between 600 and 750 m.

Gradient sampling also showed that forest structure varied by topography. Canopy heights for the four forest types ranged between 4 and 26 m, with the tallest trees on ridges in lower montane forest and the shortest on ridges in dwarf forest (table 8). Plot stem densities for the four forest types varied from 680 ha⁻¹ in lower montane forest to 4660 ha⁻¹ in dwarf forest. Moreover, plot stem densities declined from ridge through slopes to ravine topography in all forest types. Aboveground plot biomass also showed considerable variation, ranging from nearly 60 t ha⁻¹ in palm brake ravines to about 520 t ha⁻¹ on montane forest ridges. Mean biomass values within all forest types declined from ridge through slope to ravine topography. Known specific gravities for 87 LEF tree species ranged from 0.22 to 0.90 with nearly 75 percent between 0.50 and 0.79 g cm⁻³ (Reyes and others 1992) (appendix F). Estimates of mean specific gravity by forest types (i.e., weighted by number of stems per species) varied from 0.49 to 0.63 for all species combined, including palm, and from 0.60 to 0.66 for broadleaf species alone (i.e., excluding palm) (table 8). Specific gravity for all species combined tended to increase slightly from lower montane forest to dwarf forest with the exception of palm brake. Palm brakes are dominated by *Prestoea montana* and *Cecropia schreberiana*, woods that are very light in weight (appendix F).

Species' richness also varied by topography (fig. 18) (table 8). In lower montane and montane forests, ridges and slopes contain more species than ravines (Scatena and Lugo 1995; Weaver 1987a, 2000a). These differences may be partially due to greater tree density on ridges, a factor that creates

numerically larger sample sizes. Ridge topography also has better access to light and better drainage, both of which may favor the survival of rarer species, which are normally smaller in stature (Weaver 1989c). Slightly elevated terrain in palm brakes showed greater species' richness than either straight slopes or ravines, again reflecting better drainage (fig. 18). In dwarf forest, with fewer species and less relief, topographic differences are less pronounced, and species richness is limited mainly by climatic conditions and exposure.

Other studies in the LEF showed that tree density, tree taper, the amount of branch wood, and soil organic matter all increased with elevation whereas canopy height, typical d.b.h. range, total timber volumes, aboveground woody biomass, leaf biomass, leaf area index, specific leaf area, total number of tree species, and total aboveground net primary productivity (with the notable exception of palm brake) were greater at lower elevations (Wadsworth 1949; Waide and others 1998; Weaver 1991, 2000; Weaver and Murphy 1990; White 1963) (table 8). Moreover, tree biomass equations derived from field measurements in lower montane, montane, and dwarf forests differed by vegetation type (Weaver and Gillespie 1992). Surveys along the LEF's elevational gradient also showed a decreasing trend in stem respiration due to changes in tree species composition, a decrease in the surface area of trees, and lower temperatures (Harris and others 2008).

Fauna (i.e., birds, amphibians, and reptiles) also show preferential distributions according to elevation, forest type, and habitat (Joglar 1998, Raffaele 1983, Rivero 1978). Palm litter samples were richer in nutrients than broadleaf forest samples, significantly so at high elevations (Richardson and others 2005). Litter invertebrate abundance and species richness paralleled the nutrient pattern, declining with elevation in broadleaf forests but not in palm brakes. These latter differences were attributed to forest heterogeneity and its contribution to the chemical and physical nature of the litter rather than the direct effects of temperature and rainfall. Also along the gradient from sea level to Luquillo Mountain summits, the number of earthworm species increased with greater rainfall and lower temperature (González and others 2007). Differences in earthworm species richness were associated with soil pH and with the root length density (i.e., root length divided by soil volume at 30 cm depth). Worm biomass, however, was greatest at the lowest and highest elevations along the gradient.

Tree Species Ranges in Luquillo Mountains

Tree species in the LEF's different forest types form a mosaic in time and space influenced by their inherent biology, their capacity to adapt to landscape variables, competition with other vegetation, and their response to disturbances.

Knowledge of species adaptations and their longevity helps explain their occurrence and persistence in the landscape. Some abundant species are adapted to a variety of sites in the LEF whereas others have much narrower habitat preferences.

Gradient sampling showed that the 10 most common species within each forest type accounted for 72 percent of the tallied stems in lower montane forest, 64 percent in montane forest, 91 percent in palm brake, and 93 percent in dwarf forest (appendix tables 9A–9D). Of the 105 species tallied throughout the LEF, the two most abundant, *Prestoea montana* and *Henriettea squamulosa*, accounted for nearly 29 percent of all stems (appendix C). The 25 most common species, each tallied ≥ 90 times, accounted for 90 percent of the total sample. Of the less common species, eight were recorded only once, and 32 were recorded ≤ 5 times. The greatest elevational ranges (i.e., ≥ 600 m) recorded during sampling were for *Brysonima wadsworthii*, *Cecropia schreberiana*, *Cordia borinquensis*, *Croton poecilanthus*, *Haenianthus salicifolius*, *Henriettea squamulosa*, *Magnolia splendens*, *Micropholis garciniifolia*, *Ocotea leucoxylon*, *O. spathulata*, and *Prestoea montana* (appendix C).

Several mature forest species are largely confined to one or two forest types (e.g., *Dacryodes excelsa*, *Manilkara bidentata* and *Tetragastris balsamifera* in lower montane forest; *Brysonima wadsworthii*, *Matayba domingensis*, *Micropholis guyanensis*, and *Miconia laevigata* in montane forest; *Cyathea bryophila* in dwarf forest; and *Eugenia borinquensis*, *Ocotea spathulata*, and *Tabebuia rigida* in dwarf forest and higher elevations of montane forest) (appendix C). In contrast, some species intermediate in size like *Henriettea squamulosa*, *Micropholis garciniifolia*, and *Prestoea montana* have ample elevational ranges, growing in the second story at lower elevations and reaching the canopy at higher elevation. Also, secondary tree species such as *Cecropia schreberiana* and *Psychotria berteriana* have a cosmopolitan distribution occupying openings within mature forests at lower elevations but are sparsely represented in dwarf forest.

Some tree species show strong topographic preferences such as *Dacryodes excelsa* on ridges, *Cyrilla racemiflora* and *Micropholis garciniifolia* for ridges and upper slopes, and *Prestoea montana* for ravines and lower slopes. The best distributed species, *Henriettea squamulosa*, grows on all topographies in all forest types. *Cordia borinquensis*, *Croton poecilanthus*, and *Psychotria berteriana*, found on ridges and slopes at lower elevations, were not recorded on ridges within dwarf forest. Finally, *Didymopanax gleasonii* Britton & Wilson, *Podocarpus coriaceae* L.C. Rich., and *Styrax portoricensis* Krug & Urban and similar rare species are largely confined to higher elevations in montane or dwarf forests (Little and Wadsworth 1964, Little and others 1974, Weaver 1989c) (appendix C).

Eight native trees were sampled on plots well outside of their normal elevational range within the LEF (appendix C):

- *Pterocarpus officinalis*, common in coastal freshwater wetlands and along the Río Mameyes near Puente Roto, also in ravine topography at and above the confluence of the Río Mameyes and Río de La Mina.
- *Dacryodes excelsa*, common in lower montane forest, as high as 850 m on ravine topography in the Espíritu Santo watershed.
- *Sloanea berteriana*, common in lower montane forest, as high as 890 m on slope topography in the Río Blanco watershed.
- *Sapium laurocerasus*, found in lower montane and montane forests, as high as 950 m on ravine topography in the Espíritu Santo watershed.
- *Clusia clusioides*, most common in dwarf and montane forests, as low as 450 m on ridge topography in the Río Mameyes watershed.
- *Tabebuia rigida*, abundant in dwarf forest, as low as 450 m on slope topography in the Río Mameyes watershed.
- *Eugenia borinquensis*, abundant in dwarf forest, as low as 350 m on ridge topography in the Río Mameyes watershed.
- *Ocotea spathulata*, most common in dwarf and montane forests, as low as 350 m on ridge topography in the Río Mameyes watershed.

Given that the entire gradient sample covered only 5.77 ha (0.05 percent of the LEF), more extensive field observations would most likely extend the maximum ranges for virtually all of the 105 sampled species (appendix C). Past land use has obscured the natural distributions of species in lower montane forest, some of which also grew in the coastal lowlands.

Tree Life Cycles and Longevity

Tree regeneration and growth follows several pathways depending on plant life cycles and environmental conditions (Gómez-Pompa and Vázquez-Yanes 1974). Many years of research and monitoring, including observations made after disturbances, have provided insights regarding the ecological roles and longevity of several tree species. Some species



Pterocarpus officinalis (Bloodwood tree), with sinuous buttressed roots, grows at 120 m elevation along a small forest stream tributary to the Río Mameyes. (Photo by Iván Vicéns)

surviving today in lower montane forest were most likely more abundant in the lowland forests surrounding the LEF before human intervention.

Diameter growth rates of several timber species in the lower montane forest vary considerably, being comparatively rapid under favorable stand conditions (Crow and Weaver 1977, Weaver 1983). Some of these data have been used to explore population dynamics in life history studies for different species (McCormick 1995). In lower montane forest, *Dacryodes excelsa*, with its narrow crown, may reach >1 m in d.b.h. in about 500 years (Weaver 2002b). *Buchenavia tetraphylla*, considered to be a “late secondary” species with a spreading crown, favors upper slopes and ridges (Sastre-De Jesús 1979). Its growth is relatively rapid and trees may approach 1 m in d.b.h. within a couple of centuries. *Manilkara bidentata*, the remaining large species in lower montane forest, is a dense, shade tolerant tree that attains >1 m in d.b.h. (Little and Wadsworth 1964). Seedlings may persist in the understory with little growth for 40 years before they are released by openings in the canopy (You 1991). Trees 0.6 m in size were estimated to be about 250 years old. It is likely that the largest specimens >1 m in size harvested in the past approached 500 years in age (Weaver 2002b). *Inga vera*, common in areas like El Verde where shade coffee was previously grown, probably attains a d.b.h. of 0.5 m in about 65 years (Muñiz-Meléndez 1978). One specimen, however, was recorded at 0.9 m in d.b.h. (Little and Wadsworth 1964). *Cecropia schreberiana*, a secondary species, grows to largest size in lower montane forest where it reaches 30 cm in 30 years (Brokaw 1998, Doyle 1981, Silander 1979); however, the largest observed specimens reaching 80 cm probably survived > 60 years. In contrast, *Palicourea riparia* and *Schefflera morototoni* are small and medium-size gap opportunists, respectively, which regenerate and mature quickly in disturbed areas of lower montane forest (Lebrón 1977, Nieves 1979).

Cyrilla racemiflora, most common in the montane forest, grows to about 1 m in d.b.h. in 650 years (Weaver 1986b). *Magnolia splendens*, also most common in montane forest, appears to reach at least 65 cm in 500 years (Weaver 1987b). *Prestoea montana* dominates the palm brake. The oldest palms at one site located at 550 m elevation were estimated at 100 years (Lugo and Rivera Batlle 1987). The oldest specimens, however, reach 20 m tall and may persist for about 180 years (Bannister 1970, Van Valen 1975). Because several of these species grow along an elevation gradient that becomes climatically more rigorous near the summits, it is likely that some of the island’s oldest trees may be specimens of *Cyrilla racemiflora* or *Magnolia splendens* growing at high elevations within montane or dwarf forest (Weaver 1986b, 1987a). The largest specimens of most other tree species in the LEF probably do not attain ages more than a century or two, with many being comparatively ephemeral within the stands. Life

history and silvicultural information has been summarized for native and exotic trees growing in Puerto Rico, including 20 species native to the lower forests of the LEF (Francis and Lowe 2000).

Most trees growing in dwarf forest are small in stature (table 8). Of the 10 most common species, *Micropholis garciniifolia* and *Tabebuia rigida* sometimes attain larger sizes (table 12). D.b.h. growth rates for all tree species combined on a small plot in closed dwarf forest near Pico del Este averaged only 0.03 cm yr⁻¹ (Weaver 1983, 2008). Saplings of *Clusia clusioides* and *Tabebuia rigida* growing in openings, however, may average 0.15 to 0.35 cm yr⁻¹ for a few years until they begin to slow because of competition. Topography and exposure may also influence growth rates and the final size of dwarf forest trees. Estimating ages given these conditions would be tenuous.

Attempts to determine the successional status of tree species are influenced by the types of observations made (e.g., environmental conditions required for regeneration; or stand compositions, dynamics, and growth) and their duration (e.g., instantaneous vs. monitoring). Other important variables include:

- **Location (spatial factors)**—such as geographic range, and occurrence along gradients (e.g., elevation, aspect, topographic position, exposure).
- **Forest maturity (temporal factors)**—such as the status of the forest with regard to past disturbance (e.g., post-hurricane, early secondary, late secondary, mature, or possibly mixed) and its influence on reproduction and growth of species.

Past attempts at classifying the successional status of trees within the lower montane and montane forests used similar but not identical approaches and showed considerable overlap (appendix D). Both developed indices that were based on: the ratio of understory trees to canopy trees; the ratio of seedlings to canopy trees; seed size; and, wood specific gravity. Lower montane forest observations were made on 30 species in the mid-1960s, about 30 years after the passage of three hurricanes (Smith 1970). Observations in montane forest were made on 20 species during the early 1980s, about 50 years after the same hurricanes (Weaver 1992). Both indices ranked *Cecropia schreberiana* as most secondary (appendix D); *Tetragastris balsamifera* was rated most primary in lower montane forest and *Eugenia borinquensis* in montane forest. The use of stand features and autecological characteristics offered some assurance that the results would be fairly robust.

At El Verde, sampling along gradients from gaps to surrounding forest showed that gap centers, gap margins, and forest below canopy are distinct environments for the regeneration of

tree species (Devoe 1989). Several observations were made with regard to seeds and fruits, including: a greater mass and number of seeds fall below closed canopy than in the open; animal-dispersed seeds are more likely to be deposited below the canopy whereas wind-dispersed seeds are more common in openings; and heavier seeds or fruits are more likely to fall below the canopy. Thus, late successional or mature forest tree species seldom reach the center of gaps. Edge conditions along gaps are particularly favorable for the establishment of commercial timbers by seed (Devoe 1989). In terms of silviculture, clear cutting and seed tree methods, both of which clear large areas, were not considered appropriate for regenerating timber species in the lower montane forest. In contrast, shelterwood and selection methods, both of which provide shade, were deemed more likely to be successful. Native tree species in the lower montane forest were classified according to their capacity to regenerate in different light conditions, as follows (Devoe 1989):

- **High light**—*Alchornea latifolia*, *Alchorneopsis floribunda*, *Casearia arborea*, *Casearia sylvestris*, *Cecropia schreberiana*, *Dendropanax arboreus* (L.) Decne. & Planch., *Laetia procera* (Poepp. & Endl.) Eichl., *Schefflera morototoni*, *Tabebuia heterophylla*, *Trema micrantha*, and *Zanthoxylum martinicense* (Lam.) DC.

- **Intermediate light**—*Buchenavia tetraphylla*, *Byrsonima spicata*, *Calophyllum calaba*, *Chionanthus domingensis*, *Croton poecilanthus*, *Guarea guidonia*, *Guettarda scabra* (L.) Vent., *Ormosia krugii*, *Prestoea montana*, *Pterocarpus officinalis*, and *Sapium laurocerasus*.
- **Low light**—*Dacryodes excelsa*, *Drypetes glauca*, *Inga laurina*, *Manilkara bidentata*, *Ocotea moschata*, *Nectandra turbacensis* (HBK) Nees (formerly *Ocotea sintenisii* (Mez.) Alain, *Quararibea turbinata*, *Sloanea berteriana*, and *Tetragastris balsamifera*.

In addition to the above specific observations regarding tree growth and regeneration, nearly 100 tree species were recorded on numerous landslides of different sizes throughout the LEF (appendix D). Although individual site conditions vary, all slides have disturbed soils, are exposed to overhead light at least temporarily, and are situated at relatively short distances from the forest edge. In general, these conditions favor the regeneration of pioneer or secondary tree species and shrubs.

Chapter 5. MAJOR TYPES OF DISTURBANCE

The natural vegetation of the LEF has been affected by numerous disturbances, including:

- Background mortality such as sporadic treefalls.
- Climatic disturbances, including heavy rainfalls, tropical storms, and hurricanes.
- Landslides and erosion associated with climatic events and human activities.
- Human disturbances, including timber cutting, charcoal harvest, agriculture, grazing, road construction, and mining.
- Forestry activities such as silvicultural operations and planting of native and exotic tree species.
- Accidents, notably plane crashes.

Treefalls (Background Mortality)

Recording a treefall, except during a hurricane, is a rare event. While monitoring a permanent plot in lower montane forest in 1976, a Forest Service field crew mounted a tarp for protection during a heavy rainfall. Returning the next day, the tarp was found pinned to the ground by a 43-cm *Sapium laurocerasus* (see footnote 1). Typical background tree mortality such as this event form scattered gaps in the forest.

Mortality rates within the LEF may vary by forest type (Weaver 1983). The rates (in trees ha⁻¹ yr⁻¹) for trees >4 cm between 1946 and 1976 were: Lower montane forest, 24 to 32; montane forest, 17 to 20; and palm brake, 22. In contrast, mortality rates in previously thinned stands of lower montane and montane forest were 37 and 16, respectively. Although the data are very limited, it appears that mortality rates may be slightly greater in lower montane forest than in either montane forest or palm brake. The data may also suggest that post-thinning mortality rates differ by forest type.

Background tree mortality rates in the LEF are mainly influenced by typical species life cycles, competition among trees, the minimum diameters recorded, and the frequency of plot remeasurement. The above tree mortality data were determined during a post-hurricane recovery period spanning 15 to 45 years using 4 cm as the minimum d.b.h. Recurrent surveys conducted during shorter or longer periods, at different times in the life of the stands, and with different dimensions should yield different results. Current tree mortality rates in the LEF are underestimates because a 30-year remeasurement cycle invariably fails to record numerous small stems (i.e., stems that enter the minimum d.b.h. class and die before the next measurement). One typical

example would be the abundant regeneration of *Cecropia schreberiana* immediately after canopy disturbances, most of which succumb within a few years (Weaver 2002b).

Gap analyses are sometimes employed in lieu of actual tree mortality data to estimate tree turnover in the short term. In lower montane forest, gaps formed at the rate of 0.8 per hectare per year; moreover, they varied by topography, being the greatest in riparian valleys, intermediate on ridges, and the least on slopes and in upland valleys (Scatena and Lugo 1995). Estimates of gap formation for most neotropical lowland forests were slightly higher, averaging about one gap per hectare per year. It was suggested that the lower rate of gap formation in the LEF may reflect the periodic loss of weaker stems during recurrent hurricanes.

Other factors, however, are at least as important. Tropical mainland trees tend to be larger than those in the LEF, perhaps up to one-third or more in height. Some also have spreading crowns. Before Hurricane Hugo, the canopy in the LEF's lower montane forest was described as smoother and with fewer and smaller treefall gaps than were evident on Barro Colorado Island in Panama (Brokaw and others 2004). Persistent winds and recurrent hurricane impacts within the LEF appear to reduce the canopy size of dominant trees. Tree species in Dominica's lower montane forest, notably the dominant *Dacryodes excelsa*, had comparatively small crown-to-bole ratios (Bell 1976). Lower montane forest in the Caribbean Basin appears adapted to hurricanes with its "little-developed emergent story, small crowns, small crown-to-stem ratio, many stems, and small photosynthetic surface per stem, accompanied by slow stem growth rates, gradual limb loss, and in situ decomposition of standing trunks" (Odum 1970, page H-3). The gradual mortality of upright stems (Crow 1980, Odum 1970) should produce smaller gaps than those found on the mainland.

Climatic Disturbances

Hurricanes regularly impact the forests of the Caribbean Islands (Tomblin 1981). They vary in frequency, trajectory, forward movement, wind velocity, gust speed, duration, rainfall, and associated tornados. Hurricanes may impact organisms in the landscape by causing changes in forest structure, species composition, and diversity; by increasing the heterogeneity of landscapes and variability in ecosystem processes; by redirecting succession; and, inducing evolutionary change through natural selection (Lugo 2008).

Tree impacts correlate with hurricane trajectory and gust speed (Francis and Gillespie 1993). Defoliation and minor branch breakage start near 60 km hr^{-1} and increase rapidly to 130 km hr^{-1} after which they do not worsen. The most severe damage is avoided if crown surface area is diminished by the loss of leaves. Wood strength in the branches and bole contributes little resistance to breakage at high wind speeds. Palms, without branches and with leaves that trail in the wind, defoliate at high gust speeds and prove more wind resistant than broadleaf trees.

Hurricane impacts are a function of pre-storm forest composition and structure, including tree size, stem density, and root characteristics. Various factors within the LEF (i.e., topography, elevation, aspect, exposure, soil depth, soil moisture content, and past human activities) may also locally influence storm impacts. In addition, mortality rates of tree species depend on their inherent capacities to withstand major storms and to regenerate vegetatively afterwards. In some cases, however, purported differences in storm damage may actually be attributable to poor field techniques if live trees are prematurely recorded as dead.

Hurricane damage and recovery vary over the landscape. Hurricane trajectories near and over the Luquillo Mountains are frequent enough so that parts of the LEF are always in some stage of recovery from past events (fig. 12) (see table 6 for hurricane details and most citations). Field observations made in northeastern Puerto Rico immediately after the passage of Hurricane San Felipe showed defoliation, snapping, and uprooting, followed a short time later by refoliation, and for some tree species, abnormal seed production. Permanent plots established in the 1940s, 11 to 18 years after the hurricanes, showed an increase in saplings and pole-size trees after 15 years, accompanied by an increase in tree species richness and mean d.b.h. growth rates. As the forest closed, competition among surviving stems caused heavy mortality of secondary species. The survivors, mainly mature forest species, gradually dominated the stands. In montane forest, and probably in the lower montane forest as well, the mean specific gravity for the forest increased during 30 years as species composition changed. Forest volume and biomass also increased, gradually becoming asymptotic as the respective forests approached maturity. At any moment, however, the cycle could be renewed locally by treefalls, or throughout by new hurricanes (Brokaw 1985). In 1956, Santa Clara, a marginal hurricane with a trajectory over the center of the island, caused minor impacts within the LEF resulting mainly in defoliation, localized breakage, and some windthrow.

Hurricane Hugo, with a trajectory just east of the LEF, was the first major hurricane to strike the mountains in nearly 60 years (fig. 12) (table 6). Aspect and topography within the mountains sheltered pockets of trees in some places and

exposed others to high winds. Hurricane impacts included defoliation, breakage, uprooting, and loss of standing biomass, with some impacts increasing closer to the storm trajectory. Large trees were found susceptible to wind whereas smaller trees showed no consistent patterns; moreover, buttresses did not appear to protect against uprooting. Light reaching the forest floor increased immediately after the storm. Uprooting created treefall pits of variable size and vast quantities of debris and litter were deposited on the soil surface where they had variable effects on seed germination. Within a few years, canopy spaces created by broken branches were filled. Secondary tree species regenerated in gaps along with ferns and grasses. Vines also grew rapidly, often climbing dead and surviving stems.

In lower montane forest, post-Hugo observations showed an early recovery of foliage and tree crowns along with the establishment of herbaceous and woody ground vegetation. Comparative foliage profiles showed that the percentage of leaves at upper levels decreased after the hurricane and the percentage at lower levels increased. Pioneer species suffered high breakage and mortality and had a low capacity to



The effects of Hurricane Hugo (September 1989), the first major hurricane to affect the Luquillo Mountains in 57 years, was evident throughout the Luquillo Experimental Forest. Coca Falls is in the background. (Photo by Peter L. Weaver)

sprout whereas nonpioneers survived better and resprouted. *Dacryodes excelsa* and *Prestoea montana*, common in lower montane forest, appeared best adapted to recurrent storms. In contrast, many introduced species planted in ravines were severely affected.

Fine roots in the topsoil died a few months after Hurricane Hugo and much of the nutrient uptake was retained in the aboveground vegetation. Canopy development was followed by peak aboveground productivity as early successional trees grew into sapling and pole size trees. At this time, the Bisley forest had low within stand nutrient-use efficiency and the highest levels of productivity observed in the LEF. Subsequently, many of the trees impacted by the storm died. A summary of 15 years of recovery showed immediate losses of biomass, tree numbers, and species richness followed by gradual recovery.

Studies of post-Hurricane Hugo seed rain in the center and along the edges of two landslides at 370 and 520 m within lower montane forest reflected the presence of local flora (i.e., long distance dispersal was not required to explain observations). Seed rain peaks coincided with periods of high seed production and were dominated by shrubs that had increased fruit production in the surrounding forest understory.

Heavy rainfall in montane forest caused numerous landslides and the deposition of fine litter greatly in excess of pre-storm inputs (table 6). On a riparian palm forest plot, stem damage was common but mortality was low and recovery rapid. Litter deposited on the forest floor immediately after the hurricane decreased to pre-hurricane levels after 5 years. Also, post-hurricane stem density and biomass exceeded pre-hurricane values and delayed tree mortality was twice the normal background mortality.

In dwarf forest, about one-quarter of the stems that survived the hurricane suffered delayed mortality, with individual mortality rates varying by species (table 6). Pre- and post-hurricane litterfall were nearly equal, except when coarse woody debris was included in the post-hurricane tally. Loss of epiphytes in dwarf forest changes the pattern of water movement from the canopy to the ground. Hurricane Hugo stripped dwarf forest epiphytes in varying amounts depending on topography and exposure. Although not associated with Hugo, the experimental removal of dwarf forest epiphytes two decades earlier showed dramatic changes in the amounts of throughfall and stemflow during rainfall events (Weaver 1972). Before removal, epiphytes served to conduct much of the impinging rainfall as throughfall; after epiphyte removal, stemflow increased considerably. Hurricanes and the manual removal of epiphytes cause similar effects, increasing stemflow at the expense of throughfall. In addition, epiphyte

removal increases the amount of light reaching the soil surface, a change that favors immediate increases in grasses and ferns.

Hurricane Georges, with a trajectory just south of the LEF, had less impact than Hugo and received less attention (fig. 12) (table 6). Immediate post-Georges observations on permanent plot TR-1 in the lower montane forest showed a decline in tree species richness; moreover, *Dacryodes excelsa* accounted for a proportionally greater dominance in both residual stems and biomass. A post-hurricane island-wide study of sites varying in rainfall, elevation, soil type, topography, and aspect indicated high soil turnover rates caused by uprooting. Lower montane sites at Bisley and El Verde were part of the study. In dwarf forest, delayed mortality further reduced stem numbers and biomass adding to losses caused directly by Georges. Instantaneous litterfall due to Hurricane Georges ranged from about one-half to nearly the entire annual rate at six forest sites in the LEF. Subsequent decomposition returned litter levels to pre-hurricane values in about 1 year.

In addition to major impacts on the vegetation, hurricanes also affect wildlife. The direct impacts on bird populations include mortality due to wind, rain, storm surges, and geographic displacement of individuals (Wiley and Wunderle 1993, Wunderle 1995, Wunderle and Arendt 2011). For example, Hurricane Hugo reduced the wild population of *Amazona vittata* by one-half. Indirect effects include post-storm loss of food supplies or foraging sites, loss of nest or roosting sites, increased vulnerability to predators, and microclimatic changes. Birds respond in the short-term through shifts in diet, foraging sites or habitats, and changes in reproduction. Long-term responses may involve greater use of secondary vegetation. Post-hurricane recovery of bird populations depends on the amount of vegetation damaged as well as inherent species' characteristics like reproductive rates.

Bat populations are also affected by storm damage (Gannon and Willig 1994). The population levels of *Artibeus jamaicensis*, *Monophyllus redmani*, and *Stenoderma rufum*, the latter species listed as sensitive by the Forest Service, were affected by the hurricane. The first two species recovered within 2 years, but the *Stenoderma rufum* population only reached 30 percent of pre-hurricane levels after 3 years. Moreover, the size of its foraging and home range had expanded by five times implying significant increases in time and energy to secure food. A change in population age structure was also evident. Juveniles were absent after the storm indicating a decline in reproduction. Post-hurricane conditions also affected *Epicrates inornatus* (Puerto Rican boa constrictor), which wandered more after the hurricane than before (Wunderle and others 2004). Apparently, less branch density and leaf cover limited their use of arboreal sites.

Lost forest cover temporarily increased the amount of rainfall reaching the ground. Landslides and debris blocked stream channels altering habitats and food webs for aquatic fauna (Covich and others 1996, 2006). Other impacts included population changes and migrations of aquatic organisms. Hurricanes and tropical storms also affect the abundance, dispersion, and colonization of insects (Torres 1988, 1992). Outbreaks of 15 species of Lepidoptera were reported during the spring and early summer after Hurricane Hugo. All of the species fed on early successional vegetation, some of which represented new host plants within the LEF.

Landslides

More than one-half of the landslides in Puerto Rico are caused by intensive rains and winds associated with disturbances such as hurricanes, tropical storms, and tropical depressions, waves, or troughs; the remainder result from winter cold fronts or convective thunderstorms (Larsen and Torres-Sánchez 1992). The area with the greatest number of slides in the LEF lies between 600 and 800 m in elevation. Most occur during the June through October hurricane season. Their detection is not easy because many are small and are rapidly colonized by surrounding vegetation.

Highway construction and maintenance are critical factors affecting hillslope erosion and landslides. The lateral extent of impact caused by road construction is considerable. A survey of Puerto Rican roads in humid mountainous terrain showed that the rate of mass wasting increased five to eight times within a 170 m swath along road corridors as compared to more distant areas (Larsen and Parks 1997). Undercutting the foot of a slope is the most common construction-related activity that results in landslides. In the Río Blanco area, the frequency of landslides increased with (Larsen and Torres-Sánchez 1992):

- Slope angle, with more slides on precipitous slopes than less steep ones.
- Elevation, with more slides on high elevation hillslopes than on low elevation hillslopes.
- Aspect, with more slides on windward slopes facing the prevailing winds than to the leeward.

Landslides in ravines (cove slopes) are more common than those on slopes (side slopes) or ridges (nose slopes) (Simon and others 1990). Several observations have been made with regard to the growth of tree species on slides and unstable soils. In general, regeneration is more vigorous in the lower part of a slide, where light-demanding, fast-growing pioneer species dominate (Guariguata 1990). *Prestoea montana* is associated with saturated soils and grows on slopes disturbed by mass wasting (Guariguata 1990). The distribution of other

species varies with topographic form: *Clusia clusioides*, *Cyrilla racemiflora*, *Micropholis garciniifolia*, *Micropholis guyanensis*, and *Tabebuia rigida* are least common on cove slopes. Fern thickets growing on landslides low in nutrients appear to facilitate the germination of tree seedlings but later may inhibit their growth, notably on the upper portions of slides (Guariguata 1990). *Cecropia schreberiana* seeds sown under fern thickets germinated at a higher rate than those sown in adjacent open areas (Walker 1994).

Hurricane Hugo caused more than 400 landslides on nearly 60 percent of the LEF (Larsen and Torres-Sánchez 1992). Slides averaged about 150 m² and ranged between 18 and 4500 m². Estimates show that landslides are eroding the LEF at a rate that equals about 1 percent (about 113 ha) per 1,000 years. Long-term landslide estimates are tenuous, however, because the proportion of a landscape covered by slides may increase dramatically in response to prolonged heavy rainfalls or hurricanes.

The largest LEF landslide occurred in 1970 at 600 m elevation on the south side of the forest at km 21 along PR route 191 (Guariguata and Larsen 1990; Larsen 1997; U.S. Department of Agriculture, Forest Service 1997b). The ~6 ha slide was caused by a 5-day storm with an accumulated rainfall of 950 mm. In September 1979, Hurricanes David and Frederick caused additional erosion on the large slide and smaller landslides about 1.5 km to the north on PR route 191. Subsequently, the road 0.5 km north and south of the main slide has been completely covered by numerous minor landslides. In some instances, slump (i.e., mass wasting where a coherent mass of loosely consolidated materials slide a short distance down slope) has deposited mature trees on the road surface. *Cecropia schreberiana*, *Prestoea montana*, and *Psychotria berteriana* are well represented on the transported soil. Large patches of the popular flowering *Impatiens* sp. are also growing in shaded areas on the road surface.

An October 2005 survey of trees on the major slide showed >40 species (appendix D), about the same number that was detected on all other landslides within the LEF (Guariguata 1990). The large landslide shared 19 species with the remaining LEF slides, including *Cyathea arborea*, which was the most abundant species in a range of sizes. Other common species included *Alchornea latifolia*, *Cecropia schreberiana*, *Cyrilla racemiflora*, *Inga laurina*, *I. vera*, *Miconia racemosa*, *Prestoea montana*, *Psychotria berteriana*, and *Tabebuia heterophylla*. Rare species on the site included *Coccoloba schwartzii*, *Roystonea borinquena* O.F. Cook, and *Sloanea berteriana*, possibly survivors on an isolated clump of soil that remained intact during the slide. Fruit trees, such as *Psidium guajava* and *Annona* sp., were probably introduced by visitors. *Pinus caribaea* was planted about 20 to 25 years earlier, and its regeneration is common along the top and

southern fringe of the slide. By 2009, most of the major slide was covered by secondary regeneration. The steep slopes bordering the slide, however, are continuously eroding and several deep crevasses dissect it at lower levels. Because the slide is large, the substrate unstable, and rainfall both frequent and heavy, complete recovery will require considerable time.

Plant responses to nutrients and light on landslides were explored to determine if the availability of nitrogen and phosphorus limited the growth of pioneer and nonpioneer species differently (Fetcher and others 1996). The amount of nitrogen appeared to influence the growth of both pioneer and nonpioneer species, whereas the amount of phosphorus

appeared to affect the growth of pioneers. In the absence of nutrient additions, neither pioneer nor nonpioneer species appeared to be well adapted to colonize parent material because their growth was slow.

An attempt was made to predict landslide vegetation after disturbance in the LEF (Myster and others 1997). Age, aspect, elevation, and substrate were found to be important variables influencing vegetation complexity on slides. More advanced succession is found on landslides which are older, leeward to hurricane winds (i.e., southeast in the case of Hurricane Hugo), at lower elevation within the mountains, and on volcanoclastic as opposed to dioritic substrates. Biological mechanisms, such as dispersal, predation, and competition, are variables of less importance. Tree species which colonize treefall gaps within the forest are also found on landslides and their sequences are determined by decreasing light availability (Myster and Walker 1997). *Alchornea latifolia*, *Cecropia schreberiana*, *Solanum torvum*, *Tabebuia heterophylla*, and *Trema micrantha* are the most light-demanding species (appendix D); *Miconia* spp. and *Urera baccifera* are considered to be light demanding; *Piper* spp. are rated as intermediate with regard to light; and finally *Inga laurina*, *I. vera*, *Ocotea leucoxylon*, and *Prestoea montana* grow in gaps with low light. It was suggested that the aforementioned sequence might represent the order in which tree species would replace each other during the recovery process.

The major landslide at km 21 on PR route 191 closed the scenic highway on the south slopes making access to the forest interior more difficult. Simultaneously it made the forest less environmentally fragmented and gave managers greater control over forest resources, especially wildlife. Humans built the road on unstable terrain where it served visitors for almost 30 years. Nature, via heavy rains and a major landslide, has kept the road closed for >40 years.

Human Activities—Settlement and Development

Forests were the dominant vegetation cover in virtually all of Puerto Rico when Columbus arrived (Wadsworth 1950). At that time, the lower montane forest probably had an average timber volume of about 250 m³ ha⁻¹ (Wadsworth 1949, 1950, 1951). By the middle of the 20th century, however, timber harvest, agriculture, and fuelwood cutting had removed or disturbed all but 3500 ha in Puerto Rico, 65 percent of which was at higher elevations in the LEF (Wadsworth 1950). The upper LEF was always forested and experienced very little human disturbance. In contrast, much of the lower part was subjected to “the familiar routine of logging, clearing, burning, grazing, and farming which constitutes shifting agriculture” (Marrero 1948).



This major landslide at 600 m elevation (i.e., km 21 along PR route 191) occurred after heavy rains in 1970 and permanently closed the highway. TOP: The slide with little vegetation in 1981 BOTTOM: The same area with denser cover in 2005. Note the abundance of the native *Cyathea arborea* (tree fern) and the presence of introduced *Pinus caribaea* (Caribbean pine). (Photos by Peter L. Weaver)

In 1936, <50 percent of the LEF had continuous canopy cover (i.e., areas with >80 percent of the land area under forest canopy) (Foster and others 1999). This was about 100 years after major human activity began on the lower slopes and only 4 to 8 years after the passage of three major hurricanes, including one regarded as the island's legendary storm and another that passed directly over the forest. Subsequently, forestry operations like timber stand improvement and planting of native and exotic timber species were carried out at lower elevations (fig. 6) (table 13). By 1989, >97 percent of the LEF was under forest canopy.

Many other human disturbances have occurred since the period of discovery and settlement (table 13). Initially, the cutting of timber and clearing of trails for mining most likely had minor impact on the forest. At least 24 mining claims were made in the El Yunque quadrangle (Cardona 1984). Five of the sites were worked, 10 were not, and the history of the remainder is uncertain. Virtually all of the sites were situated in lower montane forest.

The construction of PR routes 186 and 191 as well as secondary roads led to the direct loss of forest. By the mid-1990s, nearly

50 ha of the LEF were occupied by roads (Kharecha 1997). Moreover, road construction and maintenance—or the extension of long corridors through the forest—has an impact on adjacent ecosystems (Heyne 2000). These include changes in soil and surface water properties, erosion, landslides, leaching of nutrients, and the addition of pollutants from road deterioration and use. Canopy openings for the roads change the local microclimate, increasing levels of radiation, temperature, and evapotranspiration and reducing humidity and water infiltration. The net effect is to dry nearby soils and to slow organic matter decomposition and nutrient release to the soil. The roads and associated landslides also provide routes for the entrance of secondary and exotic species. The development of administrative sites, recreation areas and hiking trails, and communication sites, including towers and transmission lines, disturbed at least 630 ha (table 13). These sites have similar negative impacts on the environment. In addition, they are a source of noise, garbage, and contamination of clean waters.

A case study of past land use carried out in the early 1990s disclosed some of the less obvious impacts of past human activity. The Spanish began land distribution in the 1800s to encourage the settlement of the LEF's lower slopes (García-Montiel and Scatena 1994). Select removal of timber species and the cultivation of coffee and subsistence crops followed, and in 1934, when the Forest Service acquired Bisley, forestry activities were initiated. Among the forest impacts observed at Bisley in the early 1990s were:

- Evidence of skid trails used for timber extraction.
- Shifts in the dominance and age structure of canopy trees.
- Proportional decreases in certain commercial timber species.
- Understory subsistence crops, notably the banana in riparian areas.
- Increases in the importance of *Guarea guidonia*, *Inga laurina*, and *I. vera*, tree species that were used as coffee shade in the mountains.
- Evidence of past charcoal kilns and an increase in *Prestoea montana* in the vicinity of the kilns.

Human impacts similar to those at Bisley most likely characterize other sites along the LEF's border.

Accidents

Several accidents have caused minor disturbances within the forests of the Luquillo Mountains. At least six notable incidents (i.e., with estimates of site damage and trail clearing in parenthesis) have occurred (appendix A):

- An airplane crashed in lower montane forest near the Bisley watersheds, possibly during the 1940s or 1950s (0.3 ha). No additional information could be found regarding the wreck.

Table 13—Estimated areas of historic and current disturbances within the Luquillo Experimental Forest^a

Disturbance types	Area ha
Hurricanes ^b	~11 310
Agriculture and timber ^c	6450
Administrative sites ^d	82
Communication sites ^d	79
Developed recreation ^d	468
Roads ^e	50
Landslides ^f	113
Mining ^g	3
Forest management	
Stand improvement ^h	1620
Plantations ⁱ	1510
Research manipulation ^j	5
Crashes (airplanes and vehicles) ^k	5

^aSome areas overlap.

^bOver the course of centuries, hurricanes would impact virtually all of the LEF.

^cCrops, grazing, charcoal, and wood harvest (Marrero 1948).

^dU.S. Department of Agriculture, Forest Service (1997a).

^eRoads and margins (Kharecha 1997, Scatena 1993).

^fData expressed in hectares per 1,000 years (Larsen and Torres Sánchez 1992).

^gMost was placer mining for gold (Cardona 1984).

^hThinning, girdling, tree cutting (Snyder and others 1987).

ⁱNumerous species (Marrero 1948).

^jTree cutting, trails, arboretum, and canopy trimming (Byer and Weaver 1977; Francis 1989; Howard 1968; Sheils and others 2010).

^kCrash site plus areas disturbed in clean-up operations.

- A Fairchild C-119 (Flying boxcar) departed from Roosevelt Roads and crashed in dwarf forest near Pico del Este on December 14, 1968 (0.3 ha). Subsequently, vegetative recovery has been monitored for > 40 years on the site (Weaver 2000b, 2008).
- A Havilland Heron DH-114 (Prinair flight) flying between St. Thomas and San Juan crashed in montane forest near Cacique Peak on March 5, 1969 (1.5 ha) (Rojas Daporta and Ortiz Otero 1969).
- A Cessna 441 flying between Culebra and San Juan fell in lower montane forest near the roadside restaurants on PR-191 on January 5, 2002 (0.3 ha) (Torres 2002).
- A fixed-wing Rockwell International 690B turbo commander flying between Tortola and San Juan fell in the El Toro Wilderness Area situated in lower montane forest near the northern forest border on December 3, 2008 (2.0 ha) (Hernández Pérez 2008).
- A crane parked overnight on FS-27 near Pico del Oeste slid off the road, clearing a patch of montane forest during the early 1980s (0.3 ha). The crane was not removed from the forest.

In addition, an unknown number of automobiles and trucks have crashed at several points along forest roads causing local damage. Some accidents affect considerably more area than the accident site. Crash investigations and debris removal for airplane wrecks involve trail clearing, intense trampling around the accident sites, and soil erosion. They also cause changes in herbaceous species and present opportunities for the introduction of exotic weeds. The total impact to the six forest sites above is estimated cover about 5 ha.

Post-Disturbance Recovery

Forest recovery from past disturbance depends on numerous factors. These include: site variables such as elevation, aspect, topography, and exposure; the nature of past disturbance (e.g., selective logging, agriculture, grazing, hurricane damage, or landslides, alone or in combination); size of disturbance and distance from seed sources; and duration of disturbance, especially with regard to agricultural activities or temporary settlement.



At least five airplanes have crashed within the Luquillo Experimental Forest since the 1940s, including the 1968 crash of a Fairchild C-119 (flying boxcar) in dwarf forest near Pico del Este. LEFT: The crash site after 9 years is covered by ferns and grasses. (Photo by Peter L. Weaver) ABOVE: After 35 years, debris at the same site is surrounded by many endemic broadleaf species and ferns. (Photo by Iván Vicéns)

Hurricane disturbance and recovery were modeled for the LEF's lower montane forest considering several factors (Everham 1995):

- Catastrophic wind intensity—sustained wind, maximum gusts, storm duration, total storm rainfall, the storm's proportion of total annual rainfall, and the distance between impacted sites and climatic stations.
- Biotic factors—tree species, size, and stand factors as they influence the severity of damage during a storm event.
- Abiotic factors—factors as they relate to severity of damage such as topography (i.e., channeling wind, site exposure, or vegetative preadaptation to chronic wind), soil (i.e., root growth as affected by water tables and other factors), and previous disturbance (i.e., increase in turbulence by canopy opening, the loss of susceptible trees, or shifting composition to more wind resistant species).
- Response pathways—regrowth and recruitment, the major pathways, along with some release and repression, as influenced by mainly the amount of structural and compositional damage incurred.

At small spatial scales, damage is controlled mainly by biotic factors such as species composition. At larger scales, abiotic factors such as topography and storm intensity become more important. Post-disturbance recovery is sensitive to gradients in light and water (Everham 1995). For example, sheltered valleys are humid but receive less light due to shading by surrounding slopes; ridges, in comparison, are better drained but receive more diffuse light at lower levels, differences often reflected in a greater shrub layer. Moreover, two general patterns of canopy recovery are possible. Where pioneers are recruited, a homogeneous canopy layer grows upward shading lower vegetation. Where regrowth of surrounding

trees dominates, the canopy extends outward creating a more heterogeneous profile. Seedling recruitment is also important in site recovery (Uriarte and others 2005). Recruitment reflects interactions among several factors, including distance from local parent trees, parent tree size, seeds from nonlocal trees, and density-dependent effects from conspecific seedlings.

One might speculate on the time required for complete recovery after major disturbance within the LEF's forests. Stand biomass and dynamics should recover relatively rapidly. Structure, or the typical size class distribution of trees within mature forest, would take longer. Species' compositions similar to those found at the time of discovery, especially with regard to rare endemics, could require yet more time. Lower montane forest, with the greatest structure and diversity, also has the most favorable climate. Dwarf forest at the other extreme has the least structure and fewest species but the most rigorous climate.

Time required in lower montane and montane forests may be in the order of 100 years for biomass, 300 to 400 years for structure, and perhaps 1,000 years for species composition. Palm brakes and ravines, regardless of elevation, should take less time because their total biomass is less and their species compositions are not as complex. *Prestoea montana* matures quickly and regenerates well in openings and closed forest. Recovery of biomass and structure in dwarf forest may be a little longer than for the lower forest types; however, given the paucity of total species, and the abundance of endemics during succession, recovery of typical species composition may be more rapid. Superimposed on all of these estimates are the unknown effects of future disturbances, especially global warming and probable plant and animal migrations.

Chapter 6. OTHER VEGETATION

In addition to the four major forest types, the LEF has tree plantings, timber plantations, mahogany line plantings, a mahogany provenance trial, and the Forest Service arboretum at Caracoles (figs. 13 and 19). A total of 144 tree species have been planted, including 61 in plantings or in plantations, 75 as species blocks within the arboretum, 17 during agricultural activities, and 18 as ornamentals (appendix E). Of the total, 120 tree species were introduced from elsewhere, including 112 exotics and 8 species native to other parts of Puerto Rico (appendix E).

Tree Plantings and Plantations

Beginning in the 1920s, timber and ornamental trees from other countries, both tropical and temperate, were introduced, propagated, and tested in Puerto Rico (Bates 1927; Francis 1987, 1995; Kramer 1926, 1927; Wadsworth 1970) (appendix E). In 1931, plantings began in the northwest (El Verde) and south (Del Valle) sites near the forest border (fig. 6). The major reasons for establishing plantations were timber production and watershed protection (Marrero 1947). An additional goal was the development of a multiaged forest composed of sawtimber and other species capable of natural reproduction. Local farmers recognized topographic variation (i.e., convex, straight, and concave slopes) as a critical factor in the selection of sites for agricultural crops. Likewise, topography was considered important to the survival and growth of plantation species (Marrero 1948, 1950).

The most active period for reforestation was between 1934 and 1945 when more than 4 million seedlings of 27 species were planted at 54 different plantation sites on ~2000 ha of recently abandoned farmland (Marrero 1947, 1948) (appendix E). Ten species accounted for >94 percent of the planted seedlings: *Swietenia macrophylla* and *Swietenia mahagoni* totaled 51 percent; and *Casuarina equisetifolia*, *Cedrela odorata*, *Cordia alliodora*, *Guarea guidonia*, *Montezuma speciosissima*, *Petitia domingensis*, *Tabebuia heterophylla*, and *Tectona grandis* accounted for >43 percent. The remaining 17 species totaled <6 percent. *Byrsonima spicata*, *Calophyllum calaba*, and *Tabebuia heterophylla*, tree species that invade degraded secondary sites throughout the island were also used (Marrero 1950) (appendix E). About 60 percent of the plantations were well stocked; however, many of the planted species, both natives and exotics, were not well adapted to the Luquillo Mountains. Previous inexperience with native species, misjudgments with regard to species selection, and planting on eroded and depleted soils all contributed to failures. Partial replanting was carried out on more than one-half of the

plantations. By 1960, all plantations within the LEF had been thinned (Wadsworth 2009, see endnotes).

In the late 1930s, taungya plantings (i.e., interplanting of timber species with subsistence crops) using *Calophyllum calaba*, *Swietenia macrophylla*, and *Swietenia* hybrid (i.e., *S. macrophylla* x *S. mahagoni*) were initiated at elevations between 250 and 450 m (Holdridge 1940). The purpose was to convert abandoned agricultural lands into timberland. After 50 years, some plantings that had survived the period were measured to determine their mean and current annual increments (Weaver 1989a). *Swietenia* hybrid at 250 m elevation on the Harvey site (fig. 6) had grown satisfactorily over the entire period, averaging about 400 m³ ha⁻¹ or a mean annual increment of 7.5 m³ ha⁻¹ yr⁻¹; moreover, current annual increment at 12.0 m³ ha⁻¹ yr⁻¹ was considered excellent. Mahogany seedlings and saplings were evident throughout the stand. In comparison, *Calophyllum calaba* at 450 m, like many other species in the LEF, grew slowly, averaging 200 m³ ha⁻¹, or 5.0 m³ ha⁻¹ yr⁻¹. Current annual increment was similar. Stand densities, including the ingrowth of other species, averaged about 1000 ha⁻¹ in the mahogany stand and 1450 ha⁻¹ in the *Calophyllum calaba* stand. The latter appeared stagnated but its survival demonstrated a capacity to tolerate marginal planting sites and competition.

Other studies indicate the performance of introduced species. Differences in spacing affected the height and d.b.h. growth of *Pinus caribaea* planted at Guzmán and the Caracoles arboretum along the western and southwestern boundaries of the LEF (figs. 6 and 13). The different spacings within the LEF contained trees that averaged 23 m tall after 20 years, growth rates which were slower than for sites in western Puerto Rico (Liegel and others 1985). The performance of *Anthocephalis chinensis* in spacing studies at El Verde, line plantings at Jiménez, plantations at Catalina, and at sites elsewhere on the island showed that it averaged between 16 and 21 m in height after 10 to 22 years. The best growth was attained on silty clay, nutrient-rich soil (Lugo and Figueroa 1985). Wide spacings allow trees to grow rapidly for 10 years and satisfactorily for 20, usually with excellent form. *Anthocephalis chinensis* is a recommended species for pulp in the wet tropics because of its fast growth and desirable wood characteristics.

Hibiscus elatus was surveyed at 34 sites in Puerto Rico, including the arboretum and Sabana (Francis and Weaver 1988) (figs. 6, 13, and 19). Growth rates after 25 and 26 years showed basal areas ranging between 20 and 50 m² ha⁻¹, with

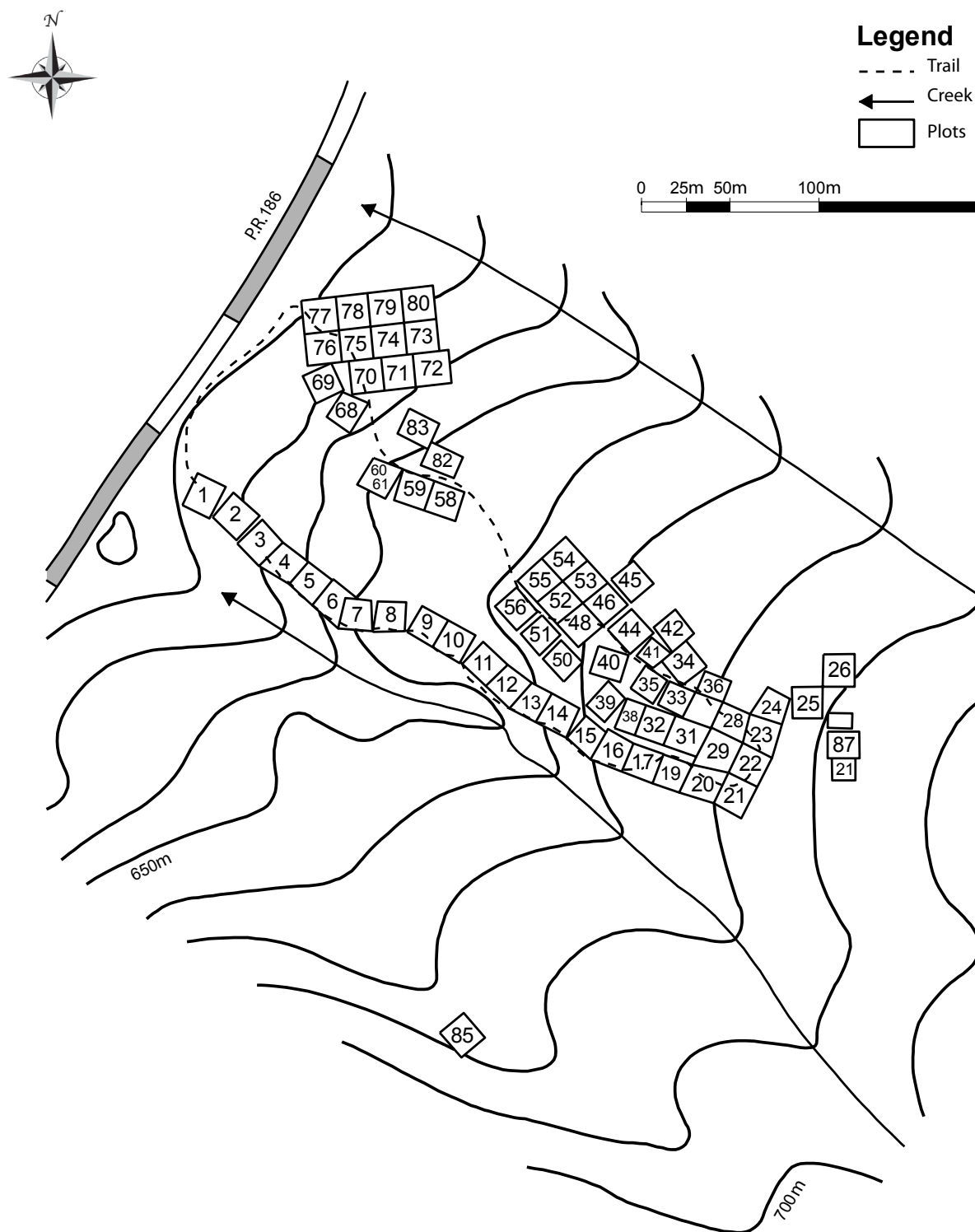


Figure 19—Design of the arboretum in the Luquillo Experimental Forest.



Mahogany plantings. LEFT: Line-planted mahogany hybrid grows on the lower slopes of the Luquillo Experimental Forest after the abandonment of agriculture. (Photo by Gerald P. Bauer) RIGHT: A 70-year old mahogany plantation at the Harvey site reflects the dedicated efforts of earlier foresters. (Photo by Peter L. Weaver)

a mean d.b.h. for dominant stems between 20 and 50 cm. *Hibiscus elatus* appeared to be adapted to a wide range of sites in Puerto Rico, including most with rainfalls >1500 mm yr⁻¹.

Tectona grandis was surveyed on 27 plantations in Puerto Rico, including a 49-year-old stand at 120 m in Sabana (Weaver and Francis 1990) (fig. 6). The merchantable volume of *Tectona grandis* at Sabana, which accounted for one-half of the 1400 stems on the plot, was ~ 110 m³ ha⁻¹. The mean height and mean d.b.h. of dominants were 17 m and 28 cm, respectively. Teak growth on the island was satisfactory on soils varying in texture from sands to heavy clays when rainfalls averaged between 1200 and 3400 mm yr⁻¹. Plantings of *Byrsonima spicata*, *Cordia alliodora*, *Guarea guidonia*, *Ocotea moscata*, *Petitia domingensis*, *Pouteria multiflora*, and *Tabebuia heterophylla* growing in the LEF were also evaluated (Wadsworth 2009, see endnotes).

Mahogany Line Planting

Several enrichment techniques, including line planting, have been used to establish at least 163 tree species in at least 12 countries or territories within the neotropics

(Weaver 1987c). The objective of enrichment planting is to improve the composition and commercial potential of secondary forests, rendering them more valuable at maturity. Because enrichment plantings require only partial clearing of secondary forests, they help conserve the soil, water, and wildlife resources during the establishment phase.

Field observations showed that secondary forest regeneration in areas with planting trials appeared to have a positive effect on the planted trees, especially mahogany (Wadsworth 1970). Consequently, line planting (i.e., underplanting or enrichment planting) trials were initiated with *Swietenia* hybrid in degraded secondary forest along the northeastern border of the LEF (Tropical Forest Experiment Station 1950) (fig. 6). *Swietenia* hybrid line plantings began in the 1960s and by 1981 they covered about 1275 ha (Weaver and Bauer 1986).

Establishment and tending methods for the mahogany plantings varied. In the earliest enrichment plantings, the overstory was gradually poisoned and seeds were planted at 3x3 m spacings. Weeds were controlled by using herbicides. Seedlings were liberated by repeated early thinnings based on tree form and spacing. Later plantings employed bare root seedlings with a spacing of 2.5 m between trees and 11 m between rows. Tree

survival and growth rates for both techniques were satisfactory. Growth differed significantly by topographic position with trees on bottomlands and lower slopes averaging about 20 m in height after 18 years, and those on mid-slopes and ridges about 17 and 10 m, respectively (Weaver and Bauer 1986). Plot density after 18 years was 370 stems ha^{-1} , basal area 28 $\text{m}^2 \text{ha}^{-1}$, and total aboveground biomass 170 t ha^{-1} .

Seedling survival rates varied between 55 and 65 percent and shoot borer infestation between 10 and 60 percent (Weaver and Bauer 1986). Better light conditions and lower surrounding basal areas positively influenced growth. However, no consistent relations were found between shoot borer damage and crown class, surrounding basal area, or topographic position. Later, volume tables based on 133 trees were developed for 16 and 20-year-old plantation-grown *Swietenia* hybrid at the Sabana and nearby Río Chiquito sites (Bauer and Gillespie 1990) (figs. 6 and 13).

Although forest plantations are widespread in the tropics and common at lower elevations within the LEF, their importance and use by avian species has not been well studied. In the early 1980s, avian community organization and resource use was surveyed in the *Swietenia* hybrid plantings at Río Chiquito (Cruz 1987). Frugivores and nectarivores foraged mostly in the understory when flowering and fruiting shrubs were present. Insectivores (foliage gleaners) were more common in the canopy whereas sally-hoverers were concentrated in the understory. Later, foraging patterns in *Pinus caribaea* plantations were found similar to those in the *Swietenia* hybrid plantings (Cruz 1988). Maintaining or encouraging a heterogeneous understory along with scattered native canopy species could improve the use of forest plantations by birds.

Enrichment plantings previously used to improve commercial timber potential in the LEF (Weaver and Bauer 1986) may also be one of the best alternatives available to enhance wildlife habitat, particularly for the avifauna. In the latter case, foraging or nesting trees, especially natives, could be favored in lieu of timber species. Another option might be experimental forest thinnings to stimulate the regeneration of critical wildlife tree species. Past basal area reductions in montane forest increased significantly the regeneration of *Cyrilla racemiflora* (Weaver 2001). Increasing foraging and nesting habitats could help all wildlife species survive future hurricanes, notably the parrot.

Mahogany Provenance Trial

Swietenia macrophylla and *S. humilis* seeds collected in the mid-1960s from 24 sites in Mexico, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, and Panama were germinated and tested at 11 sites in Puerto Rico, including

the LEF, and at two sites in St. Croix (Geary and others 1973, Glogiewicz 1986, Weaver 2006). Nineteen provenances were planted at sites ranging from dry to wet in Puerto Rico and 10 provenances were planted on dry sites in St. Croix. Seedling survival, height, and d.b.h. growth were determined after outplanting (Geary 1969, Geary and others 1973) along with wood densities from sites in Mexico, Central America, Puerto Rico, and the U.S. Virgin islands (Boone and Chudnoff 1970, Chudnoff and Geary 1973).

The objectives of the most recent analysis of the *Swietenia* spp. (i.e., *S. macrophylla*, *S. mahagoni*, and *S. humilis* Zucc.) and provenance plantings, including 20 genetic sources, were to determine the amount of phenotypic plasticity and genetic variation within and among species and populations, and to examine how species and provenance growth characteristics change across environments (Ward and Lugo 2003). Relative amounts of environmental and genetic variation in growth and size traits, survival, and insect susceptibility were estimated. Trees were planted at 14 sites in Puerto Rico and St. Croix, including two locations within the LEF. The study showed the following size and growth traits after 14 years:

- Mahogany species showed about 10 times more genetic variation than was apparent among provenances within species.
- The mean estimated environmental variance for *S. macrophylla* was 79 percent, the mean estimated genetic variance was 11 percent, and the mean interaction was 8 percent. Similar estimates for *S. humilis* were 41, 15, and 29 percent, respectively. Comparisons for *S. mahagoni* were unavailable.
- Significant correlations existed between environmental gradients at sites of origin and measures of growth suggesting natural selection in differentiating populations.
- *S. macrophylla* showed the greatest mean growth (i.e., height, d.b.h., and biomass) at 14 years across all sites. *S. mahagoni* and *S. humilis* did not differ in most measured variables.
- All species and several populations showed distinct responses to different life zones and soil types.
- For both *S. macrophylla* and *S. humilis*, 95 percent of the variation in shoot borer attack was caused by estimated large- and small-scale environmental effects.
- Provenances became more genetically distinct as distance increased (i.e., source populations ranged from 160 to 1600 km apart).

The planting site for the provenance trial represents an *ex-situ* preserve that originally contained germplasm for an average of 16 trees per 19 provenances (fig. 13). Because many of the source areas for seeds may have been logged, the collection is critical to conservation biology and strategies to preserve genetic variation in mahogany. Without the study, the genotypic

information and breeding material itself would have been lost (Glogiewicz 1986). Today, the collection provides opportunities for new studies, including future genetic, morphological, and biochemical analyses. Seed orchard establishment and clonal propagation, however, may no longer be feasible.

Forest Service Arboretum (Caracoles)

The arboretum is located between 620 and 690 m in elevation on the lower western flank of El Toro Peak (Francis 1989) (figs. 13 and 20). In its pristine state, the site was probably occupied by transition vegetation between lower montane and montane forests. Rainfall averages about 3000 mm yr⁻¹, and the soils are clays with a mean pH of 4.7 and an average organic matter content of 8.6 percent. The land was first cleared for subsistence farming in the 1920s and was partially replanted at a later date. Subsequently brush occupied much of the area.

In 1959, a small test plantation was established on the site and in 1960, different tree species, mostly exotics, were gradually planted in small blocks (fig. 19) (appendix E). Most plantings were completed by 1963, but new species were added in plots of 49 trees (7 x 7 trees) when seedlings were available. During the 1980s, seven new species were introduced. By 1989, 14 species had been lost whereas 68 species, some represented by multiple subspecies or provenances, still survived (Francis 1989).

Some of the plots were measured earlier but a complete inventory was not finished until 1987. The tallest specimens by species ranged from 6 to 46 m and their corresponding diameters from 8 to 75 cm. Grouping by height classes for the tallest specimens of all species showed that 44 percent were <20 m, 45 percent were between 20 and 30 m, and 11 percent were >30 m tall. Corresponding data for diameters showed 16 percent <20 cm, 51 percent between 20 and 40 cm, and 33 percent >40 cm (Francis 1989). The species represented 26 countries: Africa (Nigeria, Sudan, Uganda, Zimbabwe); North America (Mexico, United States); Central America (Belize, Costa Rica, Guatemala, Honduras); South America (Argentina, Brazil, Surinam, Venezuela); the Caribbean (Cuba, Jamaica, Puerto Rico, U.S. Virgin Islands); Asia and islands (China, India, Iran, Papua New Guinea, the Philippines, Sri Lanka, Taiwan); and Australia.

Several of the introduced broadleaf species at the arboretum site showed promise for timber production, including: *Anthocephalis chinensis* and *Aleuritus moluccana*, both species with low specific gravities; *Eucalyptus grandis*, *E. robusta*, and *E. saligna*; *Khaya grandifolia*, *K. nyasica*, and *K. senegalensis*; and *Hibiscus elatus*, *Maeopsis eminii*, *Swietenia macrophylla*, and *Terminalia ivorensis*. Among the conifers, *Pinus caribaea* var. *hondurensis* (also var. *caribaea*) and *P. oocarpa* performed well. Some broadleaf species also

showed potential as ornamentals, including the introduced *Pterocarpus indicus* and *Clitoria racemosa*, and the native *Hernandia sonora*. Among the conifers with potential as ornamentals were *Callitris glauca* and *C. intertropica*. Other species showed promise for planting or further testing as timber species or ornamentals. Today, the arboretum continues as an experimental site for species adaptability trials; moreover, it is also used for ecological research, seed collection, demonstration, and educational purposes.

In 1987 and 1998, species composition and structure in the arboretum understory were studied (Lugo and others 1999). Of the 83 species tallied, 20 were considered abundant, including *Maeopsis eminii*, *Palicourea riparia*, *Prestoea montana*, *Schefflera morototoni*, *Syzygium jambos*, and



Ornamentals. Roadside mahogany planted along PR route 988 in the 1960s adds some color to the surrounding foliage during the dry season. (Photo by Iván Vicéns)

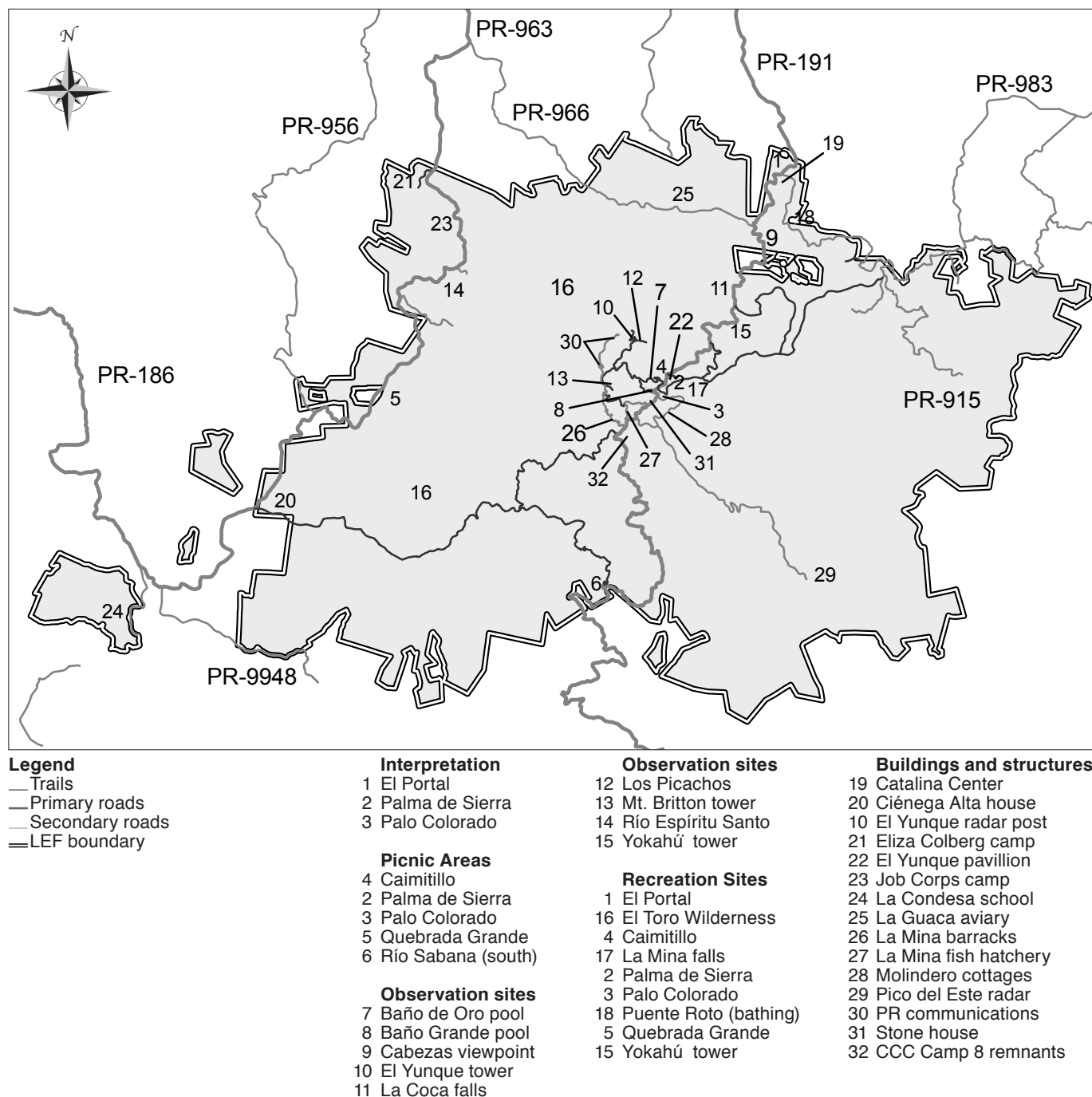


Figure 20—Management areas and structures within the Luquillo Experimental Forest.

Thespesia grandiflora. Hurricanes of 1989 and 1998 caused a decline in species numbers and plant density in the understory.

Other Tree Species and Common Herbs

Ascending PR route 191, *Bambusa vulgaris*, established during the 1930s and 1940s, is visible along the roadside and in ravines where it was planted to help stabilize the soil (Little and Wadsworth 1964). The species, however, gradually spreads along streams where its increase could impact aquatic communities that depend on leaf litterfall (O'Conner and others 2000) (appendix E). The risk of colonization was considered sufficient enough during a recent survey to recommend monitoring and research (Blundell and others 2003).

During gradient sampling, a few exotic tree species not associated with plantations were noted in closed forest. *Castilla elastica* was seen at 730 m above the La Mina recreation area. The fruit may have been carried by birds from ornamental plantings along the road. *Mangifera indica*, observed in the Mameyes valley near the forest border, was most likely introduced as fruit tree during settlement. *Syzygium jambos*, native to Southeast Asia and introduced to Puerto Rico nearly 200 years ago, yields edible fruit and fuelwood, and is not restricted by topography, soil nutrient status, or elevation (Brown and others 2006). The species is shade tolerant and gradually spreads along streams and lower slopes where it may exclude natives by allelopathy (O'Conner and others 2000). Its presence in closed forest is due to past human activity, possibly hikers or laborers traversing the forest years ago. In addition, *Psidium guajava*, *Pinus*

caribaea, and *Annona* sp. were recorded during the survey of the large landslide at km 21 along PR route 191. The pine was planted to help stabilize the soil. The other species, both edible fruits, were probably discarded by hikers.

Exotic ornamentals, including shrubs (*Hibiscus* sp.), herbs (*Impatiens* sp., *Heliconia* spp., and *Zingiber* sp.), and several grasses also grow along LEF roadsides and in recreation areas. After construction of FS-27, the exotic grass *Melinis minutiflora* Beauv. was seeded with fertilizer to reduce erosion and sedimentation (Olander and others 1998). *Pennisetum purpureum* Schumacher, another exotic grass, also grows along the same road. Interestingly, these grasses remained largely confined to the roadside. A recent survey carried out in the El Toro Wilderness tallied 82 invasive species: 23 vines, 14 trees, 11 grasses, 11 herbs, 10 shrubs, 8 ferns, 1 orchid, 1 sedge, and 3 listed as weeds (U.S. Department of Agriculture, Forest Service 2009, see endnotes).

At least 41 of the exotic tree species planted in the LEF have become naturalized in varying degrees (Francis and Liogier 1991) (appendix E). Naturalized species showing the highest degree of integration include those that are capable of competing in mature or primary forests after escaping from their original planting sites. Lesser integration is shown by those species that have entered secondary forests. The least integration includes species that reproduce infrequently or incidentally, and are dependent on human disturbance for survival. At least 35 exotic tree species were independently rated as adapted to the climate and soils of the LEF (Francis 1987) (appendix E).

Chapter 7. VERTEBRATE FAUNA

The LEF has 165 species of vertebrates of which 158 are terrestrial and 7 are aquatic (U.S. Department of Agriculture, Forest Service 1997a, 1997b). In addition, the forest has aquatic macroinvertebrates.

Mammals

The LEF has 16 species of mammals. Eleven are native bats and five are introduced species common to Caribbean islands (table 14). Of the natives, *Artibeus jamaicensis* (fruit bat) is the most common though not necessarily the most abundant bat in Puerto Rico (Joglar 2005). The species feeds on a variety of fruits and occupies caves or the lower surfaces of palms or dense foliage during the day. *Brachyphylla cavernarum* (cave bat) has similar habits, and may displace the fruit bat when foraging in the same tree. *Eptesicus fuscus* (big brown bat) is common, nocturnal, and insectivorous, foraging in openings in vegetation. It spends days in caves, and has been recorded underneath concrete structures used to channel streams. *Erophylla sezekorni* (brown flower bat) is completely nocturnal and principally frugivorous, but also consumes some insects. During the day it occupies warm caves. *Lasiurus borealis* (red bat) is insectivorous, hiding during the day in the foliage of trees. It has been encountered in coastal, urban, and very humid areas, and is difficult to capture. *Molossus molossus* (velvety free-tailed bat) is common throughout the island and often hides in houses. It is nocturnal and insectivorous, frequently feeding on beetles and moths.

Monophyllus redmanii (Greater Antillean long-tongued bat), native exclusively to the Greater Antilles, is widespread in Puerto Rico. It is nocturnal, nectivorous, and spends the day in caves. *Mormoops blainvillii* (Blainville's leaf-chinned bat) is nocturnal and insectivorous, foraging principally on moths in the forest understory. *Pteronotus quadridens* (sooty mustached bat) is insectivorous and begins its activity just before sunset. It flies in formation, following the same route each night. *Stenoderma rufum* (red fruit bat) is endemic to the Puerto Rico and offshore islands. Spending the day in trees, it begins activities at sunset, flying short distances to feed on fruits. *Tadarida brasiliensis* (Mexican free-tailed bat) is insectivorous and begins foraging in open areas at sunset. During the day, it occupies crevices in rocks or caves in dense groups.

Introduced mammals include two species of rats, one mouse, the ubiquitous *Herpestes auropunctatus* (Indian mongoose) (table 14), and an occasional feral cat. Rats have been implicated in the loss of Puerto Rican parrot eggs (Snyder and others 1987). The mongoose, introduced between 1877 and

1879 to control rats in sugar cane fields, is now Puerto Rico's most detrimental predator on ground-nesting birds and lizards (Raffaele 1983). Mongooses also consume frogs, blind snakes, and several species of invertebrates, including ants (Danforth 1926, Wolcott 1953) but apparently do not prey on parrots (Snyder and others 1987).

Birds

The LEF avifauna list includes 26 families and 107 species of which 61 are resident in Puerto Rico (54 native and 7 introduced that also reside on the island), and 46 are migratory or transient (table 15). The Parulidae with 27 species, only two of which are migrants, is the best represented family. Columbidae with nine species, Falconidae with six, and Trochilidae, Vireonidae, and Icteridae each with five species, are also well represented. Five families have only a single species recorded in the LEF.

Many species have been reported during the Fajardo Christmas count, which has been carried out as part of the National Audubon Society's Christmas bird count since 1994. The Society of Puerto Rican Ornithologists, the Puerto Rican Natural History Society, the Puerto Rican Conservation Trust, and the International Institute of Tropical Forestry are co-sponsors of the event. Several additional species were recorded during monthly point counts and incidental observations by Forest Service wildlife biologists (Wayne Arendt, see endnotes). Of the total, 25 species are common, 34 uncommon, and 48 are rare. In addition, 13 species and 2 subspecies are Puerto Rican endemics. *Corvus leucognathus*, previously reported within the LEF, is locally extirpated (Raffaele 1983). It survives, however, on other Caribbean islands.

The story of three species—*Amazona vittata*, *Margarops fuscatus*, and *Dendroica angelae*—presents interesting contrasts with regard to their discovery and adaptation to human settlement. During the time of the Tainos, hunting parrots was an occupation for youngsters (Alegría 1972). In 1493, the parrot occupied most of Puerto Rico, including the offshore islands of Vieques and Culebra. The species was most likely one of the first to be seen and heard by early explorers. Human disturbance—deforestation and habitat destruction—during the mid-to-late 19th century reduced the population considerably (Snyder and others 1987, Wunderle and others 2003). By 1900, parrots lived in only two areas on the island, and by the 1930s, only in the Luquillo Mountains (Danforth 1936; Gerhart 1936, see endnotes). In 1936, the

Table 14—Vertebrate animal species except birds with environmental and status information for the Luquillo Experimental Forest^a

Group and species	English names ^b	Status classification ^d				
		Origin ^c	USFS	Federal	Nat. Her.	PR
Mammals—native bats (11) and exotic species (5)						
<i>Artibeus jamaicensis</i>	Fruit bat	NA				
<i>Brachyphylla cavernarum</i>	Cave bat	NA				
<i>Eptesicus fuscus</i>	Big brown bat	NA				
<i>Erophylla sezekorni</i>	Brown flower bat	NA				
<i>Lasiurus borealis</i>	Red bat	NA				
<i>Molossus molossus</i>	Velvety free-tailed bat	NA				
<i>Monophyllus redmanii</i>	Greater Antillean long-tongued bat	NA				
<i>Mormoops blainvillii</i>	Blainvillee’s leaf-chinned bat	NA				
<i>Pteronotus quadridens</i>	Sooty moustached bat	NA				
<i>Stenoderma rufum</i>	Red fruit bat	NA	S		G3,L4	
<i>Tadarida brasiliensis</i>	Mexican free-tailed bat	NA				
<i>Felis catis</i>	Feral cat	EX				
<i>Herpestes auropunctatus</i>	Indian mongoose	EX				
<i>Mus musculus</i>	House mouse	EX				
<i>Rattus norvegicus</i>	House rat	EX				
<i>Rattus rattus</i>	Roof rat	EX				
Reptiles—native lizards and geckos (13) and exotic species (1)						
<i>Ameiva exsul</i>	Puerto Rican ground lizard	EN				
<i>Amphisbaena caeca</i>	Puerto Rican worm lizard	EN				
<i>Anolis cristatellus</i>	Puerto Rican crested anole	NA				
<i>Anolis cuvieri</i>	Cuvier’s (Green giant) anole	NA				
<i>Anolis evermanni</i>	Everman’s (Emerald) anole	NA				
<i>Anolis gundlachi</i>	Yellow-bearded anole	NA	M			
<i>Anolis krugi</i>	Krug’s (Olive bush) anole	NA				
<i>Anolis occultus</i>	Pygmy (Twig) anole	EN				
<i>Anolis pulchellus</i>	Grass anole	NA				
<i>Anolis stratulus</i>	Spotted anole	NA				
<i>Diploglossus pleei</i>	Puerto Rican Galliwasp	EN				
<i>Hemidactylus brooki</i>	Brook’s gecko	EX				
<i>Sphaerodactylus klauberi</i>	Klauber’s least gecko	NA				
<i>Sphaerodactylus macrolepis</i>	Big scale dwarf gecko	NA				
Reptiles—native snakes (5)						
<i>Alsophis portoricensis</i>	Puerto Rican (P.R.) racer	EN				
<i>Arrhyton exiguum</i>	P.R. garden snake	EN				
<i>Epicrates inornatus</i>	P.R. boa	EN	E	E	G1,G2,N3	E
<i>Typhlops richardii</i>	Richard’s worm snake	NA				
<i>Typhlops rostellatus</i>	P.R. wetland blind snake	EN				

(table continued on following page)

Table 14 (continued) —Vertebrate animal species except birds with environmental and status information for the Luquillo Experimental Forest^a

Group and species	English names ^b	Status classification ^d				
		Origin ^c	USFS	Federal	Nat. Her.	PR
Amphibians—native frogs (14) and exotic species (1)						
<i>Bufo marinus</i>	Marine toad	EX				
<i>Eleutherodactylus antillensis</i>	Red-eyed coqui	NA				
<i>Eleutherodactylus brittoni</i>	Grass coqui	EN				
<i>Eleutherodactylus cochranae</i>	Whistling coqui	NA				
<i>Eleutherodactylus coqui</i>	Common coqui	EN				
<i>Eleutherodactylus eneidae</i>	Mottled coqui	EN	S		G2,G3,N3	T
<i>Eleutherodactylus gryllus</i>	Green (cricket) coqui	EN				
<i>Eleutherodactylus hedricki</i>	Tree-hole coqui	EN	M			
<i>Eleutherodactylus karlschmidti</i>	Web-footed coqui	EN	S		G1,N1	T
<i>Eleutherodactylus locustus</i>	Warty coqui	EN	M,S		G2,N?	
<i>Eleutherodactylus portoricensis</i>	Upland coqui	EN				
<i>Eleutherodactylus richmondi</i>	Bronze (Ground) coqui	EN	S		G3,N?	
<i>Eleutherodactylus unicolor</i>	Elfin (Burrow) coqui	EN	M,S		G1,G2,N?	
<i>Eleutherodactylus wightmanii</i>	Melodius coqui	EN				
<i>Leptodactylus albilabris</i>	White-lipped frog	NA				
Fish—native fishes (6) and exotic species (3)						
<i>Agonostomus monticola</i>	Mountain mullet	NA	M			
<i>Anguilla rostrata</i>	American eel	NA				
<i>Awaous tajasica</i>	Sand fish, River goby	NA				
<i>Carpinus carpio</i> ^e	Koi (carp)	EX				
<i>Eleotris pisonis</i>	Spinycheek sleeper	NA				
<i>Gobiomorus dormitor</i>	Bigmouth sleeper	NA				
<i>Oncorhynchus mykiss</i> ^e	Rainbow trout	EX				
<i>Poecilia reticulata</i> ^e	Guppy	EX				
<i>Sicydium plumieri</i>	Rock sucker (goby)	NA	M			

^aSources: Brown and others (1983); Gannon and others (2005); Nieves (1998); U.S. Department of Agriculture, Forest Service (1997b); Weaver (1994); Willig and Bauman (1984).

^bBat common names (Joglar 2005).

^cOrigin: EN = endemic; EX = exotic; NA = native.

^dStatus classification: EN = endemic; Nat. Her. = Natural Heritage classification system: G = global, N = national, L = taxa formerly listed, 1 = critically imperiled, 2 = imperiled, 3 = vulnerable, 4 = apparently secure, 5 = widespread and secure, ? = species not ranked; USFS = Forest Service; PR = Puerto Rico; E = endangered; M = management indicator species; S = sensitive; T = threatened.

^eIntroduced species: Koi survived in a shallow, excavated area along Pico del Este road for several years; rainbow trout eggs were introduced during the mid-1930s but adults failed to reproduce; and, guppies are found in many of the LEF streams.

Table 15—Bird species with environmental and status information for the Luquillo Experimental Forest^a

Scientific name	Common name	Type ^b	Occur ^c	Forest ^d	Site ^e	Status classification ^f				
						Endemic	USFS	Fed.	Nat. Her.	PR
ARDEIDAE										
<i>Bubulcus ibis</i>	Cattle egret	R	R	T	E					
<i>Butorides striatus</i>	Green-backed heron	T	R	T-C	R					
<i>Egretta caerulea</i>	Little blue heron	R	R	T	R					
<i>Egretta thula</i>	Snowy egret	R	R	T	R					
<i>Nycticorax violaceus</i>	Yellow-crowned heron	R	U	T	R					
SCOLOPACIDAE										
<i>Actitis macularia</i>	Spotted sandpiper	T	U	T-C-P	R					
FALCONIDAE										
<i>Accipiter striatus</i>	Sharp-shinned hawk	R	U/R	T-C		ENSS	E,M	E	G5,N2	E
<i>Buteo jamaicensis</i>	Red-tailed hawk	R	C	T-C-P-D						
<i>Buteo platypterus</i>	Broad-winged hawk	R	C	T-C		ENSS	E,M	E	G5,N2	E
<i>Falco columbarius</i>	Merlin	T	U	T-C-P						
<i>Falco peregrinus</i>	Peregrine falcon	T	U/R	T-C-P			T	T	G2,NN	T
<i>Falco sparverius</i>	American Kestrel	R	U	T-C-PL	E					
COLUMBIDAE										
<i>Columba leucocephala</i>	White-crowned pigeon	R	R	T-C						
<i>Columba livia</i>	Rock pigeon	R-I	U	T-PL	E					
<i>Columba squamosa</i>	Scaly-naped pigeon	R	C	T-C-P-D-PL	E					
<i>Columbina passerina</i>	Common ground-dove	R	U	T-PL	E					
<i>Geotrygon montana</i>	Ruddy Quail-dove	R	C	T-C-P-PL						
<i>Patagioenas inornata</i>	Plain pigeon	R	R	T-C-P-PL	E					
<i>Zenaida asiatica</i>	White-winged dove	R	U	T-C-PL	E					
<i>Zenaida aurita</i>	Zenaida dove	R	C	PL	E					
<i>Zenaida macroura</i>	Mourning dove	R	R	T-PL	E					
PSITTACIDAE										
<i>Amazona vittata</i>	Puerto Rican parrot	R	R	T-C-P		EN	E,M	E	G1,N1	E
<i>Aratinga canicularis</i>	Orange-fronted parakeet	R-I	U	PL	E					
<i>Brotogeris versicolurus</i>	White-winged parakeet	R-I	U/R	PL	E					
<i>Myiopsitta monachus</i>	Monk parrot	R-I	R	T-PL	E					
CUCULIDAE										
<i>Coccozygus americanus</i>	Yellow-billed cuckoo	T	R	T-C-PL	E					
<i>Coccyzus minor</i>	Mangrove cuckoo	R	U	T-PL	E					
<i>Crotophaga ani</i>	Smooth-billed ani	R	U/R	T-PL	E					
<i>Saurothera vieilloti</i>	Puerto Rican lizard-cuckoo	R	C	T-C-P-D-PL	E	EN				
STRIGIDAE										
<i>Megascops nudipes</i>	Puerto Rican screech-owl	R	C	T-C-P-D-PL		EN				
<i>Tyto alba</i>	Barn Owl	R	R	T-PL	E					
CAPRIMULGIDAE										
<i>Caprimulgus carolinensis</i>	Chuck-will's widow	T	R	T-C-P						
<i>Chordeiles gundlachi</i>	Antillean nighthawk	R	R	T-PL	E					
APODIDAE										
<i>Cypseloides niger</i>	Black swift	R	C/U	T-C-P-D						
TROCHILIDAE										
<i>Anthracothonax dominicus</i>	Antillean mango	R	U/R	PL-T-C	E					
<i>Anthracothonax viridis</i>	Green mango	R	U/R	T-C-P-D	E	EN				

(table continued on following page)

Table 15 (continued)—Bird species with environmental and status information for the Luquillo Experimental Forest^a

Scientific name	Common name	Type ^b	Occur ^c	Forest ^d	Site ^e	Status classification ^f				
						Endemic	USFS	Fed.	Nat. Her.	PR
<i>Chlorostibon maugaeus</i>	Puerto Rican emerald	R	C	T-C-P-D-PL	E	EN				
<i>Eulampis holosericeus</i>	Green-throated Carib	R	R	T-PL	E					
<i>Orthorhyncus maugaeus</i>	Antillean crested hummingbird	R	R	T-PL	E					
TODIDAE										
<i>Todus mexicanus</i>	Puerto Rican tody	R	C	T-C-P-D-PL	E-R	EN				
ALCEDINIDAE										
<i>Ceryle alcyon</i>	Belted kingfisher	T	R	T	R					
PICIDAE										
<i>Melanerpes portoricensis</i>	Puerto Rican woodpecker	R	C	T-C-P-D-PL	E-R	EN				
<i>Sphyrapicus varius</i>	Yellow-bellied sapsucker	T	R	T-C-P-D-PL						
TYRANNIDAE										
<i>Elaenia martinica</i>	Caribbean elaenia	R	R	T-PL						
<i>Myiarchus antillarum</i>	Puerto Rican flycatcher	R	U	T-C-PL	E	EN				
<i>Tyrannus caudifasciatus</i>	Loggerhead kingbird	R	U	T-C-PL	E					
<i>Tyrannus dominicensis</i>	Gray kingbird	R	C	T-C-P-D-PL	E-R					
VIREONIDAE										
<i>Vireo altiloquus</i>	Black-whiskered vireo	R	C	T-C-P-D-PL	E-R					
<i>Vireo flavifrons</i>	Yellow-throated vireo	T	R	T-C-PL	E					
<i>Vireo griseus</i>	White-eyed vireo	T	R	T-PL	E					
<i>Vireo latimeri</i>	Puerto Rican vireo	R	R	T-C		EN				
<i>Vireo olivaceus</i>	Red-eyed vireo	T	R	T-PL	E					
HIRUNDINIDAE										
<i>Hirundo rustica</i>	Barn swallow	T	U/R	T-C-P-D-PL	E-R					
<i>Petrochelidon fulva</i>	Cave swallow	R	U/R	PL	E					
<i>Progne diminicensis</i>	Caribbean martin	R	R	T-C-P-D-PL	E-R					
TURDIDAE										
<i>Catharus bicknelli</i>	Bicknell's thrush	T	R	PL	E					
<i>Catharus ustulatus</i>	Swainson's thrush	T	R	T-C-PL						
<i>Hylocichia mustelina</i>	Wood thrush	T	R	T-PL	E					
<i>Turdus plumbeus</i>	Red-legged thrush	R	C	T-C-PL	E					
MIMIDAE										
<i>Dumetella carolinensis</i>	Gray catbird	T	R	T-C-PL	E					
<i>Margarops fuscatus</i>	Pearly-eyed thrasher	R	C	T-C-P-D-PL	E-R					
<i>Mimus ployglottos</i>	Northern mockingbird	R	U/R	T-PL	E					
BOMBYCILLIDAE										
<i>Bombycilla cedrorum</i>	Cedar waxwing	T	R	T-C-PL						
PARULIDAE										
<i>Coereba flaveola</i>	Bananaquit	R	C	T-C-P-D-PL	E-R					
<i>Dendroica angelae</i>	Elfin-woods warbler	R	U	C-P-D		EN	M,S		G1,G2,N?	E
<i>Dendroica caerulescens</i>	Black-throated blue warbler	T	C	T-C-P-D-PL			M			
<i>Dendroica castanea</i>	Bay-breasted warbler	T	R	T-PL	E					
<i>Dendroica coronata</i>	Yellow-rumped warbler	T	R	T-PL	E					
<i>Dendroica discolor</i>	Prairie warbler	T	U	T-C-PL	E					
<i>Dendroica fusca</i>	Blackburnia warbler	T	R	T-PL						
<i>Dendroica magnolia</i>	Magnolia warbler	T	U/R	T-C-PL	E					
<i>Dendroica pensylvanica</i>	Chestnut-sided warbler	T	R	T-C-PL	E					

(table continued on following page)

Table 15 (continued)—Bird species with environmental and status information for the Luquillo Experimental Forest^a

Scientific name	Common name	Type ^b	Occur ^c	Forest ^d	Site ^e	Status classification ^f				
						Endemic	USFS	Fed.	Nat. Her.	PR
<i>Dendroica petechia</i>	Yellow warbler	T	R	D						
<i>Dendroica pinus</i>	Pine warbler	T	R	C-P						
<i>Dendroica striata</i>	Blackpoll warbler	T	U	T-C-P-D-PL	E-R					
<i>Dendroica tigrina</i>	Cape May warbler	T	U/R	T-C-PL	E					
<i>Dendroica virens</i>	Black-throated green warbler	T	R	C						
<i>Geothlypis trichas</i>	Common Yellowthroat	T	R	T-PL	E					
<i>Helmitheros vermivorus</i>	Worm-eating warbler	T	R	T-C-P						
<i>Mniotilta varia</i>	Black-and-white warbler	T	U	T-C-P-D-PL	E-R					
<i>Oporornis formosus</i>	Kentucky warbler	T	R	T-C-D-PL	E					
<i>Parula americana</i>	Northern parula	T	C	T-C-P-D-PL	E-R					
<i>Seiurus aurocapillus</i>	Ovenbird	T	U	T-C-P-D-PL	E-R					
<i>Seiurus motacilla</i>	Louisiana waterthrush	T	U	T-C-P-PL	E-R					
<i>Seiurus noveboracensis</i>	Northern waterthrush	T	U	T-C-P	R					
<i>Setophaga ruticilla</i>	American redstart	T	C	T-C-P-D-PL	E-R					
<i>Vermivora chrysotera</i>	Golden-winged warbler	T	U	T-C-P						
<i>Vermivora peregrina</i>	Tennessee warbler	T	R	T-C-PL						
<i>Vermivora pinus</i>	Blue-winged warbler	T	R	T-C-PL	E					
<i>Wilsonia citrina</i>	Hooded warbler	T	R	T-C-PL	E					
THRAUPIDAE										
<i>Nesospingis speculiferus</i>	Puerto Rican tanager	R	C	T-C-P-D-PL	E-R	EN				
<i>Spindalis zena portoricensis</i>	Stripe-headed tanager	R	C	T-C-P-D-PL	E-R	EN				
EMBERIZIDAE										
<i>Tiaris bicolor</i>	Black-faced grassquit	R	C	PL	E					
<i>Tiaris olivaceus</i>	Yellow-faced grassquit	R	U	PL	E					
<i>Loxigilla portoricensis</i>	Puerto Rican bullfinch	R	C	T-C-P-D-PL	E-R	EN				
CARDINALIDAE										
<i>Passerina ciris</i>	Painted bunting	T	R	C						
<i>Passerina cyanea</i>	Indigo bunting	T	U/R	T-PL	E					
<i>Pheucticus ludovicianus</i>	Rose-breasted grosbeak	T	R	PL						
ICTERIDAE										
<i>Icterus dominicensis</i>	Black-cowled oriole	R	C/U	T-C-PL	E					
<i>Icterus galbula</i>	Baltimore oriole	T	R	PL	E					
<i>Icterus icterus</i>	Troupial	R	R	PL	E					
<i>Molothris bonariensis</i>	Shiny cowbird	R	U	T-C-PL	E					
<i>Quiscalus niger</i>	Greater Antillean grackle	R	R	PL	E					
FRINGILLIDAE										
<i>Euphonia musica</i>	Antillean euphonia	R	C/U	T-C-P-D-PL	E-R					
ESTRILIDAE										
<i>Estrilda melopoda</i>	Orange-cheeked waxbill	R-I	R	PL	E					
<i>Lonchura cucullata</i>	Bronze mannikin	R-I	U	PL	E					
<i>Lonchura punctulata</i>	Nutmeg mannikin	R-I	U	PL	E					

^aSources: Kepler and Kepler (1970); Recher and Recher (1966); Snyder and others (1987); U.S. Department of Agriculture, Forest Service (1997b); Wiley and Bauer (1985); monthly point counts and incidental observations (Wayne Arendt, see endnotes). White-necked crow (*Corvus leucognaphalus*) was last seen in the LEF in 1963.

^bType (in Puerto Rico): I = introduced (or exotic); R = resident; T = transient (or migratory).

^cOccurrence (in LEF): C = common; U = uncommon; R = rare.

^dForest preference: T = Lower montane rain forest; C = Montane rain forest; P = Palm brake; D = Dwarf forest; PL = plantation.

^eSite preference: E = forest edge at interface with pastures, cropland, or fallow; R = stream edge.

^fStatus classification: EN = endemic species; ENSS = endemic subspecies; USFS = Forest Service; Fed. = Federal; Nat. Her. = Natural Heritage classification system: G = global, N = national, 1 = critically imperiled, 2 = imperiled, 3 = vulnerable, 4 = apparently secure, 5 = widespread and secure, ? = species not ranked; PR = Puerto Rico; E = endangered; M = management indicator species; S = sensitive; T = threatened.



Amazona vittata (Puerto Rican parrot), once common throughout much of Puerto Rico, is currently classified as rare and endangered. (Photo by Gerald P. Bauer)

LEF was recommended as a bird sanctuary. At the same time, however, the mountains were being dissected by a major highway, which opened the area to the public, including hunters and pet seekers. With the decline in population, the parrots became more vulnerable to numerous competitors, predators, and parasites. Between 1953 and 1956, tallies made within the LEF estimated the population at 200 birds (Rodríguez Vidal 1959, 1962). At this time, the parrot was concentrated in three river valleys—Río Espíritu Santo, Río Hicaco, and Río de la Mina, where it consumed the fruits of at least 54 species of trees and vines. During the 1960s, about 50 individuals were estimated and by the early 1970s, a complete count revealed only 13 birds (Recher and Recher 1966, Snyder and others 1987).

In 1968, the parrot was designated as an endangered species—one of the 10 most endangered in the world—and in 1972 an aviary was established in the La Mina barracks on FS 10 (Snyder and others 1987) (fig. 20) (table 3). After a successful effort to increase the captive and wild populations to about 100 birds, Hurricane Hugo eliminated about one-half of the wild population (i.e., about one-quarter of the entire population) (U.S. Department of Agriculture, Forest Service 1997b). By the time that Hurricane Georges passed over the forest, several birds had been moved to the Río Abajo aviary within the commonwealth forest reserve system south of Arecibo. Four factors appear responsible for maintaining the bottleneck in the recovery of the parrot (Beissinger and others 2008): reduced hatching success due to inbreeding; failure of adults to nest; nest failure; and reduced survival of adults and

juveniles. Today, many parrot eggs are hatched and fledged in captivity both at Río Abajo aviary and the new “La Iguaca” aviary built on the lower, northern slopes of El Yunque in 2007. Birds are then conditioned for the wild and released. Three recent releases totaling 34 birds were carried out between 2000 and 2002 (White and others 2005). Slightly less than one-half of the released birds survived in the wild, with one-fifth being lost to raptors. Today’s parrot population of nearly 250 birds is found either in captivity or in the wild.

The pearly-eyed thrasher was relatively scarce and only patchily distributed in the lowlands and hills of Puerto Rico until the 1920s when biologists noted a steady increase in its numbers (Arendt 2006). The spread continued to 600 m in the LEF by 1930 and throughout the forest by the early 1950s (Snyder and others 1987). The thrasher has superior colonizing capabilities and traits characteristic of avian “tramps” (Arendt 2006). It is a strong flier, disperses well, and occupies all available habitats within Puerto Rico and other Caribbean islands. It is omnivorous, shows variability in diet and foraging, and has several reproductive strategies that facilitate its survival and expansion. Moreover, the thrasher is resilient to major disturbances such as hurricanes and droughts.

The thrasher, a most remarkable natural enemy of the parrot, nests in tree cavities (Snyder and others 1987). It also frequently enters parrot nests where it destroys eggs, attacks nestlings, and may take control of the nest site. The gradual increase of thrashers at higher elevations within the forest resulted in encounters with the parrot, especially during



Parrot aviaries. LEFT: La Mina barracks served as the U.S. Department of Agriculture Forest Service's first parrot aviary from 1972 until after 2000. RIGHT: The new Iguaca aviary opened in 2007 on PR route 9966 along the northern forest border. (Photos by Peter L. Weaver)

their coincident breeding seasons. The thrasher, along with predators such as *Buteo jamaicensis* (red-tailed hawk) and rats, and parasites and site competitors like warble flies and honey bees, caused a decline in the parrot population to record lows during the mid-1970s.

In 1971, long after the island's native bird species had been identified and described, the elfin-woods warbler was discovered in the dwarf forest and upper reaches of the montane forest in the LEF (Kepler and Parkes 1972). Interestingly, the species had been noted a short time earlier by another birder working at Roosevelt Roads. Similar to *Mniotilta varia* (black-and-white warbler), the elfin-woods warbler required specimens to assure its identification as a new species (Kepler 2009). The late discovery of the warbler decades after the identification of all other species in Puerto Rico is due in part to its limited habitat and distribution (Raffaele 1983). Later, other populations were found in the Central Mountains. Today the species is protected throughout the island.

Reptiles

Of the 19 species of reptiles found in the LEF, 14 are lizards or geckos, and 5 are snakes (table 14). Some are restricted to particular forest types or habitats whereas others have more ample foraging sites or ranges. Nearly a century ago, the diets of 11 species (i.e., an iguana, a skink, two geckos, and seven lizards), were investigated from the standpoint of agricultural economics (Wolcott 1924). Stomach contents revealed a variety of insects but no mosquitoes or house flies. The samples were based on observations made outside of the national forest.

Ameiva exsul (Puerto Rican ground lizard) is found in open areas, including roads and trails, at low elevations near the border. *Anolis cristatellus* (Puerto Rican crested anole) and *Anolis gundlachi* (yellow-bearded anole) forage on trunks and on the ground (Joglar 2005, Rivero 1978). *Anolis cuvieri* (giant green anole), the largest species in Puerto Rico, seems to prefer canopies in shady, cool areas at intermediate elevations. *Anolis evermanni* (Everman's anole) and *Anolis stratulus* (spotted anole) forage in canopies and trunks. Both *Anolis krugi* (Krug's anole) and the *Anolis pulchellus* (grass anole) frequent grassy areas, herbaceous growth, and bushes, whereas the small *Anolis occultus* (pygmy anole) forages on twigs and branches. *Amphisbaena caeca* (worm lizard) hides under vegetative debris, logs, rocks, and in roots, consuming coleopteran larvae (Reagan and Waide 1996). *Hemidactylus brooki* (Brook's gecko), widespread in the tropics, lives in leaf litter and among tree roots and buttresses where it eats spiders, cockroaches, and other insects.

Diploglossus pleei (Puerto Rican Galliwasp), the only species of its genus in Puerto Rico, hides under rocks, logs, and decaying ground vegetation where it may consume various invertebrates, including insects, and even frogs (Joglar 2005, Rivero 1978) (table 14). *Sphaerodactylus klauberi* (Klauber's least gecko) has been found above 900 m in elevation and *S. macrolepis* (big scale dwarf gecko), the most widespread of its genus, to 880 m.

Five nonpoisonous species of snakes are found in the LEF. They range from the island's shorelines to midelevations in the mountains. *Alsophis portoricensis* (Puerto Rican racer) is widely distributed, diurnal, and terrestrial, although sometimes found in trees. *Arrhyton exiguum* (Puerto Rican garden snake), the most common throughout the island, is terrestrial and somewhat secretive, typically being found

BELOW: Lizard. *Anolis evermanni* (Emerald anole), one of eight native anoles, frequents the deep, wet forests of the Luquillo Experimental Forest and humid mountainous sites elsewhere on the island. RIGHT: Snake. *Epicrates inornatus* (Puerto Rican boa constrictor), which feeds on small mammals, birds, and lizards, is the island's largest snake. The endemic boa, reaching 2.5 m in length, remains listed as an endangered species largely because of past habitat destruction. (Photos by Iván Vicéns)



under logs and tree stumps (Joglar 2005, Rivero 1978). Both consume lizards, frogs, and frog eggs. *Epicrates inornatus*, the largest species, is found on the ground or in trees where it feeds on rats, mice, birds, and sometimes bats (Rivero 1978). It is apparently less common in the LEF than other locations such as the limestone hills. *Typhlops richardii* (Richard's worm snake) and *Typhlops rostellatus* (Puerto Rican wetland blind snake) are both blind and subterranean in habit. They typically feed on termites, ants, and other invertebrates.

Amphibians

The LEF has 15 species of amphibians. All but two species of tree frogs (*Eleutherodactylus* spp., locally called coquis) are endemic to Puerto Rico and feed on a large variety of insects and snails found in the forest (table 14). Natural predators include spiders, notably on young individuals, as well as lizards, snakes, birds, rats, and mongooses.

The *Eleutherodactylus antillensis* (red-eyed coqui), widely distributed in open areas and along forest borders, occurs most frequently at low to intermediate elevations (Joglar 1998, Rivero 1978). The species typically hides below rocks, herbaceous roots, trunks, and loose bark. *E. brittoni* (grass

coqui) is most frequently found at low elevations in fields and pastures exposed to the sun, but it also may be found in herbaceous growth along roads and forest borders.

E. cochranae (whistling coqui), with distribution in both dry and wet sites on the island, occupies low elevations in the LEF where it frequents vegetation near the ground, including bushes, trees, and bromeliads. The species waits for prey and feeds mainly on arthropods and a variety of insects. The *E. coqui* (common coqui), living from the coast to mountain summits, is the best known and the best studied of the island's amphibians. During the day, it hides under fallen leaves, in bromeliads, and in the axils of palm leaves at intermediate to high elevations, and within pastures at low elevations near the LEF border.

E. eneidae (mottled coqui) occupies humid forests at elevations between 300 and the summits, where it prefers slopes along trails and moss-covered trunks near the ground (Joglar 1998). *E. gryllus* (green coqui) also occupies similar elevations. At lower elevations, it prefers open areas and forest borders whereas at higher elevations it is found in bromeliads and under moss on rocks. *E. hedricki* (tree-hole coqui) is arboreal and occupies dense, wet forests between 450 m and the summits. Diurnal refuges include cavities in trees up to 18 m in height. *E. karlschmidtii* (web-footed coqui) is found



Frog. *Eleutherodactylus coqui* (Coqui frog) is 1 of 13 native frogs in the genus, 12 of which are also island endemics that live within the Luquillo Experimental Forest. The widespread coqui is the island's best known and cherished amphibian. (Photo by Iván Vicéns)

at elevations between 50 and 650 m in rocks along streams, and near waterfalls and rocks splashed with water. Recent exhaustive searches for both the mottled coqui and the web-footed coqui have been unsuccessful and they are presumed to be extinct.

E. locustus (warty coqui) is found in wet, mountainous forest above 370 m, including dwarf forest, where it appears to be more abundant along forest borders and in open areas (Joglar 1998). *E. portoricensis* (upland coqui) is found at elevations from 180 m to the summits where it occupies bushes, palms, bromeliads, but appears to prefer the soil surface and litter. Recent data suggest that both of these species are less abundant than formerly (Joglar 1998). *E. richmondi* (bronze coqui) is found in the interior of the island at elevations from 40 m to near the summits. However, it appears to have declined at elevations above 600 m in the LEF since the early 1980s. *E. unicolor* (elfin coqui) is endemic to peaks above 675 m in the LEF, where it lives in subterranean cavities under surface roots, and in mosses growing on the ground. *E. wightmanii* (melodious coqui) is also found in the interior of Puerto Rico from 150 m to the summits. It dwells principally on or very near to the ground.

The remaining amphibians are in other genera (Rivero 1978) (table 14). The native *Leptodactylus albilabris* (white-lipped frog) is terrestrial but is seldom found away from streams or marshy areas. It passes through a tadpole stage and often calls from muddy areas. *Bufo marinus* (marine toad) was imported from Jamaica and Barbados during the 1920s to control grubs on sugar cane. A few years later, it was abundant.

The apparent extinctions of *E. eneidae* and *E. karlschmidti* in the LEF, and *E. jasperii* (golden coqui) from the Central

Mountains near Cayey (Joglar 1998) suggest island-wide problems among certain amphibian populations. This trend is substantiated by the apparent decline of other species like the *E. locustus*, *E. portoricensis*, and *E. gryllus* in the LEF (Woolbright 1997). Whether these population declines are related to normal fluctuations or migrations is uncertain. The LEF remained largely undisturbed by hurricanes from 1932 until 1989. Recent hurricanes, however, may have caused temporary changes in the understory, reducing some populations or causing migrations to other sites. More serious possibilities involve the amphibian chytridiomycosis fungus which has devastated frog populations worldwide (Daszak and others 2003).

Fish

Six native fish species were recorded in the headwaters of the Río Espíritu Santo and Río Mameyes, including the Bisley watersheds (Nieves 1998) (table 14). Three are found in the upper portions of streams—*Agonostomus monticola* (mountain mullet), *Anguilla rostrata* (American eel), and *Sicydium plumieri* (rock sucker) and the others, *Awaous tajasica* (sand fish), *Eleotris pisonis* (spinycheek sleeper) and *Gobiomorus dormitor* (bigmouth sleeper) are found below. None of the six is endemic or endangered. All feed on shrimp except the rock sucker, which is herbivorous. In addition, at least three introduced species have reached the LEF at one time or another—the common *Poecilia reticulata* (guppy), *Oncorhynchus mykiss* (rainbow trout), and a few *Carpinus carpio* (koi or carp). Rainbow trout eggs were introduced into the La Mina area nursery in 1934 and 1935 in an attempt to provide sport fishing. The effort was unsuccessful because the streams were too warm for reproduction (Gerhart 1936, see endnotes). During the 1990s, koi were placed into a shallow, 75 m² depression scraped out of impermeable soil along FS-27. Rainfall, cloud moisture deposition, and possibly runoff from the road provide enough water for the koi to survive.

With regard to migrations, the American eel is catadromous (i.e., adults live in fresh water and migrate to the sea to spawn) whereas the remaining native species are amphidromous (i.e., adults spawn in upland streams, larvae are carried downstream to sea during rainfalls, and juveniles return upstream). The headwaters of LEF streams serve as refugia from predators, sites where the fish grow, mature, and reproduce. The mountain mullet, the most important game fish found in fast flowing upland streams in Puerto Rico, is also adapted to sluggish waters (Erdman 1972, Hildebrand 1935). The rock sucker has the capacity to climb waterfalls and obstructions such as low level dams and was recorded at elevations of 650 m in the Mameyes watershed (Nieves 1998). The species is considered as a biological indicator of the ecological health of streams (Erdman 1984).

Chapter 8. SPECIES DIVERSITY—PLANTS AND ANIMALS

Plant Diversity

The LEF has a diverse plant life. Native trees number 225 (Little and Wadsworth 1964; Little and Woodbury 1976, 1980; Little and others 1974), orchids at least 79 (Ackerman 1992, 1995; Kasomenakis 1988), and ferns about 150 (Kepler 1975). The number of trees exceeds that found on all other national forests combined (U.S. Department of Agriculture, Forest Service 1997b). In addition, 120 of the 144 tree species planted in the LEF were introduced species (i.e., 112 were exotics and 8 were natives to Puerto Rico that grow outside of the forest). Only 24 of the planted species were forest natives (appendix E). Although most of these introductions were made for forestry purposes, some species were planted for agriculture or as ornamentals.

The relative abundances of tree species within the LEF vary in time and space. In 1500, before settlement, the forest contained native tree species in abundances controlled by life cycles, environmental variables, and climatic events. During the 19th and 20th centuries, agriculture and tree plantings on the lower slopes along with the construction of roads, trails, and facilities at higher elevations, introduced exotics and secondary species. The long post-hurricane recovery period after San Felipe and San Cipriano showed a gradual decline in secondary tree species on permanent plots (Crow 1980, Weaver 1983, 1989b), a trend that was reversed after hurricanes Hugo and Georges (Weaver 2002b).

Although the total number of tree species recorded by forest type decreases with ascent in the LEF (table 8), gradient sampling showed a greater number of species at elevations in montane forest rather than lower montane forest (fig. 18) (table 8) (appendix tables 9A through 9D). This is due partially to the forest classification system and partially to the sampling procedure. First, forest types are broadly defined by elevation. Species distribution in mountainous terrain, however, is also influenced by aspect and topography (Weaver 1991, 2010a, 2010b). The greatest current abundance of species occurs in highly dissected terrain in the ecotone between the lower montane and montane forest types (fig. 17). Second, more plots were sampled in the montane forest and dwarf forest types than in lower montane forest or palm brake (appendix C). Greater numbers of plots produce larger tree samples

and a greater likelihood of encountering new species. Third, plot size was limited 500 m² in order to sample on topographic features. This plot size may have been inadequate to encompass representative samples of the larger stems characteristic of lower montane forest. In addition, past human activities precluded sampling undisturbed native forest at lower elevations near the forest border (i.e., near the ecotone between the lowland coastal and lower montane forests). Species richness was most likely greatest in this area before logging and settlement. Finally, species richness in palm brake, regardless of elevation, and dwarf forest is limited by environmental conditions.

Animal Diversity

The current vertebrate fauna within the LEF is fairly diverse and includes 157 terrestrial and seven aquatic species (tables 11 and 12): 16 species of mammals; 107 birds, including 61 residents and 46 migrants; 19 reptiles; 15 amphibians; and 7 species of freshwater fishes. In addition to the fish, about 1800 km of rivers and streams in the forest support nine species of freshwater shrimp and one freshwater crab (U.S. Department of Agriculture, Forest Service 1997a, 1997b). The relative abundances of several animal species have varied in time and space as a result of human activities. Most notable are changes involving populations of *Amazona vittata*, *Buteo jamaicensis*, and *Corvus leucognaphallus*.

As with islands elsewhere, the arrival of animals from continental land masses to Puerto Rico was restricted. Bird species richness in the LEF, although fairly high, is less than in Guánica Forest in the dry southwestern part of the island (Kepler and Kepler 1970). A plausible explanation is that insect populations in the forest are controlled by abundant resident populations of lizards and frogs that effectively compete with avian species (table 14). Differences in species richness could also be partially due to past climatic conditions in Puerto Rico. During the Pleistocene, the West Indies were both larger and drier than today (Faaborg and Arendt 1990, 1992). Summaries of recent bird counts in the southwest showed at least 157 bird species in Guánica Forest, substantiating earlier observations (Weaver and Schwagerl 2009).

Chapter 9. CLASSIFIED SPECIES OF PLANTS AND ANIMALS

The Forest Service and commonwealth agencies use several terms to classify the status of plant and animal species (U.S. Department of Agriculture, Forest Service 1997b):

- **Endemic**—the characteristic of being unique to a particular geographic region (i.e., an island, a habitat, a forest, or other defined area).
- **Rare**—a species for which population viability is a concern because it exists at extremely low numbers within a forest or particular habitat.
- **Endangered**—a species that is in danger of extinction throughout or in a significant portion of its range.
- **Threatened**—a species that is likely to become endangered in the foreseeable future throughout or in a significant portion of its range.
- **Sensitive**—a species for which population viability is a concern as indicated by downward trends in population numbers or density, or in habitat availability that would further reduce the distribution of a species.
- **Management indicator species**—species whose population changes may reflect management practices.

Classified Plants

The LEF has 38 classified species of plants, including 24 trees, 2 shrubs, and 12 herbs (1 liana, 1 grass, 1 fern, 2 lycopodia, and 7 others) (table 16). Of these, 30 are endemic to Puerto Rico, and 13 are confined to the Luquillo Mountains alone. The Forest Service lists 8 as endangered, 30 as sensitive, and 11 as management indicator species (U.S. Department of Agriculture, Forest Service 1997a). Both the Federal and Puerto Rican governments also list 8 as endangered, and the Federal Government cites another as threatened and under consideration for listing. The Natural Heritage classification system ranks 30 of the species either as critically imperiled or imperiled either globally or nationally

Classified Animals

The LEF has 32 endemic animal species, including 11 amphibians, 8 reptiles, and 13 birds; moreover, there are two endemic avian subspecies (tables 11 and 12). In addition, 13 species of animals are classified, including 1 mammal (bat), 1 reptile (snake), 5 amphibians (frogs), and 6 birds. The Forest Service lists 5 animals as endangered, 7 as sensitive, 1 as threatened, and 11 as management indicator species (U.S. Department of Agriculture, Forest Service 1997a). Both the Federal and Puerto Rican governments also list 5 as endangered. Moreover, the Federal Government cites one species as threatened and the Puerto Rican government cites three as threatened. The Natural Heritage classification ranks 13 species in various classes. Finally, the Forest Service has classified five as a management indicator species (U.S. Department of Agriculture, Forest Service 1997b).

Table 16—Classified plants within the Luquillo Experimental Forest^a

Scientific name	Life form ^b	Status classification ^c				
		Endemic	USFS	Fed.	Nat. Her.	PR
<i>Brachionidium ciliolatum</i> Garay	H	ENL	S		G1,N1	
<i>Brachionidium sherringii</i> Rolfe	H		S		G1,N1	
<i>Brunfelsia portoricensis</i> Krug & Urban	T	EN	S		G1,N2	
<i>Callicarpa ampla</i> Schauer	T	EN	E,M	E	G1,N1	E
<i>Calyptanthes luquillensis</i> Alain	T	ENL	S		G1,N1	
<i>Calyptanthes woodburyi</i> Alain	T	EN	S		G1,N2	
<i>Coccoloba rugosa</i> Desf.	T		M,S	P,T	G2,N2	
<i>Conostegia hotteana</i> Urban & Ekman	T		S		G2,N2	
<i>Cordia wagnerorum</i> R. Howard	S	ENL	S		G1,N1	
<i>Cybianthus sintenisii</i> (Urban) Agostini	S	ENL	S		G1,N1	
<i>Dichantherium aciculare</i> (Desv. ex Poir) Gould & Clark	G		S		G4,G5,N1	
<i>Eugenia eggersii</i> Kiaersk.	T	EN	S		G2,N2	
<i>Eugenia haematocarpa</i> Alain	T	EN	E,M	E	G1,N1	E
<i>Ilex sintenisii</i> (Urban) Britton	T	EN	E,M	E	G1,N1	E
<i>Laplacea portoricensis</i> (Krug & Urban) Dyer	T	EN	S			
<i>Lepanthes dodiana</i> Stimson	H	EN	S		G1,N2	
<i>Lepanthes eltorensis</i> Stimson	H	EN	E,M	E	G1,N1	E
<i>Lindsaea stricta</i> (Sw.) Dryander var. <i>jamesoniiformis</i> Kramer	H		S		G1,N1	
<i>Lycopodium tenuicaule</i> Underw. & Lloyd	LY		S			
<i>Lycopodium wilsonii</i> Underw. & Lloyd	LY		S			
<i>Marliera sintenisii</i> Kiaersk.	T	ENL	S		G1,N1	
<i>Marsdenia elliptica</i> Decne.	LI	ENL	S			
<i>Maytenus elongata</i> (Urban) Britton	T	EN	S		G1,N1	
<i>Miconia faveolata</i> Cogn.	T	ENL	M,S		G1,N1	
<i>Miconia pycnoneura</i> Urban	T	EN	S		G1,N1	
<i>Myrcia holdridgeana</i> Lundell	T	EN	S		G2,N2	
<i>Pilea multicaulis</i> Urban	H	ENL	S			
<i>Pilea yunqueensis</i> Urban (Britton & Wilson)	H	EN	S			
<i>Pleodendrum macranthum</i> (Baill.) v. Tiegh.	T		E,M	E	G1,N1	E
<i>Psidium sintenisii</i> (Kiaersk.) Alain	T	EN	S		G1,N1	
<i>Ravenia urbanii</i> Engler	T	EN	S			
<i>Solanum woodburyi</i> R.A. Howard	H	EN	M,S		G1,N1,N2	
<i>Styrax portoricensis</i> Krug & Urban	T	EN	E,M	E	G1,N1	E
<i>Ternstroemia hepatasepala</i> Krug & Urban	T	ENL	S		G1,N1	
<i>Ternstroemia luquillensis</i> Krug & Urban	T	EN	E,M	E	G1,N1	E
<i>Ternstroemia subsessilis</i> (Britton) Kobuski	T	EN	E,M	E	G1,N1	E
<i>Urera chlorocarpa</i> Urban	T	EN	S		G2,N2	
<i>Xylosma schwaneckeanum</i> (Krug & Urban) Urban	T	EN	S		G1,N1	

^aSource: Liogier (1985, 1997); Little and Wadsworth (1964); Little and others (1974); U.S. Department of Agriculture, Forest Service (1997b).

^bLife form: F = fern; G = grass; H = herb; LI = Liana; LY = lycopodium; S = shrub; T = tree.

^cStatus classification: EN = Endemic Puerto Rico, ENL = Endemic Luquillo Mountains; USFS = Forest Service; Fed. = Federal; Nat. Her. = Natural Heritage classification system: G = global, N = national, 1 = critically imperiled, 2 = imperiled, 3 = vulnerable, 4 = apparently secure, 5 = widespread and secure; PR = Puerto Rico; E = endangered; S = sensitive; T = threatened; P = proposed for classification.

Chapter 10. OTHER RESOURCES

Water and Shrimp

The LEF's water resources begin with abundant rainfall and intercepted cloud moisture. Seasonal variation and climatic phenomena along with dams and intakes in the lower stretches of streams all influence the quantities that ultimately reach the island's coastal estuaries. On a typical day, 70 percent of the water originating within the LEF is diverted for use before reaching the ocean (Crook and others 2007).

Ten streams drain parts of the LEF, seven of them providing domestic and commercial water supplies to communities surrounding the forest (figs. 1 and 9) (appendix A). Since 1945, the U.S. Geological Survey has maintained at one time or another 17 flow gages on seven rivers (Crook and others 2007) (fig. 9). At the moment, 31 dams and 35 water intakes intercept flow at some point between the LEF and the surrounding lowlands (Crook 2005, Crook and others 2007):

- Puerto Rican Aqueduct and Sewer Authority, 15
- Private entities, 13
- Puerto Rican Electric Power Authority, 4
- U.S. Department of Agriculture, Forest Service, 1
- Intakes with no record of permission, 2.

In addition, water was also diverted by gravity from four streams (Río Cubuy, Río Sabana, Río Icacos, and Río Prieto) to a penstock and finally to the Río Blanco hydroelectric plant (Naumann 1994) (fig. 9). By the early 1990s, however, water removal from the first two intakes had been discontinued because of broken pipes. About 225 liters of water is required to generate 1 kilowatt hour of energy.

Shrimp are considered to be an integral part of water resources because they are the dominant animals accounting for most of the aquatic faunal biomass; moreover, shrimp range from highest elevations to coastal estuaries where they play a key role as regulators of leaf decomposition (Crook 2005). Shrimp species migrate up and down streams during the year, and are vulnerable to water withdrawal during low flows, especially on streams with multiple dams (Crook 2005). Water intakes reduce shrimp habitat, negatively affecting their populations, diversity, and distribution. The migratory nature of shrimp highlights the need to protect stream connectivity and ecosystem health.

Before 1990, dams had been constructed for water supplies on all of the LEF's major streams except the Río Mameyes (Benstead and others 1999). By 1993, however, the Puerto

Rico Water and Sewer Authority had plans to install a dam on the Mameyes (Nieves 1998). Public opposition to the proposal resulted in the installation of a series of stainless steel risers (i.e., intakes) that allow water to be pumped out of the stream. This system alters the river channel and flow less than a low-head dam and has a minimal impact on migratory species (March and others 2003).

In addition to human impacts, the mountain streams are regularly affected by natural disturbances, including hurricanes, high rainfalls, landslides, and debris accumulation such as treefalls and landslides. The abundance of palaemonid shrimp (*Macrobrachium* spp.) measured from 1988 to 2002 in Quebrada Prieta, a tributary of the Río Espíritu Santo, was lowest during the 1994 regional drought. In contrast, hurricanes and storm flows had little influence on their abundance (Covich and others 2006).

Recreation

Puerto Rico's population is approaching 4 million (U.S. Department of Agriculture, Forest Service 2009). From 1975 to 1988, visits to the LEF more than doubled, reaching an estimated 750,000. About 60 percent of the visits were between April and September in either developed recreation facilities for concentrated use or dispersed recreation activities such as hiking or picnicking (Bauer 1987). The most recent surveys are based on a monitoring process that provides visitor estimates within 15 percent at the 80 percent confidence level (English and others 2002). By 2006, total forest visits had increased to about 1.2 million, with guided tours in 2007 bringing >110,000 visitors into the forest (U.S. Department of Agriculture, Forest Service 2006, 2009). Visitor responses showed that 40 percent were from Puerto Rico, 5 percent from foreign countries and the U.S. Virgin Islands, and the remainder from 44 states and the District of Columbia in the United States. Of the latter, 30 percent were from five states—New York, Florida, New Jersey, California, and Massachusetts—in descending order. About 50 percent of the respondents were of Hispanic or Latin origin and nearly 60 percent between the ages of 20 and 50. Surveys showed that visitor use was greater on weekends and holidays than on week days, and that most of the visits were for viewing natural features or wildlife, hiking, nature activities, driving for pleasure, relaxing, or visiting historic sites. Local visitors were more common during the summer months and international visitors during the winter. Visitors expressed a high level of satisfaction with their experience on the forest.

Most developed facilities are located in the northern part of the LEF along PR route 191. The El Portal Rain Forest Center, situated at the forest entrance, has three pavilions with >900 m² of exhibit space, a theater, a gift shop, and a short nature trail through secondary forest (fig. 5) (table 17). The theme of the center is that tropical forests and its people are linked in a global community and that cooperative efforts can help conserve forests. Visitors are introduced to the beauty, diversity, and complexity of tropical forests and current activities aimed at their management. Interpretation is provided in six areas: an orientation, an introduction to tropical forests, displays promoting an understanding of the forest, connections (i.e., benefits and relations between humans and forests), forest management, and hope for conservation in the future.

Ascending PR route 191 toward the summits, two other major recreation areas border the road. The Sierra Palm Center, located a short distance past Yokahú tower, has picnic shelters, restrooms, a food concession, and access to hiking trails (fig. 20) (table 17). Slightly farther along the road, the Palo Colorado Center has similar facilities and a trail that descends to La Mina Falls. Other trails ascend to freshwater swimming pools at Baño de Oro, to nearby historic sites such as the stone house and trout rearing pools, and ultimately to Mt. Britton and El Yunque peak (fig. 20) (table 17). Parking spaces within lots is limited to about 200 spaces for the entire forest.

In addition to the developed recreation sites, LEF visitors frequent river crossings (Kartchner 2003). Surveys and vehicle counts were carried out at bridges over the Río Mameyes (i.e., Puente Roto) on PR route 988 and Río Espíritu Santo on PR route 186 (figs. 5 and 9). Most visitors enjoyed eating near the rivers and bathing. Other bridges used similarly were those at Quebrada Juan Diego on PR route 191 and at Quebrada Río Grande on PR route 186. In 1995, household and recreation surveys estimated the willingness of islanders to pay for preserving instream flows in the Río Mameyes and the Río Fajardo (González-Caban and Loomis 1999). Survey results indicated that visitors were concerned about protecting the environment for future generations; moreover, they would pay \$21 per household per year to avert dams on the rivers. Expanded island-wide, that would yield \$110 million per year. Surveys also showed that heavy withdrawals would reduce stream visitations by >90 percent.

Other recreational opportunities include bird watching, stream bathing, hiking, and primitive camping. The new El Toro wilderness protects the LEF's only population of *Amazona vittata* and offers both solitude and serenity, rare resources in modern Puerto Rico.



The El Portal Rain Forest Center is the gateway to the Luquillo Experimental Forest. The center has numerous informative displays, a theater, a souvenir store, a snack bar, and ample parking. (Photo by Peter L. Weaver)

Scenery and Trails

The summits of the Luquillo Mountains are well known landmarks visible from several parts of the island and offshore. In the past, they helped to orient sailors in surrounding waters. Today, spectacular views of different forest types and panoramas of surrounding coastal shoreline can be enjoyed from several accessible vantage points, including (figs. 5, 9, and 20) (table 17):

- The 21-m Yokahú observation tower on PR route 191 has views of the Baño de Oro Natural Area in the upper Mameyes watershed, different forest types, and the island's northeast coast.
- Mt. Britton Tower, located along FS-10, provides an overview of dwarf forest and vistas north toward El Yunque, east toward Pico del Este, and south to El Toro.
- El Yunque Peak at the end of FS-10, where military radar facilities were installed in 1942, gives visitors a panorama of Puerto Rico's northeastern coast, and all of the highest peaks and major forest types in the LEF.
- El Yunque Rock offers a vista of the Puerto Rico's northeastern coast from San Juan to Fajardo.
- Los Picachos observation point, perched on top of a volcanic pinnacle, provides both a rigorous climb and a good view of the forest.
- Pico del Oeste overview, located along FS-27, allows clear views of El Yunque Peak, patches of palm brake forest, Los Picachos, and Puerto Rico's northeastern shore.

Table 17—Facilities and structures in the Luquillo Experimental Forest^{a, b}

Major facility or structure ^c	Date(s) ^d	Notes
Interpretation centers		
El Portal Rain Forest Center	1993-96	Information center, parking, trail, theater, food concession, book store
Palma de Sierra picnic area ^e	late 1930s	Parking, wooden buildings, picnic and bathing access
	1965+	Parking, bathrooms, food concession
Palo Colorado information center ^e	late 1930s	Parking, wooden buildings, picnic and bathing access
	1965+	Parking, visitor information, interpreters, souvenirs, picnic area
Picnic areas		
Caimitillo	1963+	Picnic area, parrot interpretative trail
Palma de Sierra (locations historic) ^e	1930s+	Original wooden facilities later replaced; 8 cement overnight cabins later converted to picnic shelters
	1960-70s	Current structures - bathrooms, water systems, picnic areas
	1999	Remodelling and repairs
Palo Colorado (locations historic) ^e	1930s+	Original wooden facilities later replaced; 10 cement overnight cabins later converted to picnic shelters
	1960-70s	Current structures - bathrooms, water systems, parking lot
Quebrada Grande	1990s	Parking, picnic and day use facilities
Rio Sabana	2009	Parking, picnic and day use facilities
Observation sites		
Baño de Oro (bathhouse/bathing pool) ^f	1935	Dug in area of Spanish gold mining pits; concrete bottom
Baño Grande (bathhouse/bathing pool) ^f	1937-38	Larger facility, stone masonry dam, arch bridge
El Yunque tower	1938	Rock and mortar walls; 360 degree view of mountains
La Coca falls (26-m waterfall)	1933	Small structure at falls built about 1991 after Hurricane Hugo
Las Cabezas observation point	1930s	Roadside parking viewpoint of northeastern Puerto Rico
Los Picachos (enclosure on pinnacle)	1938	Pinnacle with panoramic view
Mt. Britton tower (9-m tower)	1937-38	Stone masonry tower, panoramic view; nearby picnic shelter
Río Espíritu Santo	NA	Panoramic view west from bridge
Yokahú tower (21-m tower)	1962-63	View of Natural Area and mountains
	~1991	Post-Hurricane Hugo parking lot and site improvements
Trailheads		
Angelito trail	2008	Trail to freshwater pools in Río Mameyes
Big Tree trail	1934	Site interpretation, trail to La Mina Falls
El Toro-Tradewinds trail	1935-36?	Montane and Dwarf forests, El Toro peak
La Coca Trail	1930?	Descend to Río Mameyes in Lower montane forest
Mt. Britton trail	1935-36?	Trail to Los Picachos, El Yunque Road, and Mt. Britton
Other structures		
Camp 8 (CCC work camp)	1930s	CCC work center remnants (stone and concrete features)
Catalina Service Center	1979-82	Forest management offices and parking lot; center enlarged during the mid-1990s
Cubuy House (Cienega Alta house)	1938?	One story CCC-constructed ranger station; later, activity center
Eliza Colberg Girl Scout camp	1948-50	Scout field activities
El Verde Field Station	1937-39	Labs (1960-70s), meteorological tower (1980s), dorm (2005)
El Yunque Pavilion (or Restaurant)	1936	Mess hall and recreation; nearby cabins built (1940); parking lot improvements (1968); closed by Hurricane Hugo (1989)
El Yunque Radar Post ^g	1938	Tower, bathroom, diesel storage, dorm
El Yunque Tower (Microfleet Company)	1975-80	50-m tower; new facilities built by 1980
La Condesa school building	late 1930s	Demolished about 1990 due to recurrent flooding
La Iguaca aviary	2007	Modern facility for parrot rearing

(table continued on following page)

Table 17 (continued)—Facilities and structures in the Luquillo Experimental Forest^{a, b}

Major facility or structure ^c	Date(s) ^d	Notes
Interpretation centers		
La Mina barracks	~1938	Military housing; used as parrot aviary from 1972-1990s
La Mina house	1940s	Ranger station; 1972-1990s, housing for parrot researchers
La Mina trout hatchery	1934	Hatching trough, circular rearing pools
Molindero Road cottages	1936-1940s	Summer vacation cottages; only 3 remain in 2010
Pico del Este radar facilities	1958-62	Two radar domes, sleeping quarters, generator building, communication facilities, kitchen
PR telephone communications tower ^h	1949	50-m tower and facilities consolidated in 1976-81
Quebrada Grande Picnic Area/parking	1978	Picnic shelters along river
Sabana house and office building	late 1930s	Ranger station; 1986-present, research offices, housing, labs
Stone house	~1934	Overnight ranger facilities; governor's rest house; oldest CCC building on forest; future potential as museum
Summer cottages	1930s +	Summer cottages built by permittees on long-term lease; program later terminated and most cottages destroyed
Youth Conservation Corps (YCC) Camp	1973-76	Forestry youth activities 16 to 18 years old; plaza, dorms, vocational shops, class rooms, mess hall, administration
Trails		
Seven historic trails	by 1936	Big tree, El Toro, El Yunque, El Yunque rock, Los Picachos, Mt. Britton, and Río de la Mina

^aPR route 191, constructed from 1926 to 1942, made other work possible along the route, including Civil Conservation Corps (CCC) activities.

^bSources: Díaz Vega (2004); Gerhart (1936), see endnotes; Huffaker (1989), see endnotes; Rivera (2010), see endnotes; Santiago Cazull (2000), see endnotes; Walker and others (1999), see endnotes. Some dates are approximate.

^cSeveral wooden structures such as work camps, overnight cottages, shelters, guard houses, and exhibition facilities were originally built. Later some were replaced with cement structures.

^dDates refer to plans, construction, or opening of facilities (El Yunque Forest 2009, see endnotes). NA = date is uncertain.

^eFirst called La Mina recreation area.

^fBathing pools were closed during the mid-1950s because of safety hazard.

^gA 1938 map shows the tower, which is missing on the 1941 map, most likely for World War II military purposes.

^hHeavy density repeater station was formerly the El Yunque communication facilities.



Swimming pools. TOP: The Baño de Oro swimming pool, the first in the La Mina area, was built in the late 1930s in pits previously excavated by Spanish gold seekers. BOTTOM: Baño Grande, a larger pool with an arch bridge, was built shortly afterwards in response to public demand. (Photos by Iván Vicéns)

- Pico del Este, situated at the radar dome facilities at the end of FS-27, has views of dwarf forest, the northeastern tip of Puerto Rico with the Fajardo lighthouse, and the area north of the old Roosevelt Roads Navy Base.

Other less familiar viewpoints require considerable hiking:

- El Toro Peak along the El Toro-Tradewinds trail provides a panorama of the mountains.
- La Mina Peak has a similar albeit lower elevation view of the LEF.
- The 1970 major landslide on PR route 191 provides a view of the Icacos watershed and secondary vegetation dominated by the tree fern *Cyathea arborea*.

In addition to the above viewpoints, the LEF has 15 hiking trails totaling >40 km that offer visitors a closeup view of major plant and animal species (U.S. Department of Agriculture, Forest Service 1997b) (fig. 5) (table 18). The trails range in elevation from about 110 to 1074 m. The Angelito and El Portal trails are <200 m in elevation and another two lie between 250 and 450 m. Eleven trails lie ≥ 500 m in elevation. Two of these are the El Toro and Tradewinds trails that meet at El Toro Peak, passing through montane and dwarf forests en route. The hiking time required to traverse all trails would take about 2 days. Five trails are classified as easy, three as moderate, and seven as challenging. At least one forest type is visible from each of the trails. Points of interest include fauna and flora, stream crossings, different peaks, old CCC structures, and panoramic vistas. One possible concern regarding the road and trail network is that it fragments wildlife habitat, notably for *Amazona vittata*.

Other hiking or walking opportunities exist along three forest roads currently limited to administrative vehicle use, or at three recreation sites (fig. 5):

- The abandoned PR route 191, which extends from the gate at the mountain divide (km 13) to the landslide at 600 m (km 21), and then traverses the slide, and descends to a new picnic area along the Río Sabana near km 23.
- FS-27, which extends from the gate at PR route 930 to the Pico del Este radar domes.
- FS-10, which climbs from PR route 191 near km 13 to El Yunque Peak.
- The Palo Colorado and the Caimitillo picnic area, both of which have hiking trails (table 17).

The LEF also has many stream crossings and small waterfalls visible along the hiking trails or from bridges like the one over the Río Espíritu Santo on PR route 186 and La Mina Falls on the La Mina trail. Finally, trails parallel stretches of the three wild and scenic rivers (i.e., Río Icacos, Río de La Mina, and Río Mameyes). Much of the scenery along the Río Icacos

lies near abandoned PR route 191, which descends from the mountain divide to the major landslide at 600 m.

Heritage

Heritage resources are archaeological sites, artifacts, or buildings that remain after past human activity, and include the LEF's cultural resources from different periods such as the pre-Columbian, Spanish colonial, and the early 20th century (U.S. Department of Agriculture, Forest Service 1997b). Since 1983, cultural resource surface inventories have been carried out on 3400 ha, revealing > 60 pre-Columbian and historic sites. Seven historic sites have been evaluated for inclusion in the National Register of Historic Places as a multiple property nomination that covers all CCC properties (Walker 1999, 2009, see endnotes).

Before colonization, pre-Columbian settlements in northeastern Puerto Rico were confined mainly to coastal areas. Foraging and fishing camps, agricultural plots, village sites, petroglyphs, and burial sites are all potential heritage resources in the vicinity of the LEF border. From the time of discovery through 1898, the Spanish were active in gold mining (e.g., placer and shaft mines) and agricultural activities in the LEF (Robinson 1997). Differences in vegetation and the presence of refuse dumps provide aboveground evidence of past mining activities. At some time in the future, subsurface archaeological remains may be excavated. The last major historical activity was the CCC work carried out during the 1930s, which included camp sites, roads, trails, buildings, and bridges. The major cultural and historical resources found today in the LEF are (Oliver 1973, Robinson 1997):

- Petroglyph groups, including the Coca watershed (two sites), near the confluence of the Río Cubuy and Río Icacos, near the confluence of the Río Camándulas and Río Sabana, in the Quebrada Jiménez watershed, and near La Mina peak.
- A gold mine shaft along Río de La Mina.
- Copper mining remains at La Mina Peak.
- CCC sites and structures dating to the 1930s.

In addition, pieces of iron and pottery were found during the construction of the Baño de Oro facilities where the Spanish had previously excavated for gold (Gerhart 1936, see endnotes).

Several structures in the La Mina and El Yunque areas are historic, including the stone house, Baño de Oro and Baño Grande pools, Mt. Britton and El Yunque towers, and the La Mina barracks (fig. 20) (table 17). The CCC camp at La Mina was later converted into parking facilities for the Sierra Palm Recreation Area (Gerhart 1936). Picnic shelters were constructed from lumber sawn during the construction

Table 18—System of trails within the Luquillo Experimental Forest^a

Trail name (trail location)	Map key ^b	Length km	Time ^c h or m	Difficulty ^d	Elevation ^e m	Forest types ^f	Points of interest
Northern forest border							
Angelito (PR-988, km 4.0)	1	0.7	15 m	E	110-150	LM	Stream crossing
El Portal (PR-191 at El Portal)	2	0.7	15 m	E	160-180	LM-S	Tree and bird species
El Toro-Tradewinds^g	3-4	11.4	6 h	C	650-1075	M, D	El Toro peak
El Toro (PR-186, km 10.8)	3	4	2 h	C	650-1074	M, D	El Toro peak
Tradewinds (PR-191, km 13.4)	4	7.4	4 h	C	740-1074	M, D	El Toro peak
El Yunque trail system							
Baño de Oro (PR-191, km 12.2)	5	0.6	20 m	M	650-720	M	CCC structures ^h , trout nursery
Caimitillo (PR-191, km 12.1) ⁱ	6	0.6	20 m	M	630-740	M	Parrot interpretation
El Yunque (PR-191 to FS-10)	7	4.4	2 h	C	630-1050	M, D	El Yunque peak, panoramic view
El Yunque Rock (on FS-10)	8	0.3	7 m	E	1030-1040	D	Panoramic view
Los Picachos (on El Yunque trail)	9	0.3	8 m	E	900-930	D	Los Picachos, panoramic view
Mt. Britton (PR-930 to FS 10, tower)	10	1.3	40 m	C	760-940	M, D	Mt. Britton tower, panoramic view
Mt. Britton link (El Yunque to FS-10)	11	0.5	10 m	E	850-900	M, P	Gradient in vegetation
La Mina trail system							
Big Tree (PR-191, km 10.4) ⁱ	12	1.4	40 m	M	500-550	LM	La Mina falls, large trees
Carillo (PR-988, km 6.1)	13	3.4	1 h 30 m	C	250-300	LM	Mameyes river, stream crossings
La Coca (PR-191, km 8.6)	14	2.9	1 h 20 m	C	250-450	LM	Stream crossings
Río de La Mina (PR-191, km 12.2)	15	1.2	30 m	C	500-650	LM, M	La Mina falls, La Mina river
Totals (15 trails)		39.9	>14 h	E-C-M	110-1074	5 types	Several

^aSource: U.S. Department of Agriculture, Forest Service (2008).

^bMap key: Numbers are keyed to figure 5.

^cTime to walk one way (h = hours, m = minutes).

^dDifficulty: C = challenging; M = moderate; E = easy.

^eElevation: minimum and maximum.

^fForest types: LM = Lower montane rain forest; LM-S = secondary Lower montane rain forest; M = Montane rain forest; P = Palm brake; D = Dwarf forest.

^gEl Toro-Tradewinds trail was designated a National Recreation trail (U.S. Department of Agriculture, Forest Service 1997b).

^hCCC = Civilian Conservation Corps.

ⁱInterpretative trails (i.e., signs or numbered posts with explanatory handout).



LEFT: Yokahú tower was completed in 1962 and the parking lot was enlarged after a landslide during the 1990s. The tower is a convenient site for viewing different forest types and the Baño de Oro Research Natural Area. RIGHT: Two hikers enjoy the panoramic view from El Yunque rock, one of the best seats in the Luquillo Mountains. On this same site 70 years earlier, entomologist George Wolcott saw a swarm of *Polistes americanus* (Paper wasp). (Photos by Peter L. Weaver)



TOP LEFT: The visitors' center at the Palo Colorado Recreation Area in the early morning hours. TOP RIGHT: The parking lot of the Sierra Palm Recreation Area at midday. The plaque commemorating the 1976 designation of the forest as a Biosphere Reserve is mounted on a boulder behind the umbrella in background. CENTER LEFT: Recreation areas have picnic shelters and hiking trails in the vicinity. RIGHT: A hiker walks on recently finished Angelito trail, a name which commemorates Angel Torres, a well-respected forest worker who lived and worked in the vicinity. The forest has 15 major trails varying in elevation, length, and scenery. (Photo by Iván Vicéns) BOTTOM LEFT: A typical trail sign within the forest includes a map of trails within the system, trail name, length (km), time to walk (hours), hiking difficulty (easy versus challenging), and change in elevation (m). (All photos by Peter L. Weaver except where noted)



TOP: The view from the Espiritu Santo bridge on PR route 186 highlights Puerto Rico's northern shoreline and coastal lowlands in the background. (Photo by Iván Vicéns) BOTTOM: La Coca Falls, located along PR route 191, is one of the best known and favorite stops for visitors. (Photo by Peter L. Weaver)

of PR route 191. Soon damaged by insects, the shelters were later replaced with concrete buildings. The picnic and parking areas, however, are historic sites; moreover, the construction of seven trails also date to CCC days. Historic structures also remain at El Verde, La Condesa, and Sabana (figs. 1 and 20) (table 17). Both the Mt. Britton and Yokahú towers are mentioned briefly in a regional guide that highlights historic structures (Instituto de Cultura Puertorriqueña 1993). The Mt. Britton tower was referenced as neo-medieval and Yokahú tower as somewhat less so in appearance.

Finally, most of the structures on Pico del Este (i.e., dormitory building, two radar domes, and communication facilities) were built around 1960 (fig. 20) (table 17). The site, abandoned by U.S. Navy personnel in 2003, is still used by the FAA. Past researchers used the dormitory building as a basis for field operations. Currently, Pico del Este serves as a field site for the collection of atmospheric data. Should the site be restored, future uses might include field trips to surrounding dwarf forest and excursions to enjoy panoramic views of northeastern Puerto Rico.

El Yunque Stories—Myth, Legend, and Curious Facts

Myths and legends are a product of time in many regions of the world and the LEF is no exception. Myths are false whereas legends may be based on observations which become enhanced, or possibly misinterpreted with time. There are also a few hard-to-believe facts associated with the forest.

First, some names used with regard to the forest have an interesting history. Tainos referred to the El Yunque peak and surrounding forest as Yuké, or white land, in reference to the cloud covered summits. The forest's current name, El Yunque (i.e., meaning anvil in Spanish), is a corrupted derivation of the Taino word (Domínguez-Cristóbal 1997a, Moran Arce 1971). Although some may believe that the mountains resemble an anvil, most will agree that the summits are a cloud covered much of the time. Also, some say that the word Luquillo is derived either from the name Yuki-yú or from Loquillo (Barnat 1987). Both refer to a previous indigenous chief of the early 1500s noted for his guerrilla warfare against the Spanish. Loquillo and his followers hid in the forests at the base of the Luquillo Mountains. In commemoration of his efforts, the municipality of Luquillo has erected a statue to the former chief.

Among the popular myths are those that associate the mountains with extraterrestrial beings and flying saucers (Domínguez-Cristóbal 1997a). Perhaps these stories are nothing more than a 3rd millennium version of pre-Columbian lore dealing with benevolent spirits hiding within Puerto

Rico's mountains (Morán Arce 1971). Another favorite myth is that El Yunque is connected to Roosevelt Roads by a complex series of tunnels. The origin of this story is uncertain. However, large natural cavities drain surface runoff into underground channels along the Tradewinds Trail and in the upper reaches of the Río Mameyes watershed. Perhaps these cavities combined with an overactive imagination and tabloid sensationalism helped generate the myth.

Four other stories have a semblance of truth. The first concerns the "Valley of the Giants," an area which "has become myth" (Robinson 1997). The valley is located in a remote part of the Río Icacos watershed, a tributary of the Río Blanco (fig. 21). The intriguing name originated in 1948 when foresters exploring the valley found several big *Cyrilla racemiflora* trees, including the LEF's largest at 2.65 m in d.b.h. (Robinson 1997). Because most montane forest trees are small, the concentration of a few large ones anywhere is noteworthy. Typical d.b.h. growth rates suggested that a couple of these large trees may have germinated about the time that Columbus discovered the island. The largest specimen, however, appeared due to the coalescence of proximate stems, a phenomenon seen elsewhere (Weaver 1986b). Among the other large trees present was a *Cordia borinquensis* measuring 44 cm in d.b.h. *Cordia borinquensis*, abundant within the LEF, rarely exceeds 6 m in height and 13 cm in d.b.h. (Little and Wadsworth 1964). A sheltered location may explain the survival of these large trees, which are hidden in a south-facing watershed protected by the forest's highest peaks—Pico del Este and Pico del Oeste to the east, El Yunque and Mt. Britton to the north, and El Cacique and El Toro to the west (fig. 9). Time and imagination have fashioned a legend from a walk in the woods >60 years ago.

The second tale is that the Luquillo Mountains protect Puerto Rico from hurricanes. Many hurricanes passing over Puerto Rico since 1700 had trajectories to the west of the Luquillo Mountains (fig. 12). Moreover, a considerable number had trajectories at some distance to the east. Only four hurricanes passed directly over the mountains, for an average of one storm per 75 years. Regardless, many hurricanes to the east or west were large enough to cause considerable damage within the mountains. The most recent examples are Hurricanes Hugo and Georges with trajectories very close to the LEF. Conjecture regarding the effect of the Luquillo Mountains on hurricane trajectories, like weather virtually anywhere, will likely be the subject of conversation well into the future.

A third story relates to loggers being able to distinguish between two types or races of *Dacryodes excelsa* trees before felling them in the field, possibly based on wood color or fruits (Francis and Lowe 2000, Wadsworth 2009, see endnotes). Similar stories have been told about other timber species, notably *Cedrela odorata* and *Swietenia macrophylla*

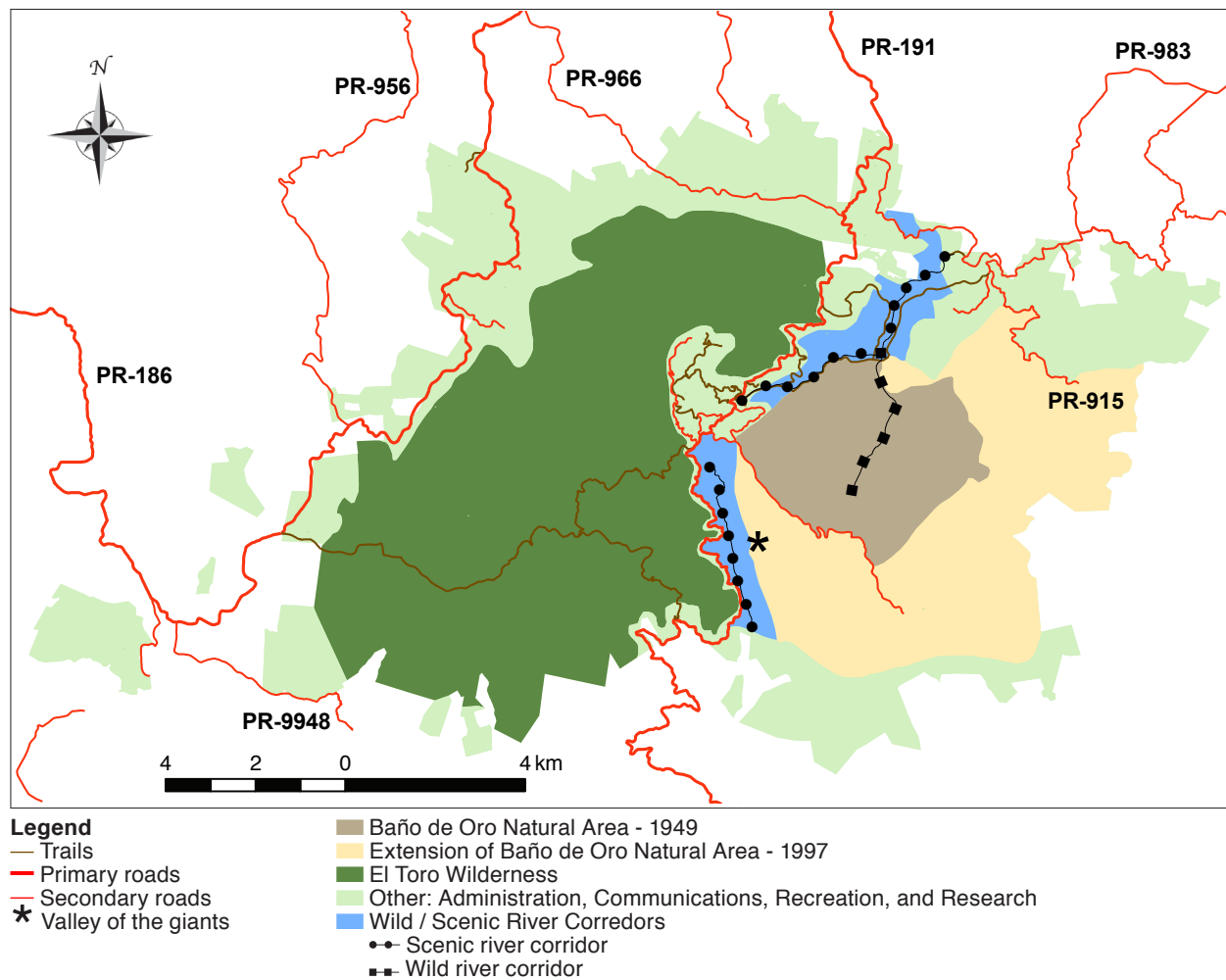


Figure 21—Major designated areas within the Luquillo Experimental Forest.

in Central and South America. One possible explanation is that trees grow at different rates according to topography (i.e., water availability and soil fertility) and consequently vary in wood density and possibly other wood properties as well. Experienced loggers may be able to detect some of these properties before cutting, or at least associate them with the landscape.

Another tale concerns a widespread farming tradition that harvesting during certain lunar phases purportedly makes tree products more durable (Anon. 1952, Brunet 1929). This belief was tested in the LEF with the palm *Prestoea montana* and showed that leaves harvested during the full moon had higher total carbon, hemicellulose, complex carbon, and lower calcium concentrations than leaves harvested at other times during the lunar cycle (Vogt and others 2002). The conclusion was that leaves cut at full moon display some chemical characteristics which should make them less susceptible to insect herbivory and more durable in use. In another study,

fence posts were harvested at different times and placed in the ground to determine if the most durable wood was produced during the waning moon (Maldonado 1962). No significant effect was determined after 4 years. When informed of the results, local farmers claimed that “the study was no good, as it did not show what everybody knew” (Wadsworth 2009, see endnotes). An earlier study based on the production of field crops concluded that the “moon is the most variable factor” (May 1924). In summary, certain chemical characteristics of wood may vary during lunar cycles but their effects on product use and longevity after harvest appears to remain a matter of opinion.

There are also a few hard-to-believe facts. After construction of the weir on the Río Icacos, early measurements indicated that the watershed produced more runoff than rainfall (Crook and others 2007; Wadsworth 2009, see endnotes). Some explanations were suggested to help account for the anomaly, including possible nonlinear relationships between the basin

and runoff, the addition of occult rainfall (i.e., the interception of cloud moisture by vegetation), or the possible occurrence of greater rainfalls slightly to the leeward of the peaks and ridges that border the eastern part of the watershed. The anomaly in the water balance, however, remains as does conjecture about its cause. Also difficult to believe is the discovery of the elfin-woods warbler within the dwarf forest nearly one-half a century after all Puerto Rican bird species were supposedly known (Kepler 2009). Communication with James Bond, an authority on West Indian birds at the time (Bond 1971), led to the suggestion that specimens be collected. Fritz Scheider, who first saw the bird in the late 1960s, didn't collect them but, Cameron and Kay Kepler did in the early 1970s, ultimately leading to the confirmation of a new species (Kepler and Parkes 1972). Later during a meeting at Cornell, Scheider showed his field notes on plumage, behavior, and song to Kepler, who asked him how he felt about the discovery. Wryly Scheider replied, "Now I know how Leif Erickson felt" (Kepler 2009).

Another intriguing fact—a sign of the times—is that the Forest Service used to arrest cows for trespassing! Although it sounds strange today, during the 1930s, forest guards led cows that had been found grazing on national forest lands

to municipal jails where they were held until owners paid a fine and related fees to repossess them (Wadsworth 2009, see endnotes). Trespass was considered an offense in conflict with efforts to protect and manage forest resources.

Finally, a current tourist promotion known as the "New 7 Wonders of Nature" includes the LEF as one of the candidate sites (El Yunque National Forest 2011). Consequently, the forest has received ample coverage in the local media and numerous first time visits from a curious public. One impressive fact, although not a wonder, is that the forest has survived, largely intact, a variety of human pressures from early gold mining and colonization through the present. El Yunque, however, must remain best known for what it was before and remains today—a revered place for the island's original occupants, and a tranquil refuge to experience nature for current visitors. Recently this feeling was eloquently stated as follows: "Para muchos de nosotros, la jornada hacia El Yunque es una forma de peregrinaje, casi religioso, en la que experimentamos el bosque virgen" (i.e., For many of us, the journey to El Yunque is a type of pilgrimage, almost religious, in which we experience virgin forest) (Valdés Pizzini and others 2011). Puerto Rico has no other place like El Yunque.

Chapter 11. DESIGNATED LAND USES

The Luquillo Mountains, with their steep elevational gradient, highly dissected topography, and wet climate provide a variety of habitats and diverse flora. During the past 60 years, the entire LEF as well as certain areas within it have been recognized or designated for particular uses (figs. 20 and 21) (table 2). These include the Baño de Oro Research Natural Area in 1949, the entire forest as a Biosphere Reserve in 1976, both Wild and Scenic Rivers in 2002, and the El Toro Wilderness Area in 2005.

The Baño de Oro Research Natural Area

Research Natural Areas (RNAs) are tracts on which natural features and processes predominate and which are preserved for scientific or educational purposes (Federal Committee of Research Natural Areas 1968). The areas need not be pristine; however, if they are disturbed, protective measures should be undertaken to restore them to their original condition through natural processes (Dyrness and others 1975). RNAs serve as a baseline to compare with areas that have been influenced by human activity (Moir 1972).

The 745 ha Baño de Oro RNA (fig. 21) was established in 1949 because it contained (Weaver 1994):

- Terrain unmodified by human activity, surrounded and buffered by other Forest Service property.
- The four forest types found within the Luquillo Mountains (i.e., lower montane forest, 56 percent; montane forest, 18 percent; palm brake, 19 percent; and dwarf forest, 7 percent).
- The lower montane forest permanent research plot (i.e., tabonuco ridge plot TR-1) established in 1946 at 350 m elevation.
- Habitat for at least 40 bird species, including populations of the endemic *Amazonia vittata* confined at that time to mid- and upper slopes of the Luquillo Mountains (Wiley and Bauer 1985).

Baño de Oro measures 3.55 km from north to south and 4.15 km east to west. Total relief is 780 m, ranging from 245 m along the Río Mameyes in the north to 1025 m in elevation at Pico del Oeste on the south. The entire area, one of the wettest areas in the LEF, receives additional moisture through fog interception on the summits. In 1968, the Baño de Oro was listed in the national directory of more than 300 RNAs (as of 2007, > 430 RNAs) set aside on Federal lands (Federal Committee of Research Natural Areas 1968; Northern Research Station 2006). In 1997, forest planners

proposed an expansion of the Baño de Oro to encompass a total of 2580 ha (U.S. Department of Agriculture, Forest Service 1997a). The proposed addition is located to the south and east of the original RNA (fig. 21).

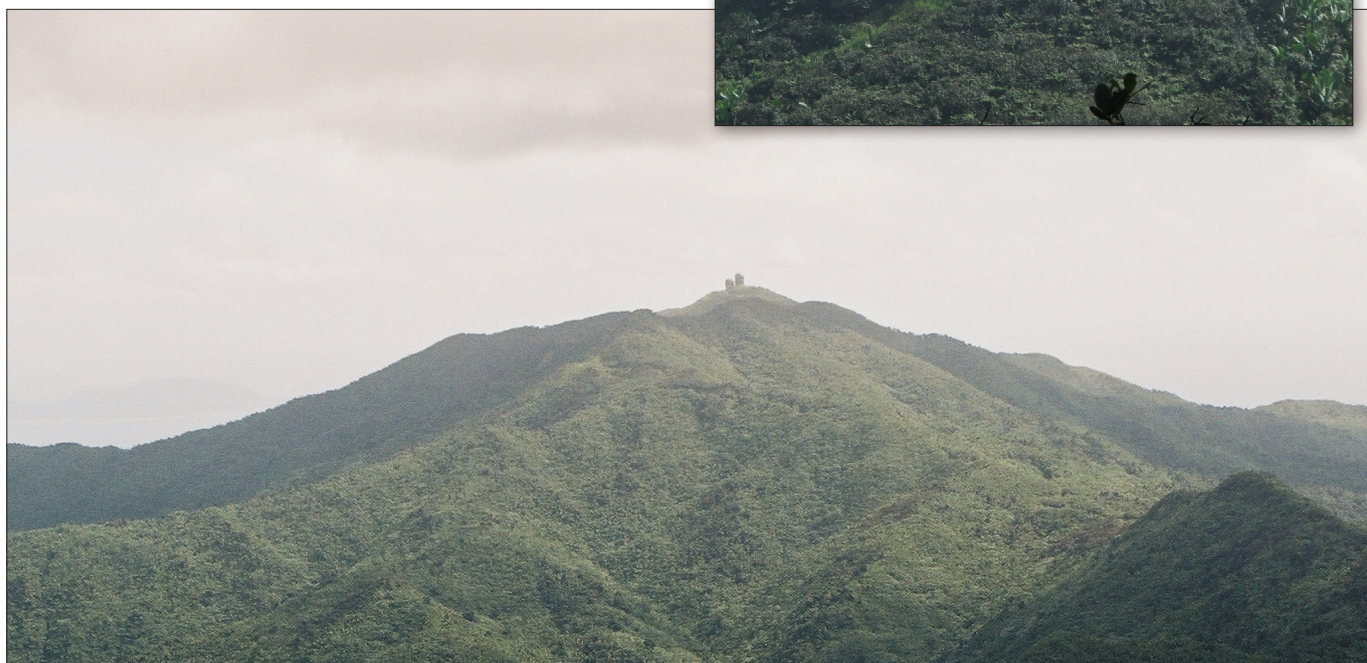
At least 10 major research activities have been implemented within or bordering the Baño de Oro during the past 60 years (figs. 9 and 21) (table 7):

- From 1946 until the present, the TR-1 permanent plot has been monitored, providing a continuous record of forest structure, species composition, tree growth, and response to hurricane impacts (Weaver 1998, 2002b).
- During the mid-1960s, the staff of the Arnold Arboretum undertook a major research effort in dwarf forest on Pico del Oeste (Howard 1968; for details see the Pico del Oeste research site).
- During the 1970s and 1980s, parrot blinds were set up in the upper reaches of the Mameyes watershed to study *Amazona vittata* (Snyder and others 1987).
- In 1984 and 1985, vertebrate and invertebrate faunal diversity was tallied in each of the RNA's forest types (Weaver 1994, Wiley and Bauer 1985).
- During the mid-1980s, about 70 tree species were tallied during gradient sampling of tree species' distributions by elevation and topography within the RNA (Weaver 1994).
- During the 1980s, studies of Black rat (*Stenoderma rufum* and *Rattus rattus*) were initiated (Layton 1986, Willig and Gannon 1991, Zwank and Layton 1989).
- From 1989 to 1993, the growth phenology of *Cyrilla racemiflora* was studied, including flowering, branch elongation, leaf litterfall, and xylem cell growth and differentiation in the lower stem. These events were related to seasonal patterns of rainfall and temperature (Drew 1998).
- In 1991, soil chemistry and the density and biomass of eight earthworm species surveyed in each of the four forest types showed different distribution patterns according to soil types (Borges and Alfaro 1997).
- In 2001-02, plots were established at eight sites along an elevational gradient between the coastal lowland and LEF summits to determine forest structure and composition. Four sites, each representing a different forest type, were situated within the RNA (Gould and others 2006) (table 7).
- In 2001-02, woody stems were sampled from 400 to 900 m in the Baño de Oro. The data were analyzed with new metacommunity tools to reveal community changes such as: clustered uphill or downhill boundaries of species distributions; coherence (i.e., fewer gaps); nestedness in species distributions; and species turnover or change in composition (Barone and others 2008) (table 7).

Luquillo Experimental Forest Biosphere Reserve

In 1976, the entire LEF was designated as a Biosphere Reserve, which is an internationally protected area managed to demonstrate the values of conservation (Lugo 1987, Weaver 1994). Biosphere Reserves are designated by the United Nations Educational, Scientific, and Cultural Organization (UNESCO) based on nominations submitted by countries participating in the Man and the Biosphere Program (MAB) launched in 1971. As of 2011, there were 564 biosphere reserves in 109 countries (UNESCO 2011). Biosphere Reserves represent voluntary cooperation among people to conserve resources for human benefit. The reserves provide a global network for cooperative research and demonstrate the sustainable use of resources. In summary, Biosphere Reserves (Man and the Biosphere 1975):

- Conserve characteristic ecosystems in one of the world's natural regions.
- Contain people as an integral component and are managed for objectives that vary from complete protection to intensive, sustainable production.
- Serve as regional centers for research, monitoring, and educational activities for natural and managed ecosystems.
- Serve as places where local people, government officials, scientists, and managers cooperate in developing land management programs that conserve biological resources (i.e., soil, water, flora, and fauna) and natural processes while providing for human needs.



ABOVE: El Yunque tower provides a view of the upper part of the Baño de Oro Research Natural Area (center left) and Pico del Este radar domes in the distance. (Photo by Peter L. Weaver) ABOVE RIGHT: The Pico del Este radar domes, built in the early 1960s, overlook northeastern Puerto Rico. (Photo by Iván Vicéns)

Wild and Scenic Rivers

The Wild and Scenic Rivers Act (October 2, 1968) states “that certain selected rivers of the Nation which, with their immediate environments, possess outstandingly remarkable scenic, recreational, geologic, fish and wildlife, historic, cultural or other similar values, shall be preserved in free-flowing condition, and that they and their immediate environments shall be protected for the benefit and enjoyment of present and future generations” (U.S. Department of Agriculture, Forest Service 1983).

In 2002, more than 15 km of the Río Icacos, Río Mameyes, and Río de la Mina Rivers, along with about 2800 ha of their

watershed areas, were designated as wild or scenic rivers (figs. 9 and 21) (table 2). These are the only tropical rivers in the National Wild and Scenic River System, which currently protects 17 600 km of 166 rivers in 38 states and Puerto Rico (National Park Service 2005).

The Río Icacos is in the Río Blanco watershed. Lying within an intrusion of tertiary quartz diorite, the river has a sandy bed, numerous pools, and large boulders at lower elevation (U.S. Department of Agriculture, Forest Service 1997b). Riparian palm stands are common. The stream gradient is less steep near the headwaters than at the LEF border. The Río Mameyes is characterized by numerous large boulders, waterfalls, and pools of water; moreover, below its confluence with Río de la Mina, it passes through scenic narrows about 1.5 km in length. The Mameyes contains several species of fish and shrimp, and the LEF's only freshwater crab. Río de la Mina, a tributary of the Río Mameyes, has outstanding scenery, including large boulders, rapids, waterfalls, and small pools of water. Departing from the picnic areas at higher elevation, the La Mina trail descends to La Mina Falls, one of the most attractive sites within the forest. All three watersheds were used in the past by *Amazona vittata*, and are currently inhabited by *Epicrates inornatus* and other endangered plant and animal species.

Wild segments of designated rivers are managed free of impoundments and are assessable only by trail. In general, wild segments are managed with the following limitations:

- No road construction or development, and primitive standards for trails.
- No motorized or mechanized vehicle use.
- No timber harvest, water development, or mining.
- No manipulative research.
- No developed recreation—recreation is managed for primitive experiences, anticipating low use.

The El Toro Wilderness Area

The Wilderness Act (September 3, 1964) states that “A wilderness, in contrast with those areas where man and his own works dominate the landscape, is hereby recognized as an area where the earth and its community of life are untrammelled by man, where man himself is a visitor who does not remain” (U.S. Department of Agriculture, Forest Service 1983). The 757 wilderness areas in the United States occupy about 443,500 km² and range in size from Pelican Island, FL with 2.4 ha to Wrangell-Saint Elias, AK with 3 675 577 ha (Wilderness.net 2011). Although difficult to define, wilderness appeals to virtually everybody (Watson 2004). Wilderness areas provide clean air and water, natural

habitats for flora and fauna, scenic beauty, solitude, and direct economic benefits to nearby communities (Dombeck 1999). In 1999, the Forest Service proposed a wilderness agenda to increase and diversify areas, and improve monitoring programs, recreational opportunities, stewardship, and collaboration among managers.

During the mid-1930s, the visiting Forest Service chief referred to the area encompassing El Toro as “the ruggedly beautiful wilderness of the Luquillo Mountains” (Silcox and Kircher 1936). Today, El Toro is the only tropical wilderness in the U.S. National Forest System. El Carmen in Mexico, set aside 2 months earlier, was the first tropical wilderness (Robles Gil 2006). Although occupying only 4050 ha and averaging 15 times smaller than U.S. wildernesses, El Toro:

- Covers 36 percent of the LEF, making it proportionally large.
- Extends from 370 m elevation at the Quebrada Grande along the northern forest border to 1074 m at El Toro Peak and is traversed by one trail but no roads.
- Encompasses the largest block of undisturbed vegetation in Puerto Rico and is largely buffered by the LEF,
- Lies within an area of tropical wet forests and contains the headwaters of 10 streams that provide pristine water supplies to surrounding communities.
- Contains four forest types and an impressive number of tree species, ferns, orchids, and rare plants and animals. Among the endemics are populations of *Amazona vittata* and *Dendroica angelae*.
- Lies 40 km east of San Juan and is surrounded by towns and suburbs, providing a steep gradient between populated landscapes and virtual solitude (fig. 1).

El Toro has a long history of research beginning >60 years before the wilderness was officially declared (figs. 13 and 21) (table 7):

- Permanent plots: Between 1946 and 1981, changes in stand structure, species composition, and tree growth were monitored on seven permanent forest plots totaling 2.8 ha within lower montane, montane, and palm brake forests, ranging in elevation between 570 and about 900 m (Weaver 2011) (table 7).
- D.b.h. distributions: D.b.h. distributions on a permanent lower montane forest plot were studied over a 30 year period with a matrix model (Wadsworth 1977).
- Gradient sampling: Variation in forest structure and species composition was studied by elevation and topography on 48 temporary plots within the wilderness, where 5,105 trees and 89 species were recorded on only 2.25 ha (Weaver 1991, 2011).
- Riparian palm stand: Forest structure, species composition, ecological cycles, and hurricane impacts were described for a small, riparian palm plot at 750 m elevation (Frangi and Lugo 1985, 1991, 1998).

Special Use Permits

During the early 1990s, about 80 special use permits had been issued in the LEF: electronics and communications, 7; outfitters and guides, 24; water supply, 15; summer cottages, 3; research, 11, including the El Verde field station; road easements, 6; organization camps, 3, including the Eliza Colberg Girl Scout Camp; and various others, 11 (U.S. Department of Agriculture, Forest Service 1991, see endnotes; 1997b, 2008). In comparison, during fiscal year 2006, 97 special use permits were issued. Long-term permits included: outfitters and guides, 29; research, 20; communication facilities, 7; recreational residences, 4; water diversion and pipelines, 2; and 1 a piece for an organization camp, a road right-of-way, an electrical transmission line, and a food service concession (El Yunque National Forest 2010). Temporary permits included: research, 3; filming and photography, 14; and recreation and group events, 14. In addition, renewal of the Puerto Rico Aqueducts and Sewer Authority permits for water storage and diversion systems were being evaluated. Although not considered a special use, permits are also required for camping.

Nearly 13 ha of land, previously covered with dwarf forest, have been designated for electronic and communication sites on top of El Yunque and Pico del Este. The El Yunque area, first

occupied by the U.S. Army during World War II, is used by government and private entities and the Pico del Este site by the Federal government, including the FAA. The summer cottages are located along PR routes 9938 and 930. One structure previously used as a summer cottage serves as a field station for the Biology Department of the University of Puerto Rico.

Earlier special use permits were issued for a variety of activities, including the use of former Spanish concessions on the Arroyo and Sandoval tracts, fuelwood cutting, subsistence agriculture and agroforestry, public roads, screening airborne arboricides, and mineral exploitation (Wadsworth 2009, see endnotes). In contrast to permits that were granted, several formal requests that were considered inconsistent with the sustainable management of a public forest were denied. Among the major rejected proposals were a hotel complex along PR route 191, an aerial tramway from the coast to El Yunque, a “parrot jungle” attraction at La Mina recreation area, more communication towers near El Yunque, and as many as 249 summer cottages above La Mina recreation area (Huffaker 1989, see endnotes; Wadsworth 2009, see endnotes).



ABOVE: Built in the late 1940s and consolidated in the early 1980s, the island's major communication towers are situated at nearly 1000 m elevation along the spur road to El Yunque peak. (Photo by Iván Vicéns) ABOVE RIGHT: The Eliza Colberg girls scout camp, dedicated in 1950, has provided an outdoor training center for generations of youngsters. (Photo by Peter L. Weaver)

Chapter 12. MAJOR FOREST RESEARCH SITES

Several sites have been used at one time or another for research activities within the LEF. Permanent plots exist in all of the forest types (table 7). Ecological studies, however, are concentrated at lower montane forest locations like Bisley and El Verde, in riparian palm stand in the upper Espíritu Santo watershed, and in dwarf forest on Pico del Este. Although much is known about certain areas, detailed floral and faunal surveys are lacking for the upper watersheds lying to the north, east, and south of FS-27 (fig. 5). Unknown wildlife species similar to the frog reported 50 years ago could exist (Rivero 1963). Rare orchids, for example, are occasionally confined to relatively small areas, at times a single mountain peak (Kasomenakis 1988).

El Verde Ecological Studies

After purchasing the land in the 1930s, the Forest Service built the El Verde field station to provide research personnel with their first permanent overnight facilities on the forest (fig. 13) (appendix A). Laboratory facilities were added, renovated, and expanded in the 1960s and 1970s, and a dormitory was built in 2005. A canopy walkway and a permanent walk-up tower with monitoring equipment were erected nearby during the 1980s. Canopy weather data, currently monitored on the 22-m tower, are stored in a data logger and later sent to the El Verde field station. Two nearby streams are gaged, one by station

personnel and the other by the U.S. Geological Survey (fig. 9). Stream discharge is also monitored and stored in a data logger.

Between 1943 and 1946, plant collecting for the Institute herbarium, field surveys for timber species, and the establishment of permanent plots were initiated near the El Verde field station (table 7). Plot monitoring and limited research were carried out in the 1950s. The next major effort was between 1961 and 1967 when controlled underground nuclear explosions were proposed for the excavation of a sea level canal in Panama (Mowbray 2008). Researchers at the University of Puerto Rico Nuclear Center in Río Piedras established studies to determine how the lower montane forest functions before, during, and after gamma irradiation (Odum and Pigeon 1970). The LEF was selected because it was the only government-owned national forest with tropical vegetation. The study was set up at El Verde and concentrated



ABOVE: The Institute's first long-term plot of 0.72 ha was established above the El Verde field house in 1943. Note person next to large *Dacryodes excelsa* at left middle of photo. (Photo by Iván Vicéns) ABOVE RIGHT: The El Verde field station served as the research center for the tropical rain forest project during the 1960s. Today it is a National Science Foundation long-term ecological research (NSF-LTER) site. The building in the background dates to 1937 when it was used by the forestry staff during field surveys. (Photo by Peter L. Weaver)

on plant and animal populations, mineral cycles, metabolism, and energy flow within the ecosystem, as follows:

- **Chapter A**—energy-circuit modules, systems ecology, and radiation stress.
- **Chapter B**—past research; climate; plant species diversity, stand structure, and distributions; aerial photography; plant geometry and plant assemblages; woody plant identification keys and autecological studies; pollen analyses; herbicide effects; tropical forest associations; and other Caribbean forests.
- **Chapter C**—radiation experiment and the cesium source; and dosimetry, patterns of exposure, and a model of radiation response.
- **Chapter D**—effects of radiation on plant species; tree phenology; and hemispherical canopy photographs.
- **Chapter E**—radiation effects on animals; and studies on forest mammals, bird diversity, frogs, and insects.
- **Chapters F and G**—effects of radiation on microorganisms and cytological studies.
- **Chapter H**—mineral cycling in soils; forest biomass and chemical contents; litterfall; hydrogen budget; tritium movement; phosphorus cycle; electrical conductivity and flow rates of soil water; stomatal variation; foliar metabolite leaching; mycorrhiza; myxomycetes; fallout radioactivity and epiphytes; and the effects of ionizing radiation on leaf-fall and soil organisms.
- **Chapter I**—forest metabolism and energy flows; forest-floor organisms; insect herbivory, termites, and snails; photosynthesis; forest metabolism and evapotranspiration; and the ecological system at El Verde.

Although irradiation was the major emphasis of the project, many of the studies on control plots and elsewhere provided a wealth of information on tropical forest structure and function.

During the 1970s, the Terrestrial Ecology Division of the Center for Energy and Environmental Research at the University of Puerto Rico continued nutrient cycling and energy flow studies at El Verde. Between 1980 and 1987, the Rain Forest Cycling and Transport Project dealt with terrestrial and aquatic food webs. After a decade of observations, participants summarized their observations on the abundance, food habits, and the ecological roles of vertebrates and invertebrates (Reagan and Waide 1996). After Hurricane Hugo in 1989, research at El Verde focused on post-storm recovery (Walker and others 1991, 1996) (table 6). Investigations concerning climate, flora, fauna, or mineral cycling were summarized as project documents, research reports and theses, or as scientific publications in journals.

Since the mid-1950s, the El Verde field station has also been used by forestry professionals, scientists, students, and

teachers for educational programs. In the 1950s, participants from all over the world visited the site during tropical forestry short courses (Anon. 1954, Barres 1963, Lamb 1959, Wadsworth and others 1955). In the early 1960s, the field station was used by professors and summer students from U.S. universities. Recently, student volunteers have cooperated in data collection, as summer interns, or as participants in university research programs, workshops, and field trips. Workshops for K-12 (i.e., kindergarten through grade 12) teachers have also been held at El Verde and at the Eliza Colberg Girl Scout Camp (U.S. Department of Agriculture, Forest Service 2009).

Luquillo Forest Dynamics Plot (LFDP) at El Verde

The LFDP, established in 1990 under the auspices of the LTER, occupies 16 ha (500 x 320 m) near El Verde field station (Soil Survey Staff 1995) (fig. 13). The plot, located between 333 and 428 m, has been forest covered since the 1930s (Brokaw and others 2004; Thompson and others 2002, 2004). About one-third was selectively logged and 7 percent farmed. The remainder had been cutover to varying degrees and partially planted to shade coffee and fruit trees (Thompson and others 2007). In the 1960s, about 320 m² was clearcut as part of experimental work (Odum and Pigeon 1970). Today, the plot is part of a network of tropical forest plots managed by the Center for Tropical Forest Science. An order 1 soils survey carried out on the plot showed that upland soils composed 95 percent of the total, ranging from gently sloping to very steep (Soil Survey Staff 1995). The remaining soils, characteristic of stream channels, ranged from gently sloping to moderately steep. Past charcoaling activity was evident in certain areas. The LFDP and similar large plots elsewhere are needed to:

- Encompass a sufficient number of common and rare species to evaluate population changes.
- Determine typical plant spatial relationships.
- Monitor populations of plants to reveal their life history characteristics (growth, phenology, and age).
- Determine forest response to disturbances such as treefalls, landslides, and hurricanes as well as long-term environmental changes associated with global phenomena (Zimmerman and others 1994).

The Institute for Tropical Ecosystem Studies (ITES), a unit within the Faculty of Natural Sciences at the University of Puerto Rico's Río Piedras campus, currently carries out research at the El Verde field station and elsewhere in the LEF. Research is concentrated on long-term ecological studies relevant to the management of natural ecosystems. Specific areas of study are (Institute for Tropical Ecosystem Studies 2011):

- Population biology, community structure, and the effects of disturbance on tropical forests.
- Properties of atmospheric aerosols and their effects on clouds and climate on Pico del Este.
- Evolution of floral traits and the effects of invasive plants on community structure.
- Properties of inland waters, stream metabolism, biogeochemistry, hydrology, and water quality.
- Aquatic insects, their taxonomy, systematics, and role in forest ecosystems.
- Satellite image analysis and use of geographic information systems for habitat characterization.
- Soil processes and fauna, and the effects of natural and human disturbances on soils.
- Vegetation growth and changes on the Luquillo Forest Dynamics Plot (LFDP).
- Canopy trimming experiment, involving structural modification of trees, variable detritus loads on the forest floor, and regeneration.

A recent study was undertaken on the LFDP to determine the fate of 12 planted tree species after hurricanes Hugo and Georges (Thompson and others 2007). The species were: *Citrus paradise* Macfadyen, *Mangifera indica*, *Musa* sp., *Simarouba glauca* DC., *Artocarpus altilis*, *Calophyllum calaba*, *Genipa americana* L., *Hibiscus pernambucensis*, *Swietenia macrophylla*, *Syzygium jambos*, *Spathodea campanulata*, and *Coffea arabica*. The first four species remained relatively stable over time and the next six species first declined and then increased. *Spathodea campanulata* gradually increased and *Coffea arabica* declined. *Swietenia macrophylla* and *Syzygium jambos* were the only species that increased under shade. The rates of recruitment, mortality, and growth for all introduced species indicated that they would likely persist for some time, and in the event of greater hurricane frequency, could increase in population.

The canopy trimming experiment, with surrounding plot buffers, was set up on >1 ha of land. Different treatments totaled nearly 0.50 ha of pruned canopy (Richardson and others 2010, Shiels and others 2010). Stand manipulation increased light levels, throughfall, and total moisture but decreased litter moisture. Seedling density, ingrowth, and mortality were affected as *Cecropia schreberiana* and *Psychotria berteriana* quickly increased in abundance. The short interval of canopy openness and its influence on the regeneration of pioneer trees was the principal factor driving short-term recovery. Canopy opening was also the major determinant negatively impacting the diversity and biomass of the invertebrate communities within forest litter. Debris deposition played a secondary role. The effects of disturbance on some invertebrate taxa were still evident after 19 months when the experiment ended.

Long Term Ecological Research (LTER) at Bisley

In 1980, the NSF established the LTER program to provide scientists, policy makers, and society with a network of sites that would provide knowledge for the conservation and management of the nation's ecosystems, especially with regard to maintaining their biodiversity and social benefits. The 26 selected sites include a variety of ecosystems and researchers with a common mission. The Luquillo LTER was authorized in 1985 to explore tropical forest structure, dynamics, and the role of disturbance (Scatena 1989). Part of the program was set up in the Bisley experimental watersheds situated near Sabana in the northeastern part of the LEF (fig. 13). Both watersheds range in elevation between 265 and 455 m (Scatena 1989, Scatena and Lugo 1995). The soils are classified as clayey, highly leached, and well-weathered ultisols. Logging and the planting of subsistence crops like coffee, bananas, and upland rice occurred between 1830 and 1890. In the early 1930s, the



Since 1985, the Bisley watersheds have been a center for National Science Foundation long-term ecological research (NSF-LTER) regarding climate, water resources (i.e., water quantity, quality, and regimen), nutrient cycling, flora and fauna, and other topics. (Photo by Peter L. Weaver)



Biomass sampling was carried out several times in different parts of the Luquillo Experimental Forest, including Bisley, El Verde, Pico del Este, and this area of line planted mahogany near the Río Chiquito. (Photo by Peter L. Weaver)

Forest Service purchased the tracts (Zimmerman and others 1995). Subsequently, agriculture was abandoned and farmlands reverted to secondary forest. *Khaya nyasica* and *Swietenia macrophylla* were planted in gaps and openings. After 50 years, the net result of human activities was an increase in *Guarea guidonia*, *Inga laurina*, and *I. vera*, all previously used as coffee shade, and the presence of exotic timber species. In summary, “although the experimental drainages were never completely cleared or drastically altered, they have been selectively logged, fished, and probably exploited for placer ores” (Scatena 1989).

Much of the early research concerned introductory work and ecosystem responses to Hurricane Hugo, as follows:

- Physiography and history of the watersheds, and the effects of human activity on the structure and composition of the forest (García Montiel and Scatena 1994, Scatena 1989).
- Climate and water discharge monitoring (Scatena 1990).
- Hurricane impacts on tree species regeneration, biomass, litterfall, and nutrient contents (Chinea 1999, Lodge and others 1991, Scatena and others 1995).
- Flora, with an annotated plant list with 102 plant families, 255 genera, and 336 species of tree species, herbaceous plants, vines, and lianas (Chinea and others 1993, Rice and others 2004).
- Wildlife, including freshwater fish, frogs, and snails (Nieves 1998).
- Biomass and nutrient cycling, including the spatial variability in nutrients, factors controlling their availability to vegetation, and their distribution in soil and plants (Scatena 1998a, Scatena and others 1993).

Since 1986, LTER researchers have written >800 abstracts, research papers, theses, and dissertations (Almanac 2009) (LUQ LTER 2011). Today, program cooperators are exploring:

- Climatic effects on litter quality and the regulation of decomposition.
- Response of terrestrial and aquatic food webs to detrital pulses.
- Impact of disturbances on nutrient cycling, plant communities, and organic matter accumulation.
- Carbon export relations in watersheds and their association with soil characteristics and detrital dynamics.
- Effects of climatic changes over an elevational gradient on detritivore communities and their feedback on litter inputs and decomposition.
- Critical zone dynamics, a recently funded project, to address how processes, flow, and transformation of materials differ in landscapes with different bedrock but similar climates, land use, and geologic histories.

Riparian Palm Stand

In 1980, riparian palm research began on a 0.25-ha plot located at 750 m in the headwaters of the Río Espíritu Santo (Frangi and Lugo 1985, 1991, 1998). The studies revealed:

- About 765 stems >1 cm in d.b.h. of 27 tree species grew on the plot.
- *Prestoea montana* accounted for 40 percent of the tallied stems.

- About 68 percent of the vegetation biomass was in the wood, 10 percent in leaves, and 22 percent in the roots.
- Details regarding the carbon, phosphorus, and water cycles (i.e., rainfall, throughfall, stemflow, interception, runoff, transpiration, and evapotranspiration).

Periodic flooding, poor soil aeration, heavy annual rainfall, and low atmospheric saturation pressure deficits were suggested as the controlling factors in the growth of the palm. After Hurricane Hugo, the palm plot, protected by topographic position, showed only 1 percent tree mortality. About 30 percent of the trees had suffered notable impacts, mainly in the canopy, with 10 percent of the aboveground biomass being transferred to the forest floor. Changes in necromass (i.e., the weight of dead organisms) and nutrients on the forest floor were also summarized for a 20-year period (Lugo and Frangi 2003). A point of interest—the riparian palm plot included a portion of permanent plot CV-1, which was established along with other permanent plots in 1946 (fig. 13) (table 7).

Pico del Oeste Dwarf Forest

Beginning in mid-1960s, research was undertaken in dwarf forest on Pico del Oeste to answer questions regarding the composition of plant species, their growing conditions, and their adaptations for survival in the summit environment (Howard 1968, 1970a). From 1968 to 1977, the *Journal of the Arnold Arboretum* published 17 articles on the following topics:

- An introduction and review of cloud forest habitats, a list of vascular flora found on Pico del Oeste and their geographic distribution, and observations on stem growth and form, and on leaf structure, damage, and herbivory (Howard 1968, 1969).
- The microclimate of the summit, including rainfall, temperature, relative humidity, solar insolation, and cloud moisture interception (Baynton 1968, 1969).
- Transpiration rates (Gates 1969), chromosome numbers in flowering plants (Nevling 1970a), chemical studies of colored leaves (Wagner and others 1969), and phytochemical screening (Persinos and others 1970).
- Aerial roots (Gill 1969), and relations among soils, roots, and earthworms (Lyford 1969).
- Numerous plant studies, including two species of *Marcgravia* (Howard 1970b), a new species of *Gonocalyx* (Nevling 1970b), epiphytic mossy vegetation (Russell and Miller 1977), leafy Hepaticae (Fulford and others 1970, 1971), and algae (Foerster 1971).
- The dwarf forest flowering and fruiting cycles and an interpretation of seasonality (i.e., wet-dry periods) in a high rainfall environment (Nevling 1971).

The vascular flora on Pico del Oeste numbered 85 species, including 40 Dicotyledoneae (22 endemic to Puerto Rico), 14 Monocotyledoneae (2 endemic), and 31 ferns (3 endemic) (Howard 1969). Pico del Oeste contained 62 of the 156 leafy Hepaticae tallied within the LEF. Also encountered were 18 epiphytic mosses and 129 epiphytic algal species.

Heavy rainfall, the high incidence of fog, cloud moisture interception, and attenuation of solar radiation were considered as unusual climatic features on Pico del Oeste (Baynton 1968, 1969), leading one observer to suggest that the dwarf forest was a “large natural culture unit” (Foerster 1971, page 107). Soil leaching was considered a possible contributor to reduced tree stature whereas wind, although persistent, was not.

Pico del Este Dwarf Forest

Research near Pico del Este, about 1.5 km distant from Pico del Oeste, started in 1968 and has covered three major topics:

- Cloud moisture interception (i.e., deposition of fog) by vegetation on windward, ridge, and leeward sites in 1968-69 (Weaver 1972).
- Monitoring of dwarf forest recovery after a 1968 airplane wreck (Byer and Weaver 1977; Weaver 1990, 2000b, 2008; Weaver and others 1973).
- Monitoring post-Hurricane Hugo recovery after 1990 on six small plots, two each on ridge, slope, and ravine topography (Weaver 2000a, 2008).

The cloud moisture study revealed that intercepted cloud water added about 10 percent to the annual moisture budget of dwarf forest soils, and highlighted the importance of summit vegetation in the water balance of the LEF. Continuous monitoring at the airplane wreck and on the small plots near Pico del Este showed that the growth and recovery of dwarf forest trees from past disturbance was very slow; moreover, monitoring indicated that delayed mortality continued for several years after the passage of Hurricane Hugo.

In 1968, much of the 2-m wide trail leading 0.5 km to the plane wreck was under dwarf forest canopy. Grass and ferns, however, dominated two exposed areas. These patches, still evident 40 years later, now contain scattered tree seedlings and small saplings. By 2000, after Hurricanes Hugo and Georges, most trees shading the trail had perished, leaving much of the area in thickets of regenerating stems. Nearly a century ago, hurricanes were suggested as a factor in dwarf forest occurrence when La Mina Peak was found stripped of vegetation (Murphy 1916, Wadsworth 1970).

Chapter 13. FOREST PLANNING AND MANAGEMENT

Puerto Rico's forests declined dramatically from nearly complete cover at the time of European discovery to about 6 percent forested in the early 1940s (Birdsey and Weaver 1982, Wadsworth 1970). The small forest areas that survived reasonably intact were at highest elevations. In the case of the LEF, most of the montane, palm brake, and dwarf forests survived along with more isolated areas of lower montane forest.

By 2000, the combined population of the greater San Juan metropolitan area and larger towns surrounding the Luquillo Mountains was approaching 1.6 million, or more than 40 percent of the island's inhabitants (CEEPUR 2009) (fig. 1). The different forest types, attractive vistas, abundant water resources, and cool climate, especially near the summits, make the LEF one large, conveniently located refuge where visitors can glimpse into the island's past before human settlement and major modifications to the environment.

A survey of the >75 800 ha within eight municipalities surrounding the LEF during the 1990s showed 54 percent classed as agriculture, 26 as forest, 13 as developed or available for development, and 7 percent as protected (Lugo and others 2000). Lands in the area were undergoing two major trends: an increase in urban and suburban development; and a decline in agriculture and pasture accompanied by an increase in forest regeneration (Ramos González 2001). The Puerto Rican Planning Board suggested a buffer zone around the LEF in 1983, amended in 1991, to promote its conservation. Development, however, continued in violation of the suggested norms (Lugo and others 2000, 2004). Continued development near the border along with the uncertain effects of global change may make the LEF warmer and drier in the future (Crook and others 2007, Scatena 1998b). The hydrologic cycle could be altered, affecting water availability for ecological processes and human activities. Moreover, some global models project that hurricanes may become more intense and frequent. Such phenomena could have a dramatic impact on the LEF's forests causing migrations or losses of flora and fauna as well as changes in tree species abundances and distributions favoring secondary species with shorter life spans at the expense of primary species (Connell 1978, Scatena 1998b). Several species of frogs have already declined or disappeared (Joglar 1998). Increased temperatures, particularly during the summer months, could also negatively affect lizards that are normally active at low body temperatures, such as those that occupy tropical lowland forests (Huey and others 2008).

As part of the National Forest System, management of the LEF must follow the principal laws relating to Forest Service

activities such as the Multiple-use Sustained-Yield Act of 1960 and the National Forest Management Act of 1976 (U.S. Department of Agriculture, Forest Service 1983). In 1992, the Forest Service adopted a new operating philosophy called ecosystem management aimed at an ecologically balanced view of its responsibilities (Wellock 2010). Fashioned by the Northern Spotted Owl controversy, the Forest Service outlined four key principles to successful land management: (1) sustainability; (2) public involvement through comments and partnerships; (3) integration with interdisciplinary approaches; and (4) collaboration among all interested parties.

Puerto Rico is an island, not a continent, and the LEF is a small mountainous landscape located in the northeastern corner of that island. Some "multiple uses" that are sustainable in larger national forests may be incompatible in the LEF. Management modifications have been suggested for the LEF based on climate, parrot breeding, migrations of aquatic organisms, and seasonal use of recreation sites (Scatena 2002). Some suggestions relating to wildlife (i.e., the Puerto Rican parrot) are already in use; others dealing with stream fauna, water use, and recreation could have future application.

As part of the planning process, the Forest Service solicited comments regarding management alternatives for the draft version of the forest management plan. Public comments were submitted by 23 individuals, 16 Federal and commonwealth government agencies, and 14 organizations. The following topics, tentatively ranked according to the number of responses, were viewed by the public as major forest issues (U.S. Department of Agriculture, Forest Service 1997b, pages H-1 to H-142):

- Timber extraction—mostly against, with a few suggesting restrictions or site changes before implementation.
- Primary forest, wilderness, wild and scenic rivers, and the research natural area—all positive, highlighting the public's concern for forest protection.
- Mass transportation (trams or buses)—all in favor of alleviating traffic congestion along the highway but most against reopening PR route 191 blocked by a landslide 40 years ago.
- Property—all in favor of regulation of land development surrounding the forest and acquisition of property, including inholdings.
- Wildlife and habitat—all in favor of rare, endangered, and threatened wildlife protection, especially the parrot.
- Water and watersheds—some concerned about soil erosion, sedimentation, and water quality, quantity, and regimen during the year.

- Recreation—some concerned about recreation sites, trails, field interpretation, public education, tours, camping, site overuse, garbage, and noise.
- Research—most with favorable responses regarding research and the use of new information.
- Culture and history—a few concerned about forest history and protection of cultural resources.
- Special use permits—a few with comments about access roads and forest permits, including electronic sites.
- Law enforcement—some with comments on control at the forest border, entrance fees, and field monitoring to help maintain the forest.
- Other topics—stated at least once, biodiversity, biosphere reserve, use of native plants, species introductions or reintroductions, the fish hatchery, vacation cottages, forest swimming pools, nontimber products, use of herbicides, scenery, flights over the forest, volunteers or scouts in the forest, the planning process, and reclassification the LEF under the U.S. National Park Service or commonwealth environmental agencies.

The LEF's revised management plan provided direction and management guidelines under several topics—primary forest, sustainable timber production, wildlife, water, recreation, wild and scenic rivers, wilderness, access roads, and research—for the next 10 to 15 years (U.S. Department of Agriculture, Forest Service 1997a, 1997b) (table 19). The plan divided

the forest into two major uses: protection, including the wilderness, the research natural area, and wild and scenic rivers, totaling about 65 percent of the LEF; and human activities, including administration, communications facilities, recreation, and research (fig. 21) (table 19). The planning directives are considered below under nine headings.

Primary Forest

Primary forests are undisturbed by humans and contain the original structure and composition of species that characterized the island before settlement, including many rare and endemic plants and animals. Today, Puerto Rico's undisturbed primary forests cover < 1 percent of the entire island (Wadsworth 1949, 1950). About 50 percent of the LEF, or 5550 ha, contains forested lands that are virtually in primary condition.

The LEF's most valuable resource is its pristine forest land. Much of the primary forest has already been set aside as the El Toro Wilderness, totaling 4050 ha, or as part of the current Baño de Oro Research Natural Area (fig. 21) (table 2). The Baño de Oro, with a total of 2580 ha, includes the original 1949 tract of 745 ha and the proposed 1997 expansion of 1835 ha (U.S. Department of Agriculture, Forest Service 1997a; Weaver 1994). The scarcity of primary forest on the island

Table 19—Management areas in the Luquillo Experimental Forest^a

Management area ^b	Area ha ^c	Description
Protected areas		
Research Natural Area	2580	Existing and proposed expansion of Baño de Oro (i.e., non-manipulative research)
Wild and scenic rivers	524	Designated in 2002
Wilderness	4196	Designated in 2005; boundaries not marked in field
Subtotal	7300	All areas designated primarily for protection (64.6 percent)
Other areas		
Administrative sites	83	El Portal, Catalina Work Station, other Forest Service administrative facilities
Communication sites	79	El Yunque and Pico del Este communication facilities, associated roads, electrical transmission lines (special use permits total only 13 ha)
Developed recreation	469	Picnic sites, trailhead parking, decentralized interpretative facilities
Integrated activities	2517	Dispersed recreation and research
Research	372	Long-term ecological research (LTER) watersheds, forest dynamics plot, permanent forest plots, treatment-control studies
Timber demonstration	472	Sustainable timber production (inactive at moment)
Subtotal	3992	All areas designated primarily for human activity (35.4 percent)
Total	11 292	All areas combined

^aData from management plan (U.S. Department of Agriculture, Forest Service 1997a, 1997b).

^bAreas shown on maps (figs. 21 and 22).

^cBased on total land area during planning activities in the mid-1990s.

and its intrinsic value to society are major concerns. During the past, virtually every square kilometer of Puerto Rico was heavily impacted by human activity. Another issue is the unknown future impact of global warming on the island's forests and its possible impact on the LEF's wildlife.

"Casual observers underestimate the role of continuous use of trails and recreation use in modifying the ecology of forest stands, behavior of animals, abundance of species, and spread of exotic species" (Lugo 1994). It is encouraged that if trail development or other increases in human activity are proposed for the wilderness that all potential impacts are considered with a focus on endangered and endemic species, notably the parrot. The main island of Puerto Rico has no other place that qualifies for wilderness. Careful monitoring of flora and fauna within the wilderness, however, could yield important information for improved forest management.

Demonstration of Sustainable Timber Production

Sustainable production of wood is needed throughout the tropics and the LEF has the potential to demonstrate the productivity of managed secondary forests. Previously logged and cultivated, the lower slopes of the forest have either recovered naturally or have been planted with timber species, mainly *Swietenia* hybrid and a few other species. Earlier versions of the forest management plan suggested that a small scale sustainable commercial timber harvest could be implemented on lands reforested since the 1920s. The proposal for commercial timber harvest, however, was highly controversial and was suspended in the revised plan due to public outcry (U.S. Department of Agriculture, Forest Service 1997b).

As urban expansion continues, the LEF's forest ecosystems become increasingly more valuable as an integral unit to protect flora, fauna, and water resources benefiting the heavily populated northeastern part of the island. Timber harvest could negatively impact roads, soils, water quality, wildlife habitat, and recreation. Logging could remove future foraging and nesting sites, and slow the expansion of the parrot back into previous habitat along the LEF border. Sustainable timber harvest could be demonstrated on privately owned forest lands and at selected sites within the drier forests of the commonwealth reserve system.

Wildlife

Puerto Rico's dense human population either cleared or modified most of the island's forests during settlement and development. Today, secondary forests are gradually recovering outside of the LEF, but most of those areas differ

significantly in species composition and are privately owned (Birdsey and Weaver 1982, Brandeis and others 2007, Franco and others 1997). The upper LEF contains not only the largest block of undisturbed forest on the island but also the wettest. Moreover, it has a diverse flora and fauna, including several island endemics some of which are confined to the LEF. Endangered, threatened, and sensitive species living within the LEF are primary management concerns (U.S. Department of Agriculture, Forest Service 1997a).

Recent research suggested that estimates of avian extinctions based on species-area relations overestimated actual extinction rates caused by habitat conversion whereas the use of a species-area relationship based on endemics improved those estimates (Kinzig and Harte 2000). Moreover, a critical level for extinctions appeared after 40 percent of an original habitat has been cleared. In summary, "At low levels of habitat destruction, estimates of species loss using the endemics-area relationship are significantly lower than existing estimates, but a rapid rise in predicted species loss when a threshold of habitat loss is exceeded suggests that extrapolation of recent rates of species loss may underestimate future species extinctions under continuous land clearing" (Kinzig and Harte 2000). The possible implications of these derived relationships for the LEF are uncertain. It is noteworthy, however, that the LEF contains many endemics, that about half of the LEF has already been disturbed by past human activities, and that development continues in areas surrounding the forest.

Some proposed activities within the LEF could involve disturbance and habitat change. Among them is an increased presence of humans whose impact may extend as far as 0.5 km beyond the roads and recreation areas that have been built for their activities (Snyder and others 1987). An endemic parakeet (*Aratinga maugei*) was last recorded late in the 19th century and *Corvus leucognaphallus* in 1963. By 1968, *Amazona vittata* was listed as rare and endangered. Today, two of the LEF's frog species, *Eleutherodactylus eneidae* and *E. karlschmidti* are threatened, or possibly even extinct. Three others, *E. gryllus*, *E. locustus*, *E. portoricensis*, have declined in numbers. Moreover, *Dendroica angelae* is being considered for listing as an endangered species (tables 11 and 12). Most wildlife has survived to the present because the mountainous interior remained largely isolated and intact.

Future management would benefit from the suggestions of experts who have studied wildlife, notably the parrot. One pointed out the importance of *Dacryodes excelsa* fruits as parrot food from August through November (Rodríguez-Vidal 1959). Others stated that "attempts to spread recreational activities more evenly through the forest could have disastrous consequences. Parrots are exceedingly sensitive to human disturbance near their nests ..." (Snyder and others 1987). They added that "most of the present parrot range in Luquillo

Forest is well protected. Still unresolved is the question of what areas of lower elevation forest might be reserved for parrot use if the population should recover from its present depressed condition” (Snyder and others 1987). They also pointed out that the undisturbed Cristal-Camándulas area in the northeastern part of the forest appeared to be a good site for the future release of parrots. An important point to consider for parrot management is that the species may never recover in the LEF if better lands are not made available at lower elevations.

The critically small parrot population is largely confined to only 1500 ha within the El Toro Wilderness Area. The area is bounded east and west by two roads, FS-10 and PR route 186, with their associated human presence and noise (U.S. Department of Agriculture, Forest Service 1997a, 1997b). The lands surrounding the LEF—abandoned pasture, suburban housing, and secondary vegetation—are currently not occupied by the parrot. Extinction is most likely for species that require large territories for survival, especially in areas like the LEF which experience recurrent hurricanes. Isolated landscape remnants can experience an influx or “supersaturation” (Saunders and others 1991) of species, including predators, from surrounding areas. Red-tailed hawks, a major threat to the parrot’s survival, abound in the LEF where they find adequate prey like lizards and forest birds, including parrots. In addition, they have access to a “buffet of domestic prey: chickens, pigeons, sundry pets including puppies and kittens, scavenging rats, mongooses, and no longer truly wild native doves, grackles, and other birds that have come to survive on table scraps and the panhandled crumbs of human largess” in the suburbanized areas surrounding the forest (Watlington 2008). There would be great value in seeking a means to extend the parrot’s range throughout the LEF and into lower elevations near the forest. One approach could involve an integrated landscape that protects the forest intact and incorporates land stewardship efforts on the part of surrounding landowners (Saunders and others 1991). Critical parrot habitat in mature lower montane forest must remain protected. Also, some suggest that secondary forest along the LEF’s border “is critical to the recovery of the PR parrot (especially advanced secondary Tabonuco [i.e., lower montane] forest ...” (U.S. Department of Agriculture, Forest Service 1997b).

Other current management concerns for LEF wildlife are:

- Defining, expanding, and demarcating critical wildlife habitats as a priority, including lower montane forest for the future expansion of parrot populations.
- Monitoring management practices to assure the protection of wildlife habitat, especially in the heavily used forest interior where refuse can support introduced pests like mongooses and rats.
- Enforcing Puerto Rican Parrot restrictions at all times, notably during the breeding season (i.e., “plan other activities ... at least 500 m from [parrot] nest sites” (U.S. Department of Agriculture, Forest Service 1997a).
- Restricting entry into Amazona vittata areas during nesting season.
- Cooperating with the FAA to restrict flights over the LEF to help protect the parrot during the recovery program.
- Controlling and monitoring access to the wilderness area (i.e., the currently occupied parrot habitat) because of associated problems of noise, refuse, and introduced exotics.
- Ameliorating downstream barriers to fish and shrimp migrations, and control of poaching.
- Establishing and enforcing norms for site use and monitoring access to favorite recreation areas to assure that resource quality is maintained (e.g., La Mina Falls and the issues of congestion, sanitation, water quality, and noise).

Water

Densely populated northeastern Puerto Rico receives water supplies from intakes within and just below the LEF boundary (Naumann 1994). Moreover, forest streams provide habitat for aquatic organisms, including fish and shrimp, throughout much of their extent. The maintenance of aquatic linkages between coastal lowlands and higher elevations is imperative if these organisms are to be protected. Diversion of water for domestic and other uses reduces streamflow and impedes migrations of aquatic organisms.

Population growth, urban and suburban development, and tourism will increase water demands in the future. Moreover, leaky pipes cause water losses within the island’s current delivery system. Losses between the reservoirs and the island’s domestic and commercial users average about 43 percent (Crook 2005). Better water management requires (Crook 2005, Naumann 1994):

- Monitoring of LEF’s water resources and biota to assure sufficient flow for aquatic organisms, notably in dry years.
- Recognizing the cumulative effects of water withdrawal and the limited capacity of streams to simultaneously provide sufficient water for aquatic wildlife and municipal water supplies.
- Developing alternative “ecologically friendly” water control devices that facilitate wildlife migrations where feasible (e.g., in-channel intakes consisting of stainless steel risers or intakes with outlets for minimum flow in lieu of dams).
- Requiring construction of future water intakes at or below the LEF border to maintain the ecological integrity of the forest.
- Requiring maintenance of all water intakes, informing users of findings, and imposing fines in cases of negligence.

- Requiring local government agencies to assume responsibility for reducing island water demand, including repair and maintenance of pipes to reduce water losses during delivery.
- Taking appropriate measures against illegal water removals.
- Considering further price increases for water to help reduce consumption.

“Puerto Rican public water supply has been poorly maintained and managed” in the past (Naumann 1994). The ecological integrity of the LEF depends on the appropriate conservation and management of its water resources. The local government is well aware of water distribution problems and is attempting to implement conservation measures.

Wild and Scenic Rivers

Three stretches of rivers within the LEF—the Río Icacos, Río de La Mina, and Río Mameyes—have been set aside as exceptionally attractive scenic areas; moreover, the upper portion of the Río Mameyes has been designated as wild (fig. 21). These are the only tropical rivers within the national Wild and Scenic Rivers system and should remain protected through management guidelines. Future water extraction from these streams is prohibited (Crook 2005).

Río de La Mina is not only a scenic river, but its attractive waterfalls border an area currently classified in the management plan as occupied parrot habitat (U.S. Department of Agriculture, Forest Service 1997b). The distance of the waterfalls from PR route 191 is about 30 minutes for most hikers. Local holidays draw massive influxes of people for bathing and picnicking near the waterfalls. Noise from the site may be heard for a considerable distance providing an experience incongruent with the solitude of the forest. Moreover, on crowded days, heavy human use around the falls may temporarily alter the stream’s chemical composition (e.g., human wastes, body lotions, discarded food, and refuse) and affect population of algae and aquatic organisms in the vicinity. Large groups can also negatively impact riparian vegetation causing streambank and soil erosion, especially in instances where crowded conditions force some bathers to seek alternative bathing sites downstream. Finally, some more daring bathers climb the slippery rocks behind the falls, an activity that could result in serious injury.

Past experience with water-based activities at higher elevation within the same watershed—the near the La Mina Recreation Area—were disastrous. “During the 10 years that the pools were open we found it impossible to control safe use (e.g., drinking and nighttime use) and there were several fatalities” (U.S. Department of Agriculture, Forest Service 1997b). Swimming and bathing in the freshwater pools have been

prohibited since the 1950s. The current heavy use of the La Mina waterfall site for bathing and water play involves issues of water pollution, safety, and future use of the forest by the parrot. More accessible bathing sites are available at lower elevations near the forest border.

Wilderness

Naturalness, wildness, and protection from human influence highlight the values of wilderness to society. However, during the past 17 years, rapid suburban development has occurred in areas adjacent to the El Toro Wilderness (Lugo and others 2004, Ramos González 2001). Active cooperation with the local government will be required to enforce buffer zone legislation around the forest (Lugo and others 2000, 2004).

Future management of the wilderness needs to define goals and desired conditions, and needs to recognize the issues or problems that lie between existing and desired conditions (McCool and Cole 1997). Several planning processes, including the limits of acceptable change, have been proposed as a means of improving recreation management in protected areas (i.e., specifically, the issue of recreation carrying capacity in wilderness areas).

The El Toro-Tradewinds trail, first constructed during the CCC days, traverses the wilderness area (figs. 5 and 21). Heavy rainfalls and recurrent storms cause treefalls, trail erosion, and landslides, notably in drainages and ravines. Future trail maintenance expenses could affect access to the wilderness. Limiting and monitoring access could reduce encounters among hikers (U.S. Department of Agriculture, Forest Service 1997a) and would help assure that the wilderness remains what the term implies—an experience with nature. Recently, a noninvasive plant management plan was drafted. The tentative plan indicated that at least 82 exotic plants were already growing in the wilderness area (U.S. Department of Agriculture, Forest Service 2009, see endnotes).

Other issues to consider are (U.S. Department of Agriculture, Forest Service 1983, 1997b):

- Marking wilderness boundaries according to Congressional designation.
- Preparing a wilderness plan, including limits of acceptable change.
- Maintaining primitive standards for maintenance work (e.g., nest cavities in coordination with the Puerto Rican Parrot program).
- Conducting research on the flora, fauna, insects, and disease, and the mapping of wildlife habitats and cultural sites according to management guidelines.

- Requiring permits for plant or animal collections.
- Prohibiting timber harvest, timber salvage, and manipulative forest research.
- Prohibiting road construction or other developments (e.g., water and electrical transmission lines), mineral activity, and motorized or mechanized bicycle use.
- Authorizing recreation management for low use and primitive experiences such as special use permits for nonoccupancy activities compatible with wilderness character. The issue of aircraft flying low over the LEF recently came to the attention of forest managers and the public. Although such flights are presumably prohibited to help recovery of the Puerto Rican Parrot, they apparently take place recurrently as witnessed by two recent accidents, the last of which occurred in 2008 within the wilderness area (Hernández Pérez 2008, Torres 2002). Low-flying aircraft must be excluded from the airspace above the entire LEF for safety and wildlife reasons. In the case of wilderness, low flying aircraft could also be viewed as issues of air quality or noise pollution such as an intrusion on the natural soundscape (Landres and others 2008).

Recreation and Conservation Education Programs

Current recreation activities include driving, scenic viewing, picnicking, hiking, stream bathing, and nature study. Use of summer cottages near La Mina and camping are minor activities. Most current forest visits are confined to daylight hours.

Most recreation sites are concentrated along the major roads resulting in traffic congestion at most sites. Although hiking trails are sufficient, trailhead parking is restricted and interpretive signs are few and limited in content. More interpretation and environmental education would benefit many forest visitors. However, increased recreational development could adversely affect the natural qualities of the forest that many visitors find appealing (U.S. Department of Agriculture, Forest Service 1997b). Proposed developments should not alter the main experience that the LEF can provide—an involvement with nature. Guidelines are needed for commercially operated visits to the forest. These could involve recurrent meetings to discuss safety, forest protection, and accuracy of information provided to the public.

Several potential themes are available for interpretation at El Portal Rain Forest Center and elsewhere on the forest, including:

- Geology and soils: The formation of the Luquillo Mountains spans millions of years and has produced different rock formations and soil types evident at different locations within the forest.
- Climate and water: Rainfall is heavy and residents depend

on water resources of the Luquillo Mountains for domestic and commercial uses. Management is concerned with balancing the water needs for aquatic organisms and the island's growing human population. One major objective is to maintain water quantity and quality during the year.

- Hurricanes: Forest conditions vary with time ranging from pre-hurricane structure and composition through damage on the day of the storm to post-storm recovery (i.e., a few days, a few months, and a few years later). Information from permanent plots on the forest would allow reconstruction of likely forest conditions during different phases of recovery.
- Gradient phenomena: The abundance of flora and fauna with changes in elevation, aspect, topography (e.g., ridge, slope, and ravine), and exposure within the mountains is influenced by climatic factors and soil types.
- Species diversity, classification, and life history: The LEF has a rich plant and animal diversity maintained by mild temperatures and heavy rainfall. The fauna and flora may be abundant, rare, endemic, or endangered. Moreover, species vary considerably in size and life span and have different strategies for reproduction, survival, and growth.
- Global warming: Changes that the LEF could experience during global warming remain speculative and include an increase in temperature, a change in rainfall, more frequent and violent hurricanes, changes in cloud cover on the summits, alteration in forest species and types, an increase in secondary tree species, decline of amphibians, and changes in the distributions of bird and reptile species.
- Dwarf forest: Among the most interesting forest types on the planet, dwarf forest tells a fascinating tale of wind, rain, cloud drip, saturated soils, stunted trees, aerial roots, thick leaves, endemic flora, and abundant epiphytes. The forest, characterized by generally low productivity, is adapted to survive in the inclement environmental conditions that characterize the summits.
- History: Pre-Columbian use of and Spanish settlement



Members of the Natural History Society enjoy a short visit to the dwarf forest at Pico del Este on a typical wet, cloudy day. During the year, cloud cover intercepted by the summit vegetation (i.e., trees and epiphytes) adds 10 percent more water to the soil than is provided by rainfall. (Photo by Peter L. Weaver)

within the Luquillo Mountains, and the impacts of both on forest resources make an interesting story. Structures, facilities, and sites built or used during the CCC days could also be explained with interpretative signs.

- Research and management issues: The role of the Forest Service, with its activities in both research and management, is not well known by forest visitors. Research in the LEF has included climate, geology, soils, water, flora, fauna, human history, ecology, and other topics. This information is available to managers to help formulate management plans.
- Puerto Rican handicrafts: The onsite production and sale of carved native woods, paintings in natural settings, and other handicrafts could benefit local artisans and serve to educate the public.
- Law enforcement: The need for regulations and restrictions within the LEF are valid topics for public education. Others include habitat needs and regulations to protect wildlife, prohibition of hunting, and the need for carrying capacity estimates and monitoring to conserve and sustain forest ecosystems.
- Natural areas in Puerto Rico: Access to other major outdoor areas such as the commonwealth forests, Puerto Rico Conservation Trust properties, U.S. Fish and Wildlife refuges, and botanical gardens.

Conservation education is distinct from interpretation in that it targets particular audiences using different methods in a structured, formal setting (U.S. Department of Agriculture, Forest Service 2009). These efforts are often age specific and provide a series of experiences such as classroom presentations, teacher training, and curriculum and media development. Some of the most widely used conservation education programs include Smokey Bear, Woodsy Owl, Project Learning Tree, Nature Watch, Partners in Flight, Leave No Trace Inc., Passport in Time, The Natural Inquirer, Sustainable Operations/Climate Change, More Kids in the Woods (substituted by teacher training programs since 2000), and Eastern National-EYNF Interpretative Association. In 1999, the Caribbean National Forest published a training document for teachers (Ruiz Díaz and others 1999). Among the objectives were to familiarize participants with different forest types, the services that they provide, and their importance in political, economic, and social events on the island. Students would be made aware of the island's renewable natural resources and possible ways that they could be involved in their conservation. Ecosystems, erosion, limiting factors, and carrying capacities were among the topics reviewed. Finally, students were introduced to ways that they could reduce human demands on natural resources.

Puerto Rico has many other sites for outdoor recreation. These include (Ventosa-Febles and others 2005, Weaver and Schwagerl 2008):

- The commonwealth forest reserve system, totaling about 25 000 ha, contains 15 forests located in coastal mangroves, the limestone hills, and in the central mountains.
- The Puerto Rico Conservation Trust has >9800 ha that include 20 properties and four easements scattered through the island.
- The U.S. Fish and Wildlife Service have five refuges that total about 9500 ha. Two are located in southwestern Puerto Rico, and the remainder on the offshore islands of Culebra, Desecheo, and Vieques.

Outdoor recreation in Puerto Rico would benefit from improved collaboration among the island's management agencies and private entities. A shared vision of resources and their potential could improve recreational opportunities. Several activities would be best done at locations elsewhere in Puerto Rico, such as competitive bicycle racing, outdoor camping, and geocaching (i.e., GPS location of sites). More accessible and safer sites exist for stream bathing on both public and private properties outside of the LEF.

Access (Roads, Trails, Aquisitions)

The 50-km network of existing roads dissects the forest north to south, and then west to east from PR route 191 to Pico del Este, about 1 km from the southeastern forest boundary (fig. 5). Maintenance of the present road system is imperative, particularly PR route 191 from Palmer to the recreation and communication sites. The large 1970 landslide closed PR route 191 between km 13 and km 21 (fig. 13). The current situation leaves the southern part of the LEF as an integral, roadless block of forest. Motor vehicle access to the forest interior is controlled at a single point—the intersection of PR route 191 and PR route 9966 (fig. 5). The slide fortuitously helps to protect habitat for the future expansion of the Puerto Rican parrot to lower elevations in drier parts of the forest.

Mother Nature—rugged, isolated terrain and heavy rainfall—allowed the interior of the LEF to survive during the past century. The current recreation plan states that “the forest has a greater capacity for people (picnicking, hiking, sightseeing, etc.) than it has for transiting and parked vehicles” (U.S. Department of Agriculture, Forest Service 2009). On the same page, the plan mentions that heavy forest use during the month of July currently results in “incident” traffic control measures to avert clogging of PR route 191. On July 25, 2009, the number of cars parked above Coca Falls was estimated at > 500 (see footnote 1). Available parking spaces, including specially designated overflow parking areas normally closed to vehicles, accommodates less than half that amount.

The plan recognizes transportation needs to help alleviate congestion and to provide access, especially on holidays and

busy weekends (Parés Arroyo 2010; U.S. Department of Agriculture, Forest Service 1997b). Re-opening PR route 191 would involve costly construction because of geologically unstable substrate and would also complicate the operation of a mass transit system. Moreover, the public does not favor reopening the road. Highways skirting the border still provide access to the northern, western, and southern fringe of the forest for those interested in driving along other scenic roads. In the interim, current restrictions will remain for vehicular traffic on the FS-10 and FS-27 roads leading to communication towers. Also, foot traffic on permanent plot monitoring sites in the Bisley watersheds should be restricted to designated trails.

At least four properties totaling about 62 ha are included in the current land acquisition strategy: (1) the 13 ha Cartagena tract along PR route 186; (2) the Río Fajardo tracts, two adjacent parcels of 20 ha; (3) the 2 ha Río Sabana tract near the Sabana Research Station; and (4) the 27 ha Charco Frío tract adjacent to the Río Fajardo (El Yunque National Forest 2010). All of these lands border the LEF and would serve several purposes such as the consolidation of the LEF, expansion of parrot habitat, protection of wildlife, and future recreational opportunities.

Research

Research carried out in the LEF during the past century has made a valuable contribution to the conservation and management of tropical forests worldwide. Much of the earlier work concentrated on identification of the flora and fauna, reforestation of abandoned agricultural lands, and silviculture. Today, the emphasis is on ecosystem management, landscape ecology, wildlife, and issues of global warming (U.S. Department of Agriculture, Forest Service 2008). Current

global concern regarding deforestation and its consequences has highlighted the need for a greater understanding of the ecology of tropical forests to facilitate their recovery, improve their management, and provide educational experience for future managers and researchers. Research should help to answer critical management concerns such as:

- Maintaining and updating inventories of native vascular plants and vertebrate fauna.
- Identifying the habitat needs of native species with special attention to endangered species.
- Determining the carrying capacity and monitoring use of the forest interior, especially its trails and waterways.
- Monitoring water diversions and use, and effects on aquatic wildlife.
- Maintaining and publishing records of tree planting and growth.
- Monitoring forest health (i.e., insects and disease) via surveys of the flora and fauna, including invasive species.
- Investigating and summarizing forest history, including information on settlement, previous resource use, and existing structures.
- Fostering research on the flora and fauna within parts the LEF that have been overlooked in the past.
- Monitoring the effects of global change on the LEF's climate, flora, and fauna.

In addition to the above, the IITF maintains a continuous research program that involves ecology, disturbance, ecosystem functioning, biodiversity, watershed dynamics, migratory birds, and invasive species (U.S. Department of Agriculture, Forest Service 2008). Much of this research is carried out with cooperators in Puerto Rico, the United States, and elsewhere



LEFT: For many years, heavy use of the forest roads during holidays and weekends has caused congestion in the upper forest. RIGHT: Dr. Frank H. Wadsworth, Institute of Tropical Forestry director from 1956 to 1979, explains the results of thinning in secondary lower montane rain forest to visitors from the World Wildlife Fund, InterAmerican University, and U.S. Department of Agriculture Forest Service offices in Washington and Atlanta. (Photos by Peter L. Weaver)

EPILOGUE—*QUO VADIS?*

The LEF, with its flora, fauna, water supplies, and opportunities for recreation and education, has largely survived the disturbances caused by settlement and development of the island. Human influence within the LEF, however, is ubiquitous and includes administration buildings, the El Portal Rain Forest Center, main and tributary roads, trails, radar and communication towers, recreation areas, picnic areas, summer cottages, small dams for water supplies, stream gage stations, experimental and permanent plots, and people driving, walking, picnicking, and bathing. Moreover, the forest is not pristine—at least one-half was disturbed in varying degrees by human activity, which included gold mining, logging, farming, tree planting, silviculture, and recreational developments. Since the 1980s, many homes have been built on the lower slopes surrounding the forest. All of these activities serve to isolate or fragment the LEF and expose its fauna to increased human influence. One bird species has been lost, another is listed as rare and endangered, and yet another is being considered for listing. Two frog species are presumed extinct and three others have declined in numbers. Moreover, since 1975, ecologists have warned about the future effects of global warming, including rising temperatures, more devastating hurricanes, and possible migrations or losses of flora and fauna.

Multiple-use planning has designated uses for the LEF. Attempts to accommodate more visitors in the forest, however, would place a heavier burden on what most needs to be protected—wildlife, water, and a tranquil outdoor

experience. The LEF is not like the other 171 national forests located in the United States. First, those forests average 40 times larger than the LEF and do not contain its abundance of endangered or threatened flora and fauna. Second, the LEF is surrounded by towns, cities, and summer homes with a population density approaching 1250 km⁻² (fig. 1). The LEF's natural and human setting requires that attention be given to tradeoffs among management alternatives because its size and existing pressures do not allow the forest to accommodate all options. The LEF is small, representing about 1 percent of the island. Sustainable human carrying capacities need to be determined, and forest educational programs should strive to make the forest a memorable experience with nature. Comprehensive land management planning for the island should involve all of Puerto Rico's natural resource entities and their land units (i.e., the LEF, the Commonwealth Forest Reserve system, the Conservation Trust, and other public and private areas).

In summary, the LEF has two major designations—experimental forest and national forest—and a variety of possible uses. Better alternatives for some recreational activities exist outside of the forest. No feasible alternatives, however, are available for most of the LEF's endemic or classified flora and fauna. Public input to the management plan has shown that protection of primary forest (i.e., the wilderness, the research natural area, and wild and scenic rivers), wildlife (e.g., the parrot and rare frogs), and water resources are major concerns.

ACKNOWLEDGMENTS

Several individuals helped with information regarding the LEF: Wayne Arendt and Joseph M. Wunderle, Jr. with information on the occurrence of bird species seen during field studies and annual Christmas counts; Tom Brandeis with the survey information; Carlos Domínguez Cristóbal and Jeffrey Walker with historic and cultural information; William Gould with comparable datasets; Carolyn Krupp and Sidney Salyer with property acquisition records and special uses; Edgardo Martínez with property details and access to old forest maps; Alan Mowbray with details about past military activities; Maya Quiñones with preparation of new figures and maps; Luis Rivera with information on forest plantings; Iván Vicéns with field assistance and photographs; and Frank H. Wadsworth with details regarding species trials, past plantation records, and numerous anecdotes regarding the forest. Reference information was acquired from the Archivo General de Puerto Rico in old San Juan and the Puerto Rican collection in the University of Puerto Rico main library. Jorge Morales and Gisel Reyes helped locate references in the Institute's library, and Liz M. Pagán in the Agricultural Experiment Station library.

Reviewers who offered valuable comments on the draft manuscript were: Thomas J. Brandeis, U.S. Department of Agriculture, Forest Service, Southern Research Station, Knoxville, TN; Nicholas V.L. Brokaw, University of Puerto Rico, Río Piedras; Peter G. Murphy, retired professor at Michigan State University; Héctor Manuel Torres-Camacho, U.S. Department of Agriculture, Forest Service, Camp Santiago Training Center; and Sheila E. Ward, Mahogany for the Future, Inc., San Juan. Additional reviewers were Wayne J. Arendt, Frank H. Wadsworth (retired), Skip Van Bloem, and Joseph M. Wunderle Jr., colleagues in the U.S. Department of Agriculture, Forest Service in Río Piedras; Felipe Cano, Carolyn Krupp, José R. Ortega, Carolyn Pabón, and Blanca I. Ruiz in the El Yunque National Forest; and Thomas Schmidt at the Northern Research Station. This work was done in cooperation with the University of Puerto Rico at Río Piedras.

ENDNOTES

- Anon.** 1941. Annual report of the Tropical Forest Experiment Station. 21 p. Unpublished report. On file at: U.S. Department of Agriculture, Forest Service, International Institute of Tropical Forestry Library, Jardín Botánico Sur, 1201 Calle Ceiba, San Juan, PR 00926-1119.
- Arendt, W.** 2008. Birds—El Yunque National Forest. 8 p. Unpublished list. On file at: U.S. Department of Agriculture, Forest Service, International Institute of Tropical Forestry Library, Jardín Botánico Sur, 1201 Calle Ceiba, San Juan, PR 00926-1119.
- Bruner, E.M.** 1918. Report upon the preliminary examination of the timber and fuel resources of the Luquillo National Forest. 11 p. Unpublished report. On file at: U.S. Department of Agriculture, Forest Service, International Institute of Tropical Forestry Library, Jardín Botánico Sur, 1201 Calle Ceiba, San Juan, PR 00926-1119.
- Caribbean National Forest.** 1994. Evaluation of emergency water withdrawal for Caribbean National Forest. 5 p. Unpublished report. On file at: El Yunque National Forest, Route 191, Intersection 988, km 4.4, Barrio Barceloneta, Río Grande, PR 00721.
- Chudnoff, M.** 1981. Unpublished list of specific gravity estimates for several species of Puerto Rican woods. Information available at: U.S. Department of Agriculture, Forest Service, Forest Products Laboratory, One Gifford Pinchot Drive, Madison, WI 53726.
- El Yunque National Forest.** 2008. Birds—El Yunque National Forest. 3 p. Unpublished list. On file at: El Yunque National Forest, Route 191, Intersection 988, km 4.4, Barrio Barceloneta, Río Grande, PR 00721.
- El Yunque National Forest.** 2009. Map record file. El Yunque National Forest. Maps on file at: El Yunque National Forest, Route 191, Intersection 988, km 4.4, Barrio Barceloneta, Río Grande, PR 00721.
- Gerhart, G.A.** 1936. Caribbean National Forest: La Mina Recreational Area, accomplishments and proposed recreational developments. Washington, DC: U.S. Department of Agriculture, Forest Service; Government Printing Office. 27 p. + maps and photographs. On file at: U.S. Department of Agriculture, Forest Service, El Yunque National Forest, Route 191, Intersection 988, km 4.4, Barrio Barceloneta, Río Grande, PR 00721.
- Huffaker, L.E.** 1989. "Hollow shells"—an analysis of the summer home program on the Caribbean National Forest. 45 p. Unpublished document. On file at: U.S. Department of Agriculture, Forest Service, El Yunque National Forest, Route 191, Intersection 988, km 4.4, Barrio Barceloneta, Río Grande, PR 00721.
- Kramer, W.P.** 1932. Policy statement—Luquillo National Forest, Porto Rico. 57 p. Unpublished document. On file at: U.S. Department of Agriculture, Forest Service, International Institute of Tropical Forestry Library, Jardín Botánico Sur, 1201 Calle Ceiba, San Juan, PR 00926-1119.
- Muñoz, J.E.** 1965. Timber management plan for the Luquillo Experimental Forest. San Juan, PR: U.S. Department of Agriculture, Forest Service, Caribbean National Forest. 54 p. Unpublished document. On file at: U.S. Department of Agriculture, Forest Service, International Institute of Tropical Forestry Library, Jardín Botánico Sur, 1201 Calle Ceiba, San Juan, PR 00926-1119.
- Rivera, L.** 2010. Personal communication. Luis Rivera, Forester, U.S. Department of Agriculture, Forest Service, El Yunque National Forest, Route 191, Intersection 988, km 4.4, Barrio Barceloneta, Río Grande, PR 00721.
- Santiago Cazull, H.** 2000. Architectural conservation assessment for repairs to ranger dwelling (Cubuy House), Caribbean National Forester, Puerto Rico. 27 p. Unpublished document. On file at: U.S. Department of Agriculture, Forest Service, El Yunque National Forest, Route 191, Intersection 988, km 4.4, Barrio Barceloneta, Río Grande, PR 00721.
- Upson, A.** 1949. The Caribbean Forest atlas. Río Piedras, PR: U.S. Department of Agriculture, Forest Service, Tropical Region. 43 p. + tables and maps. Unpublished document. On file at: U.S. Department of Agriculture, Forest Service, El Yunque National Forest, Route 191, Intersection 988, km 4.4, Barrio Barceloneta, Río Grande, PR 00721.
- U.S. Department of Agriculture, Forest Service.** 1991. El Yunque peak electronic site plan. Unpublished document. On file at: U.S. Department of Agriculture, Forest Service, El Yunque National Forest, Route 191, Intersection 988, km 4.4, Barrio Barceloneta, Río Grande, PR 00721.
- U.S. Department of Agriculture, Forest Service.** 1995. Tabulation of National Forest lands—Caribbean National Forest: 5490 Status (conveyance file). 4 p. Unpublished table. On file at: U.S. Department of Agriculture, Forest Service, El Yunque National Forest, Route 191, Intersection 988, km 4.4, Barrio Barceloneta, Río Grande, PR 00721.
- U.S. Department of Agriculture, Forest Service.** 2009. El Yunque National Forest, El Toro Wilderness, nonnative invasive plant management plan. 38 p. Unpublished document. On file at: U.S. Department of Agriculture, Forest Service, El Yunque National Forest, Route 191, Intersection 988, km 4.4, Barrio Barceloneta, Río Grande, PR 00721.
- Vélez, I.L.; Villaluzo, R.; Walker, J.; Valenzuela, F.** 1992. Caribbean National Forest interpretative plan. 75 p. Unpublished document. On file at: U.S. Department of Agriculture, Forest Service, El Yunque National Forest, Route 191, Intersection 988, km 4.4, Barrio Barceloneta, Río Grande, PR 00721.
- Wadsworth, F.H.** 2009. Personal communication. Past director, U.S. Department of Agriculture, Forest Service, International Institute of Tropical Forestry, Jardín Botánico Sur, 1201 Calle Ceiba, San Juan, PR 00926-1119.
- Walker, J.B.; Leone, J.P.; Ortega, J.R. [and others].** 1999. Strategic plan for the New Deal era historic properties on the Caribbean National Forest. 52 p. Unpublished document. On file at: U.S. Department of Agriculture, Forest Service, El Yunque National Forest, Route 191, Intersection 988, km 4.4, Barrio Barceloneta, Río Grande, PR 00721.
- Walker, J.** 2009. Personal communication. Jeffery Walker, Past Archaeologist, U.S. Department of Agriculture, Forest Service, El Yunque National Forest, Route 191, Intersection 988, km 4.4, Barrio Barceloneta, Río Grande, PR 00721. Current address: Heritage Program Lead, Pacific Northwest Region, U.S. Department of Agriculture, Forest Service, 333 SW 1st Ave., Portland, OR 97208.

LITERATURE CITED

- Anon.** 1939. New tropical forest experiment station. *Caribbean Forester*. 1(1): 29.
- Anon.** 1952. The twelfth annual report. *Caribbean Forester*. 13: 1-20.
- Anon.** 1954. Fourteenth Annual Report. *Caribbean Forester*. 15(1-2): 1-13.
- Anon.** 1957. Seventeenth Annual report. *Caribbean Forester*. 18(1-2): 1-11.
- Anon.** 1958. The status of forestry and forest research in Puerto Rico and the Virgin Islands, the eighteenth annual report of the Tropical Forest Research Center. *Caribbean Forester*. 19(1-2): 1-24.
- Anon.** 1963. Annual report for 1962, Institute of Tropical Forestry. *Caribbean Forester*. 24(1): 1-17.
- Acevedo-Rodríguez, P.** 2005. Vines and climbing plants of Puerto Rico and the Virgin Islands. Smithsonian Institution contributions from the United States National Herbarium. 51: 1-483.
- Acevedo-Rodríguez, P.; Woodbury, R.O.** 1985. Los bejucos de Puerto Rico. Gen. Tech. Rep. SO-58. New Orleans: U.S. Department of Agriculture Forest Service, Southern Forest Experiment Station. 331 p.
- Ackerman, J.D.** 1992. The orchids of Puerto Rico and the Virgin Islands. San Juan, PR: University of Puerto Rico Press. 167 p.
- Ackerman, J.D.** 1995. An orchid flora of Puerto Rico and the Virgin Islands. Bronx, NY: Memoirs of the New York Botanical Garden. 73: 1-203.
- Aide, T.M.; Zimmermann, J.K.; Pascarella, J.B. [and others].** 2000. Forest regeneration in a chronosequence of tropical abandoned pastures: implications for restoration ecology. *Restoration Ecology*. 8(4): 328-338.
- Aide, T.M.; Zimmerman, J.K.; Rosario, M.; Marcano, H.** 1996. Forest recovery in abandoned cattle pastures along an elevational gradient in northeastern Puerto Rico. *Biotropica*. 28(4a): 537-548.
- Alegría, R.E.** 1972. Historia de nuestros Indios. Barcelona, España: Talleres Gráficos de Manuel Pareja. 84 p.
- Alegría, R.E.; Rivera Quiñones, E., eds.** 1999. Historia y cultura de Puerto Rico desde la "época pre-colombina hasta nuestros días. San Juan, PR: Fundación Francisco Carvahal. 307 p.
- Almanac.** 2009. NSF funding for critical zone observatory project in Puerto Rico. University of Pennsylvania Almanac. 56(16): December 22, 2009.
- Anderson-Córdova, K.** 2000. The aftermath of conquest—the Indians of Puerto Rico during the early sixteenth century. In: Siegel, P.E., ed. Ancient Borinquen: archaeology and ethnohistory of native Puerto Rico. Tuscaloosa, AL: University of Alabama Press: 337-352.
- Angulo-Sandoval, P.; Fernández-Marín, H.; Zimmerman, J.K.; Aide, T.M.** 2004. Changes in patterns of understory leaf phenology and herbivory following hurricane damage. *Biotropica*. 36(1): 60-67.
- Anthony, H.E.** 1925-1926. Mammals of Porto Rico, living and extinct. In: Scientific Survey of Porto Rico and the U.S. Virgin Islands New York: New York Academy of Sciences. 9(1-2): 1-238 p. + plates.
- Arendt, W.J.** 2006. Adaptations of an avian supertramp: distribution, ecology, and life history of the Pearly-eyed thrasher (*Margarops fuscatus*). Portland, OR: U.S. Department of Agriculture Forest Service, Pacific Northwest Research Station. 404 p.
- Axelrod, F.S.** 2011. A systematic vademecum to the vascular plants of Puerto Rico. Fort Worth, TX: BRIT Press. 428 p. + maps.
- Bagué, J.** 1962. Presencia de los montes en nuestra historia – apuntes conjuntivos. *Revista de Agricultura de Puerto Rico*. 49(1): 4-77.
- Baker, F.S.** 1950. Principles of silviculture. New York: McGraw-Hill. 414 p.
- Bannister, B.A.** 1970. Ecological life cycle of *Euterpe globosa* Gaetrn. In: Odum, H.T.; Pigeon, R.F. A tropical rain forest: a study of irradiation and ecology at El Verde, Puerto Rico. Springfield, VA: U.S. Department of Commerce: 299-314. Chapter B-18.
- Barnat, J.** 1987. Puerto Rico A-Zeta: encyclopedia alfabética. Barcelona, España: Ediciones Nauta, SA. p. 249. Vol. 4.
- Barone, J.A.; Thomlinson, J.; Anglada Cordero, P.; Zimmerman, J.K.** 2008. Metacommunity structure of tropical forest along an elevation gradient in Puerto Rico. *Journal of Tropical Ecology*. 24: 525-534.
- Barres, H.** 1963. The 1962 tropical forestry short course. *Caribbean Forester*. 24(1): 38-39.
- Basnet, K.** 1992a. An experimental study of the slope stability of the rain forest in Puerto Rico. *Tropical Ecology*. 33(2): 181-185.
- Basnet, K.** 1992b. Effect of topography on the pattern of trees in tabonuco (*Dacryodes excelsa*) dominated rain forest of Puerto Rico. *Biotropica*. 24(10): 31-42.
- Basnet, K.** 1993a. Recovery of a tropical rain forest after hurricane damage. *Vegetatio*. 109: 1-4.
- Basnet, K.** 1993b. Controls of environmental factors on pattern of Montane rain forest in Puerto Rico. *Tropical Ecology*. 34(1): 51-63.
- Basnet, K.; Likens, G.E.; Scatena, F.N.; Lugo, A.E.** 1992. Hurricane Hugo: damage to a tropical rain forest in Puerto Rico. *Journal of Tropical Ecology*. 8: 47-55.
- Basnet, K.; Scatena, F.N.; Likens, G.E.; Lugo, A.E.** 1993. Ecological consequences of root grafting in tabonuco (*Dacryodes excelsa*) trees in the Luquillo Experimental Forest, Puerto Rico. *Biotropica*. 25(1): 28-35.
- Bates, Charles Z.** 1927. Árboles exóticos que han prosperado en Puerto Rico desde que fueron introducidos por el Servicio Forestal. *Revista de Agricultura de Puerto Rico*. 18(2): 105-113.
- Bates, C.Z.** 1929. Efectos del huracán del 13 de septiembre de 1928 en distintos árboles. *Revista de Agricultura de Puerto Rico*. 23: 113-117.
- Bauer, G.P.** 1987. Recreation resources management in the Caribbean National Forest, Puerto Rico. In: Lugo, A.E.; Ford, L.B., eds. Forest recreation in the Caribbean islands. Río Piedras, PR: U.S. Department of Agriculture Forest Service, Southern Forest Experiment Station, Institute of Tropical Forestry; Caribbean National Forest: 31-42.
- Bauer, G.P.; Gillespie, A., Jr.** 1990. Volume tables for young plantation-grown hybrid mahogany (*Swietenia macrophylla* x *S. mahagoni*) in the Luquillo Experimental Forest of Puerto Rico. Res. Pap. SO-257. New Orleans: U.S. Department of Agriculture Forest Service, Southern Forest Experiment Station. 8 p.
- Bawiec, W.J., ed.** 2001. Geology, geochemistry, geophysics, mineral occurrences and mineral resource assessment for the Commonwealth of Puerto Rico. Open-file Report 98-38. Washington, DC: U.S. Geological Survey. 337 p.
- Baynton, H.W.** 1968. The ecology of an elfin forest in Puerto Rico, 2. The microclimate of Pico del Oeste. *Journal of the Arnold Arboretum*. 49(4): 419-430.
- Baynton, H.W.** 1969. The ecology of an elfin forest in Puerto Rico, 3. Hilltop and forest influences on the microclimate of "Pico del Oeste." *Journal of the Arnold Arboretum*. 50(1): 80-92.
- Beard, J.S.** 1944. Climax vegetation in tropical America. *Ecology*. 25: 127-158.

- Beard, J.S.** 1949. Natural vegetation of the Windward and Leeward Islands. Oxford Forestry Memoirs. 21: 1-192.
- Beard, K.H.; Vogt, K.A.; Vogt, D.J. [and others].** 2005. Structural and functional responses of a subtropical forest to 10 years of hurricanes and droughts. *Ecological Monographs*. 75(3): 345-361.
- Beinroth, F.H.** 1969. An outline of the geology of Puerto Rico. Bulletin 213. Mayaguez, PR: University of Puerto Rico; Río Piedras, PR: Agricultural Experiment Station. 31 p.
- Beissinger, S.R.; Wunderle, J.M., Jr.; Meyers, M. [and others].** 2008. Anatomy of a bottleneck: diagnosing factors limiting population growth in the Puerto Rican parrot. *Ecological Monographs*. 78(2): 185-203.
- Bell, G.S.** 1976. Notes on natural generation in Dominica, Windward Islands. *Commonwealth Forestry Review*. 55: 27-36.
- Bennett, S.P.** 1996. An overview of Hurricane Hortense and its aftermath. San Juan, PR: National Weather Service, Weather Forecast Office. 4 p. http://www.srh.noaa.gov/sju/?n=1996_hortense. [Date accessed: September 8, 2010].
- Benstead, J.P.; March, J.G.; Pringle, C.M.; Scatena, F.N.** 1999. Effects of a low-head dam and water abstraction on migratory tropical stream biota. *Ecological Applications*. 9(2): 656-668.
- Birdsey, R.A.; Weaver, P.L.** 1982. The forest resources of Puerto Rico. Res. Bull. SO-85. New Orleans: U.S. Department of Agriculture Forest Service, Southern Forest Experiment Station. 59 p.
- Blundell, A.G.; Scatena, F.N.; Wentsel, R.; Sommers, W.** 2003. Ecorisk assessment using indicators of sustainability. *Journal of Forestry*. 101(1): 14-19.
- Boccheciamp, R.A.** 1977. Soil survey of the Humacao area of eastern Puerto Rico. San Juan, PR: U.S. Department of Agriculture, Soil Conservation Service. 103 p.
- Bogart, D.B.; Arnow, T.; Crooks, J.W.** 1964. Water resources of Puerto Rico: a progress report with a hydrogeologic map by Reginald P. Briggs and J.P. Akers. San Juan, PR: U.S. Geological Survey; Legislative Assembly of Puerto Rico; Puerto Rico Water Resources Authority; Puerto Rico Aqueduct and Sewer Authority; Puerto Rico Industrial Development Company. 102 p. + 18 appendices.
- Bond, J.** 1971. Birds of the West Indies. Boston, MA: London: Collins. 256 p.
- Boone, R.S.; Chudnoff, M.** 1970. Variations in wood density on the mahoganies of Mexico and Central America. *Turrialba*. 20: 369-371.
- Borges, S.; Alfaro, M.** 1997. The earthworms of Baño de Oro, Luquillo Experimental Forest, Puerto Rico. *Soil Biology and Biochemistry*. 29(3-4): 231-234.
- Brandeis, T.J.; Helmer, E.H.; Oswalt, S.N.** 2007. The status of Puerto Rico's forests, 2003. Res. Bull. SRS-119. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station. 72 p.
- Brennan, J.W.** 1991. Meteorological summary of Hurricane Hugo. *Journal of Coastal Research. Special Issue*. 8: 1-12.
- Briscoe, C.B.** 1966. Weather in the Luquillo Mountains of Puerto Rico. Res. Pap. ITF-3. Río Piedras, PR: Institute of Tropical Forestry. 250 p.
- Briscoe, C.B.; Wadsworth, F.H.** 1970. Stand structure and yield in the tabonuco forest of Puerto Rico. In: Odum, H.T.; Pigeon, R.F. A tropical rain forest: a study of irradiation and ecology at El Verde, Puerto Rico. Springfield, VA: U.S. Department of Commerce: 79-89. Chapter B-6.
- Britton, N.L.; Wilson, P.** 1923-1930. Botany of Porto Rico and the Virgin Islands: Spermatophyta and Pteridophyta. Scientific Survey of Porto Rico and the Virgin Islands. New York: New York Academy of Sciences. 5(1-4): 1-626; 6(1-4): 1-663.
- Brokaw, N.V.L.** 1985. Treefalls, regrowth and community structure in tropical forests. In: Pickett, T.A.; White, P.S., eds. The ecology of natural disturbance and patch dynamics. New York: Academic Press: 53-69. Chapter 4.
- Brokaw, N.V.L.** 1998. *Cecropia schreberiana* in the Luquillo Mountains of Puerto Rico. *The Botanical Review*. 64(2): 91-120.
- Brokaw, N.; Fraver, S.; Grear, J.S. [and others].** 2004. Disturbance and canopy structure in two tropical forests. In: Losos, E.C.; Leigh, E.G., Jr., eds. Tropical forest diversity and dynamism: findings from a large-scale plot network. Chicago, IL: The University of Chicago Press: 177-194. Chapter 13.
- Brokaw, N.V.L.; Grear, J.S.** 1991. Forest structure before and after Hurricane Hugo at three elevations in the Luquillo Mountains, Puerto Rico. *Biotropica*. 23(4a): 386-392.
- Brown, K.A.; Scatena, F.N.; Gurevitch, J.** 2006. Effects of an invasive tree on community structure and diversity in a tropical forest in Puerto Rico. *Forest Ecology and Management*. 222: 145-152.
- Brown, S.; Lugo, A.E.; Silander, S.; Liegel, L.H.** 1983. Research history and opportunities in the Luquillo Experimental Forest. Gen. Tech. Rep. SO-44. New Orleans: U.S. Department of Agriculture Forest Service, Southern Forest Experiment Station. 128 p.
- Bruner, E.M.** 1919. El Bosque Nacional de Luquillo. *Revista de Agricultura de Puerto Rico*. 2(5): 33-42.
- Bruner, E.M.** 1923. El problema de la restauración forestal de Puerto Rico. *Revista de Agricultura de Puerto Rico*. 10(3): 15-21.
- Brunet, J.** 1929. Influencia de las fases de la luna sobre ciertas prácticas agrícolas. *La Hacienda (Puerto Rico)*. 24(6): 254-256.
- Byer, M.D.; Weaver, P.L.** 1977. Early secondary succession in an elfin woodland in the Luquillo Mountains of Puerto Rico. *Biotropica*. 9(1): 35-47.
- Calvesbert, R.J.** 1970. Climate of Puerto Rico and the U.S. Virgin Islands. Silver Spring, MD: U.S. Department of Commerce, Environmental Services Administration, Environmental Data Service. 29 p.
- Cardona, W.A.** 1984. El Yunque mineral prospects, eastern Puerto Rico. *Caribbean Journal of Science*. 20(1-2): 79-87.
- CEEPUR.** 2009. Población de Puerto Rico por municipios: 1930-2000. <http://www.ceepur.org/censo2000/1930-200.html>. [Date accessed: May 13, 2009].
- Chinea, J.D.** 1999. Changes in the herbaceous and vine communities at the Bisley Experimental watersheds, Puerto Rico, following Hurricane Hugo. *Canadian Journal of Forest Research*. 29: 1433-1437.
- Chinea, J.D.; Beymer, R.J.; Rivera, C. [and others].** 1993. An annotated list of the flora of the Bisley area, Luquillo Experimental Forest, 1987 to 1992. Gen. Tech. Rep. SO-94. New Orleans: U.S. Department of Agriculture Forest Service, Southern Forest Experiment Station. 12 p.
- Chudnoff, M.; Geary, T.F.** 1973. On the heritability of wood density in *Swietenia macrophylla*. *Turrialba*. 23: 359-362.
- Connell, J.H.** 1978. Diversity in tropical rain forests and coral reefs. *Science*. 199: 1302-1310.
- Cook, M.T.** 1928. Ecological survey of the flora of Porto Rico. The Journal of the Department of Agriculture of Porto Rico. 12(1-2): 3-139.
- Covich, A.P.; Crowl, T.A.; Heartsill-Scalley, T.** 2006. Effects of drought and hurricane disturbances on headwater distributions of palaemonid shrimp (*Macrobrachium* spp.) in the Luquillo Mountains of Puerto Rico. *Journal of the North American Benthological Society*. 25(1): 99-107.

- Covich, A.P.; Crowl, T.A.; Johnson, S.L.; Pyron, M.** 1996. Distribution and abundance of tropical freshwater shrimp along a stream corridor: response to disturbance. *Biotropica*. 28(4a): 484-492.
- Cox, D.P.; Briggs, R.P.** 1973. Metallogenic map of Puerto Rico. San Juan, PR: U.S. Department of the Interior, U.S. Geological Survey. 6 p. + map I-721.
- Cox, S.B.; Willig, M.R.; Scatena, F.N.** 2002. Variation in nutrient characteristics of surface soils from the Luquillo Experimental Forest of Puerto Rico: a multivariate perspective. *Plant and Soil*. 247: 189-198.
- Crook, K.E.** 2005. Quantifying the effects of water withdrawal on streams draining the Caribbean National Forest, Puerto Rico. Athens, GA: University of Georgia. 88 p. M.S. thesis.
- Crook, K.E.; Scatena, F.N.; Pringle, C.M.** 2007. Water withdrawn from the Luquillo Experimental Forest, 2004. IITF-GTR-34. Río Piedras, PR: U.S. Department of Agriculture Forest Service, International Institute of Tropical Forestry. 26 p.
- Crow, T.R.** 1980. A rain forest chronicle: a thirty year record of change in structure and composition at El Verde, Puerto Rico. *Biotropica*. 12: 42-55.
- Crow, T.R.; Grigal, D.F.** 1979. A numerical analysis of arborescent communities in the rain forest of the Luquillo Mountains, Puerto Rico. *Vegetatio*. 40: 135-146.
- Crow, T.R.; Weaver, P.L.** 1977. Tree growth in a moist tropical forest of Puerto Rico. Res. Pap. ITF-22. Río Piedras, PR: Institute of Tropical Forestry. 17 p.
- Cruz, A.** 1987. Avian community organization in a mahogany plantation on a neotropical island. *Caribbean Journal of Science*. 23(2): 286-298.
- Cruz, A.** 1988. Avian resource use in a Caribbean Pine plantation. *Journal of Wildlife Management*. 52(2): 274-279.
- Dallmeier, F.; Comisky, J.A.; Scatena, F.N.** 1998. Five years of forest dynamics following Hurricane Hugo in Puerto Rico's Luquillo Experimental Forest. In: Dallmeier, F.; Comisky, J.A., eds. *Forest biodiversity in North, Central and South America, and the Caribbean: research and monitoring. Man and the Biosphere Series Vol. 21*. Paris: UNESCO; Pearl River, NY: The Parthenon Publishing Group. 231-248.
- Dallmeier, F.; Comisky, J.A.** 1998. Forest biodiversity in North, Central and South America, and the Caribbean: research and monitoring. *Man and the Biosphere Series Vol. 21*. Paris: UNESCO; Pearl River, NY: The Parthenon Publishing Group. 768 p.
- Daly, C.; Helmer, E.H.; Quiñones, M.** 2003. Mapping the climate of Puerto Rico, Vieques and Culebra. *International Journal of Climatology*. 23: 1359-1381.
- Danforth, S.T.** 1926. An ecological study of Cartagena Lagoon, Porto Rico, with special reference to the birds. *The Journal of Agriculture of Porto Rico*. 10(1): 1-136.
- Danforth, S.T.** 1936. *Los pájaros de Puerto Rico*. Chicago, IL: Rand McNally and Company. 99-100.
- Dansereau, P.** 1966. Studies on the vegetation of Puerto Rico. Description and integration of plant-communities. Mayagüez, PR: Institute of Caribbean Science Special Publication 1. 45 p.
- Daszak, P.; Cunningham, A.A.; Hyatt, A.D.** 2003. Infectious disease and amphibian population declines. *Diversity and Distributions*. 9(2): 141-150.
- Devoe, N.N.** 1989. Differential seeding and regeneration in openings and beneath closed canopy in sub-tropical wet forest. New Haven, CT: Yale University, Faculty of the School of Forestry and Environmental Studies. 307 p. Ph.D. dissertation.
- Díaz Vega, A.** 2004. Misteriosa vivienda en El Yunque. *El Nuevo Día*. Octubre 31, 2004: 8-9.
- Dombeck, M.** 1999. Soul of the wilderness: a wilderness agenda and legacy for the U.S. Forest Service. *International Journal of Wilderness*. 5(3): 4-6.
- Domínguez Cristóbal, C.** 1989. Situación forestal de Puerto Rico durante el siglo XIX. *Acta Científica*. 3(1): 24-25.
- Domínguez Cristóbal, C.** 1997a. La historia de la Sierra de Luquillo (Bosque Nacional del Caribe), Parte 1. *Tiempo Libre*. 11(1): 5-10.
- Domínguez Cristóbal, C.** 1997b. Sinopsis histórico de la Sierra de Luquillo (Bosque Nacional del Caribe) Parte 2. *Tiempo Libre*. 11(2): 20-25.
- Domínguez Cristóbal, C.** 1997c. El Bosque Nacional del Caribe (1898-1963) (El Yunque). *ICONOS*. 11 (13-14): 15-24.
- Domínguez Cristóbal, C.** 2000. Panorama histórico forestal de Puerto Rico. San Juan, PR: Editorial de la Universidad de Puerto Rico. 680 p.
- Donnelly, T.W.** 1996. The development of geology in Puerto Rico: an historical sketch. In: Figueroa Colón, ed. *The scientific survey of Puerto Rico and the Virgin Islands—an 80-year reassessment of the island's natural history*. Annals of the New York Academy of Sciences. 776: 17-40.
- Doyle, T.W.** 1981. The role of disturbance in the gap dynamics of a montane rain forest: An application of a tropical forest succession model. In: West, D.C. [and others], eds. *Forest succession concepts and application*. New York: Springer-Verlag. 56-73.
- Drew, A.P.** 1998. Growth rings, phenology, hurricane disturbance and climate in *Cyrilla racemiflora* L., a rain forest tree of the Luquillo Mountains, Puerto Rico. *Biotropica*. 30(1): 35-49.
- Drew, A.P.; Boley, J.D.; Zhao, Y. [and others].** 2009. Sixty-two years of change in Subtropical wet forest structure and composition at El Verde, Puerto Rico. *Interciencia*. 34(1): 34-40.
- Dyrness, C.T.; Franklin, J.F.; Maser, C. [and others].** 1975. Research natural area needs in the Pacific Northwest: a contribution to land use planning: report on natural area needs workshop. Gen. Tech. Rep. PNW-38. Portland, OR: U.S. Department of Agriculture Forest Service, Pacific Northwest Forest and Range Experiment Station. 231 p.
- Eggers, H.F.A.** 1883. Porto Rico: description of the vegetation of the Luquillo Mountains. *Nature*. 29: 129-130.
- El Yunque National Forest.** 2009. Interpretation and conservation education master plan. Río Grande, PR: U.S. Department of Agriculture Forest Service, El Yunque National Forest. 92 p. + 9 appendices.
- El Yunque National Forest.** 2011. El Yunque National Forest—centennial timeline. www.fs.fed.us/r8/.../aboutcentennial.shtml. [Date accessed: March 17, 2011].
- English, D.B.K.; Kocis, S.M.; Zarnoch, S.J.; Arnold, J.R.** 2002. Forest Service national visitor use monitoring process: research method documentation. Res. Pap. SRS-57. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Station. 14 p.
- Erdman, D.S.** 1972. Inland game fishes of Puerto Rico. San Juan, PR: Department of Agriculture, Centralized and Ancillary Operation Services. 4(2): 1-96.
- Erdman, D.S.** 1984. The green stream goby *Sicydium plumieri* in Puerto Rico. *Tropical Fish Hobbyist*. 34: 70-74.
- Everham, E.M., III.** 1995. Hurricane disturbance and recovery: an empirical and simulation study of vegetation dynamics in the Luquillo Experimental Forest. Syracuse, NY: SUNY College of Environmental Science and Forestry. 363 p. Ph.D. dissertation.
- Ewel, J.J.; Whitmore, J.L.** 1973. The ecological life zones of Puerto Rico and the U.S. Virgin Islands. U.S. Department of Agriculture Forest Service. Res. Pap. ITF-18. Institute of Tropical Forestry, Río Piedras, Puerto Rico. 72 p.

- Faaborg, J.; Arendt, W.J.** 1990. Long-term studies of Guánica Forest birds. *Acta Científica*. 4(1-3): 69-80.
- Faaborg, J.; Arendt, W.J.** 1992. Rainfall correlates of bird population fluctuations in a Puerto Rican dry forest: a 15 year study. *La Revista de la Sociedad de Ornitología Caribeña*. 3: 10-19.
- Federal Committee of Research Natural Areas.** 1968. A directory of research natural areas on Federal lands of the United States of America. Washington, DC: Federal Committee on Research Natural Areas. 129 p.
- Fernández, D.S.; Fletcher, N.** 1991. Changes in light availability following Hurricane Hugo in a subtropical montane forest in Puerto Rico. *Biotropica*. 23(4a): 303-399.
- Fletcher, N.; Haines, B.L.; Cordero, R.A. [and others].** 1996. Responses of tropical plants to nutrients and light on a landslide in Puerto Rico. *Journal of Ecology*. 84: 331-341.
- Figueroa Colón, J.C.** 1996. Phytogeographical trends, centers of high species richness and endemism, and the question of extinctions in the native flora of Puerto Rico. In: Figueroa Colón, J.C., ed. The scientific survey of Puerto Rico and the Virgin Islands—an eighty-year reassessment of the island's natural history. *Annals of the New York Academy of Sciences*. 776: 89-102.
- Foerster, J.W.** 1971. The ecology of an elfin forest in Puerto Rico, 14. The algae of Pico del Oeste. *Journal of the Arnold Arboretum*. 52: 86-109.
- Foster, D.R.; Fluet, M.; Boose, E.R.** 1999. Human or natural disturbance: landscape-scale dynamics of tropical forests in Puerto Rico. *Ecological Applications*. 9(2): 555-572.
- Francis, J.K.** 1987. Performance of exotic tree species in Puerto Rico. In: Figueroa, J.C.; Wadsworth, F.H.; Branahan, S., eds. Management of the forests of tropical America: prospects and technologies. San Juan, PR: Institute of Tropical Forestry: 377-388.
- Francis, J.K.** 1989. The Luquillo Experimental Forest Arboretum. Res. Note SO-358. New Orleans: U.S. Department of Agriculture Forest Service, Southern Forest Experiment Station, Institute of Tropical Forestry. 8 p.
- Francis, J.K.** 1995. Forest plantations in Puerto Rico. In: Lugo, A.E.; Lowe, C., eds., *Tropical forests: management and ecology*. New York: Springer-Verlag: 210-223. Chapter 8.
- Francis, J.K.; Gillespie, A.J.R.** 1993. Relating gust speed to tree damage in Hurricane Hugo, 1989. *Journal of Arboriculture*. 19(6): 368-373.
- Francis, J.K.; Liogier, H.A.** 1991. Naturalized exotic tree species in Puerto Rico. Gen. Tech. Rep. SO-82. New Orleans: U.S. Department of Agriculture Forest Service, International Institute of Tropical Forestry. 12 p.
- Francis, J.K.; Lowe, C.A.** 2000. Bioecología de árboles nativos y exóticos de Puerto Rico y las Indias Occidentales. Río Piedras, PR: U.S. Department of Agriculture Forest Service, International Institute of Tropical Forestry. 582 p.
- Francis, J.K.; Weaver, P.L.** 1988. Performance of *Hibiscus elatus* in Puerto Rico. *Commonwealth Forestry Review*. 67(4): 327-338.
- Franco, P.A.; Weaver, P.L.; Eggen-McIntosh, S.** 1997. The forest resources of Puerto Rico, 1990. Res. Bull. SRS-22. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station. 45 p.
- Frangi, J.L.; Lugo, A.E.** 1985. Ecosystem dynamics of a subtropical floodplain forest. *Ecological Monographs*. 55(3): 351-369.
- Frangi, J.L.; Lugo, A.E.** 1991. Hurricane damage to a flood plain forest in the Luquillo Mountains of Puerto Rico. *Biotropica*. 23(4a): 324-335.
- Frangi, J.L.; Lugo, A.E.** 1998. A flood plain palm forest in the Luquillo Mountains of Puerto Rico five years after Hurricane Hugo. *Biotropica*. 30(3): 339-348.
- Fulford, M.; Crandall, B.; Stotler, R.** 1970. The ecology of an elfin forest in Puerto Rico, 11. The leafy Hepaticae of Pico del Oeste. *Journal of the Arnold Arboretum*. 51: 56-69.
- Fulford, M.; Crandall, B.; Stotler, R.** 1971. The ecology of an elfin forest in Puerto Rico, 15. A study of the leafy Hepatic flora of the Luquillo Mountains. *Journal of the Arnold Arboretum*. 52 (3): 435-458.
- Gannon, M.R.; Kurta, A.; Rodríguez-Durán, A.; Willig, M.R.** 2005. Bats of Puerto Rico: an island focus and a Caribbean perspective. Lubbock, TX: Texas Tech University Press. 239 p.
- Gannon, M.R.; Willig, M.R.** 1994. The effects of Hurricane Hugo on bats of the Luquillo Experimental Forest of Puerto Rico. *Biotropica*. 26(3): 320-331.
- García-Martinó, A.R.; Warner, G.S.; Scatena, F.N.; Civco, D.L.** 1996. Rainfall, runoff and elevation relationships in the Luquillo Mountains of Puerto Rico. *Caribbean Journal of Science*. 32(4): 414-424.
- García-Montiel, D.C.; Scatena, F.N.** 1994. The effect of human activity on the structure and composition of a tropical forest in Puerto Rico. *Forest Ecology and Management*. 63: 57-78.
- Gates, O.M.** 1969. The ecology of an elfin forest in Puerto Rico, 4. Transpiration rates and temperature of leaves in cool humid environment. *Journal of the Arnold Arboretum*. 50(1): 93-98.
- Geary, T.F.** 1969. Adaptability of Mexican and Central American provenances of *Swietenia* in Puerto Rico and Saint Croix. FAO/IUFRO FO-FTB-69-2/19. In: Second World Consultation of Forest Tree Breeding. Rome, Italy: Food and Agriculture Organization of the United Nations. 9 p.
- Geary, T.F.; Barres, H.; Ybarra-Coronado.** 1973. Seed source variation in Puerto Rico and Virgin Islands grown mahoganies. Res. Pap. ITF-17. Río Piedras, PR: U.S. Department of Agriculture Forest Service, Institute of Tropical Forestry. 24 p.
- Gerhart, G.A.** 1936a. Desarrollo de actividades recreativas. *Revista de Agricultura de Puerto Rico*. 27: 31-35.
- Gerhart, G.A.** 1936b. El Cuerpo Civil de Conservación en Puerto Rico. *Revista de Agricultura de Puerto Rico*. 28: 292-299.
- Gifford, J.C.** 1905. The Luquillo Forest Reserve, Porto Rico. U.S. Department of Agriculture, Bureau of Forestry, Bulletin No. 54. Washington, DC: Government Printing Office. 52 p.
- Gill, A.M.** 1969. The ecology of an elfin forest in Puerto Rico, 6. Aerial roots. *Journal of the Arnold Arboretum*. 50(2): 197-209.
- Gill, T.** 1931. Tropical forests of the Caribbean. Baltimore, MD: Tropical Plant Research Foundation; Charles Lathrop Pack Forestry Trust. 318 p.
- Gleason, H.A.; Cook, M.T.** 1927. Scientific Survey of Porto Rico and the Virgin Islands: Plant ecology of Porto Rico.. New York: New York Academy of Sciences. 7(1-2): 3-173 + plates.
- Glogiewicz, J.S.** 1986. Performance of Mexican, Central American, and West Indian provenances of *Swietenia* grown in Puerto Rico. Syracuse, NY: State University of New York College of Environmental Science and Forestry. 69 p. M.S. thesis.
- Gómez-Pompa, A.; Vázquez-Yanes, C.** 1974. Studies of the secondary succession of tropical lowlands. Life cycle of secondary species. In: Proceedings of the First International Congress of Ecology: structure, functioning and management of ecosystems. Wageningen, Netherlands: Cente for Agricultural Publishing and Documentation. 336-342.
- González, G.; García, E.; Cruz, V.; Borges, S.; Zalamea, M.; Rivera, M.** 2007. Earthworm communities along an elevational gradient in northeastern Puerto Rico. *European Journal of Soil Biology*. 43: S24-S32.

- González-Cabán, A.; Loomis, J.** 1999. Measuring the economic benefit of maintaining the ecological integrity of the Río Mameyes in Puerto Rico. Res. Pap. PSW-RP-240. Albany, CA: U.S. Department of Agriculture Forest Service, Pacific Southwest Research Station. 61 p.
- Gould, W.A.; Alarcón, C.; Fevold, B.; [and others].** 2008. The Puerto Rico Gap Analysis Project, Volume 1: land cover, vertebrate species distributions, and land stewardship. IITF-GTR-39. Río Piedras, PR: U.S. Department of Agriculture Forest Service, International Institute of Tropical Forestry. 165 p.
- Gould, W.A.; González, G.; Carrero Rivera, G.** 2006. Structure and composition of vegetation along an elevational gradient in Puerto Rico. *Journal of Vegetation Science*. 17: 653-664.
- Grubb, P.J.** 1971. Interpretation of the "Massenerhebung Effect" on tropical mountains. *Nature*. 229: 44-45.
- Grubb, P.J.** 1977. Control of forest growth and distribution on wet tropical mountains with special reference to mineral nutrition. *Annual Review of Ecology and Systematics*. 8: 83-107.
- Guariguata, M.R.** 1990. Landslide disturbance and forest regeneration in the upper Luquillo Mountains of Puerto Rico. *Journal of Ecology*. 78: 814-832.
- Guariguata, M.R.; Larsen, M.C.** 1990. Preliminary map showing landslides in the El Yunque quadrangle, Puerto Rico. Open-file report 89-257. 1:20,000. San Juan, PR: U.S. Geological Survey. 1 sheet.
- Guzmán-Grajales, S.M.; Walker, L.R.** 1991. Differential seedling responses to litter after Hurricane Hugo in the Luquillo Experimental Forest, Puerto Rico. *Biotropica*. 23(4a): 407-413.
- Harris, N.L.; Hall, C.A.S.; Lugo, A.E.** 2008. Estimates of species- and ecosystem-level respiration of woody stems along an elevational gradient in the Luquillo Mountains, Puerto Rico. *Ecological Modelling*. 216: 253-264.
- Heartsill Scalley, T.; Estrada Ruiz, C.R.; Moya, S.** 2006. Patrones de lluvia, transcolación y flujo de nutrientes en las cuencas de Bisley, Bosque Experimental de Luquillo, Puerto Rico. *Acta Científica*. 20(1-3): 67-88.
- Heartsill Scalley, T.; Scatena, F.N.; Lugo, A.E. [and others].** 2010. Changes in structure, composition, and nutrients during 15 years of hurricane-induced succession in a subtropical wet forest in Puerto Rico. *Biotropica*. 42(4): 455-463.
- Hernández Pérez, M.** 2008. Se estrella bimotor en El Yunque. *Primera Hora*. December 4, 2008. 2-3
- Heyne, C.M.** 2000. Soil and vegetation recovery on abandoned paved roads in a humid tropical rain forest, Puerto Rico. Las Vegas, NV: University of Nevada. 152 p.
- Hildebrand, S.F.** 1935. An annotated list of fishes of the fresh waters of Puerto Rico. *Copeia*. 1935(2): 49-56.
- Hill, R.T.** 1899. Notes on the forest conditions of Porto Rico. *Forestry Bulletin* No. 25. Washington, DC: U.S. Department of Agriculture. 48 p.
- Holdridge, L.R.** 1940. The possibility of close cooperation for mutual benefit between agriculture and forestry in the American tropics. *Caribbean Forester*. 1(3): 25-29.
- Holdridge, L.R.** 1967. Life zone ecology. Revised edition. San José, Costa Rica: Tropical Science Center. 206 p.
- Howard, R.A.** 1968. The ecology of an elfin forest in Puerto Rico, 1. Introduction and composition studies. *Journal of the Arnold Arboretum*. 49(4): 381-418.
- Howard, R.A.** 1969. The ecology of an elfin forest in Puerto Rico, 8. Studies of stem growth and form and of leaf structure. *Journal of the Arnold Arboretum*. 50(2): 225-266.
- Howard, R.A.** 1970a. The "alpine" plants of the Antilles. *Biotropica*. 2(1): 24-28.
- Howard, R.A.** 1970b. The ecology of an elfin forest in Puerto Rico, 10. Notes on two species of *Marcgravia*. *Journal of the Arnold Arboretum*. 51(1): 41-55.
- Huerga, A.** 2004. *Historiadores de Puerto Rico (1492-1600)*. Ponce, PR: Pontificia Universidad de Puerto Rico. 350 p.
- Huey, R.B.; Duetsch, C.A.; Tewksbury, J.J. [and others].** 2008. Why tropical forest lizards are vulnerable to climate warming. London, UK: *Proceedings of the Royal Society B Biological Sciences*. 1-10.v. 276(1664): 1939-1948. Date accessed: April 2, 2009.
- Instituto de Cultura Puertorriqueña.** 1993. *Patrimonio histórico edificado de la región este: guía de recursos históricos del este*. Humacao, PR: Instituto de Cultura Puertorriqueña, Sede Regional del Este. 49 p.
- Institute for Tropical Ecosystems Studies.** 2011. Research. www.web.ites.upr.edu/staff-information. [Date accessed: March 16, 2011].
- Joglar, R.L.** 1998. *Los coquíes de Puerto Rico: su historia natural y conservación*. San Juan, PR: Editorial de la Universidad de Puerto Rico. 232 p.
- Joglar, R.L., ed.** 2005. *Biodiversidad de Puerto Rico: vertebrados terrestres y ecosistemas*. San Juan, PR: Editorial del Instituto de Cultura Puertorriqueña. 563 p.
- Johnston, M.H.** 1990. Successional change and species/site relationships in a Puerto Rican tropical forest. Syracuse, NY: State University of New York College of Environmental Science and Forestry. 253 p. Ph.D. dissertation.
- Jordan, C.F.** 1970. Flow of soil water in the lower montane tropical rain forest. In: Odum, T.; Pigeon, R.F., eds. *A tropical rain forest*. Springfield, VA: U.S. Government Printing Office: 199-200. Chapter H-18.
- Kartchner, S.C.** 2003. Recreational use of montane streams of the Caribbean National Forest. *Acta Científica*. 17(1-3): 39-57.
- Kasomenakis, S.** 1988. Native orchids of the Luquillo Mountains of eastern Puerto Rico. *American Orchid Society Bulletin*. 57(9): 979-988.
- Kepler, A.K.** 1975. *Helechos communes del bosque de Luquillo, Puerto Rico*. San Juan, PR: InterAmerican University Press. 128 p.
- Kepler, C.** 2009. Hidden in the clouds: the discovery of the Elfin Woods Warbler. *Winging it*. 21(5): 1, 4, 5.
- Kepler, C.B.; Kepler, A.K.** 1970. Preliminary comparison of bird species diversity and density in Luquillo and Guánica forests. In: Odum, H.T.; Pigeon, R.F., eds. *A tropical rain forest*. Springfield, VA: U.S. Department of Commerce: 183-191. Chapter E-14.
- Kepler, C.B.; Parkes, K.C.** 1972. A new species of warbler (Parulidae) from Puerto Rico. *Auk*. 89: 1-18.
- Kharecha, P.** 1997. Energy evaluation of the effects of human activities on Luquillo Experimental Forest, Puerto Rico. Gainesville, FL: University of Florida, Center for Environmental Policy and Environmental Engineering Sciences. 38 p. M.S. thesis.
- Kinzig, A.P.; Harte, J.** 2000. Implications of endemics-area relationships for estimates of species extinctions. *Ecology*. 81(12): 3305-3311.
- Kramer, W.P.** 1926. Cincuenta especies de árboles exóticos que han prosperado en Puerto Rico desde que fueron introducidos por el Servicio Forestal de Puerto Rico. *Revista de Agricultura de Puerto Rico*. 17(5): 42-43.
- Kramer, W.P.** 1927. Cincuenta especies de árboles exóticos que han prosperado en Puerto Rico desde que fueron introducidos por el Servicio Forestal de Puerto Rico. *Revista de Agricultura de Puerto Rico*. 18(1): 56-61.

- Kramer, W.P.** 1928. Nuestro bosque tropical nacional. *Revista de Agricultura de Puerto Rico*. 20(2): 54-55.
- Krug, F.** 1930. El proyecto de Río Blanco. *Revista de Obras Públicas de Puerto Rico*. 7(7): 172-177.
- LaBastille, A.; Pool, D.J.** 1978. On the need for a system of cloud-forest parks in Middle America and the Caribbean. *Environmental Conservation*. 5(2): 183-190.
- Lamb, F.B.** 1959. The 1959 tropical forestry training course. *Caribbean Forester*. 20 (1-2): 11-16.
- Landres, P.; Hennessy, M.B.; Schlenker, K. [and others].** 2008. Applying the concept of wilderness character to national forest planning, monitoring, and management. Gen. Tech. Rep. RMRS-GTR-217 WWW. Fort Collins, CO: Rocky Mountain Research Station. 45 p.
- Larsen, M.C.** 1997. Tropical geomorphology and geomorphic work: A study of geomorphic processes and sediment and water budgets in montane humid-tropical forested and developed watersheds, Puerto Rico. Boulder, CO: University of Colorado. 341 p. Ph.D. dissertation.
- Larsen, M.C.** 2000. Analysis of 20th century rainfall and streamflow to characterize drought and water resources in Puerto Rico. *Physical Geography*. 21(6): 494-521.
- Larsen, M.C.; Parks, J.E.** 1997. How wide is a road? The association of roads and mass-wasting in a forested montane environment. *Earth Surface Processes and Landforms*. 22: 835-848.
- Larsen, M.C.; Torres Sánchez, A.J.** 1992. Landslides triggered by Hurricane Hugo in eastern Puerto Rico, September 1989. *Caribbean Journal of Science*. 28(3-4): 113-125.
- Larsen, M.C.; Torres-Sánchez, A.J.** 1998. The frequency and distribution of recent landslides in three montane tropical regions of Puerto Rico. *Geomorphology*. 24: 309-331.
- Lavandero, C.F.** 1998. Campamentos de ciudadanos para conservación en Puerto Rico. *Acta Científica*. 12(1-3): 43-57.
- Lawton, R.O.** 1984. Ecological constraints on wood density in a tropical montane forest. *American Journal of Botany*. 71(2): 261-267.
- Layton, B.W.** 1986. Reproductive chronology and habitat use by black rats (*Rattus rattus*) in Puerto Rican parrot (*Amazona vittata*) habitat. Baton Rouge, LA: Louisiana State University, School of Forestry, Wildlife and Fisheries. 98 p.
- Lebron, M.L.** 1977. An autecological study of *Palicourea riparia* Benth (Rubiaceae): an ecologically important species in the recovery of a disturbed tropical rain forest in Puerto Rico. Chapel Hill, NC: University of North Carolina. 238 p. Ph.D. dissertation.
- Lenart, M.T.; Falk, D.A.; Scatena, F.N.; Osterkamp, W.R.** 2010. Estimating soil turnover rate from tree uprooting during hurricanes in Puerto Rico. *Forest Ecology and Management*. 250(6): 1076-1084.
- Lewisohn, F.** 1964. Divers information on the romantic history of St. Croix. Fredericksted, St. Croix: St. Croix Landmarks Society. 71 p.
- Liegel, L.H.; Balmer, W.E.; Ryan, G.W.** 1985. Honduras pine spacing trial results in Puerto Rico. *Southern Journal of Applied Forestry*. 9(3): 69-75.
- Linsley, R.K., Jr.; Kohler, M.A.; Paulhus, J.L.H.** 1949. *Applied hydrology*. New York, McGraw-Hill Book Company. 689 p.
- Liogier, H.A.** 1985-1997. Descriptive flora of Puerto Rico and adjacent islands – Spermatophyta. San Juan, PR: Editorial de la Universidad de Puerto Rico. 2347 p. Vols. 1-5.
- Liogier, H.A.** 1996. Botany and botanists in Puerto Rico. In: Figueroa Colón, ed. The scientific survey of Puerto Rico and the Virgin Islands – an eighty-year reassessment of the island's natural history. *Annals of the New York Academy of Sciences*. 776: 41-53.
- Little, E.L., Jr.** 1970. Relationships of trees of the Luquillo Experimental Forest. In: Odum, H.T.; Pigeon, R.F. A tropical rain forest: a study of irradiation and ecology at El Verde, Puerto Rico. Springfield, VA: U.S. Department of Commerce: 47-58. Chapter B-3.
- Little, E.L., Jr.; Wadsworth, F.H.** 1964. Common trees of Puerto Rico and the Virgin Islands. Agric. Handb. No. 249. Washington, DC: U.S. Department of Agriculture Forest Service. 548 p.
- Little, E.L., Jr.; Woodbury, R.O.; Wadsworth, F.H.** 1974. Trees of Puerto Rico and the Virgin Islands. Agric. Handb. 449. Washington, DC: U.S. Department of Agriculture Forest Service. 1024 p.
- Little, E.L., Jr.; Woodbury, R.O.** 1976. Trees of the Caribbean National Forest. Forest Service Research Paper ITF-20. Río Piedras, PR: U.S. Department of Agriculture Forest Service, Institute of Tropical Forestry. 27 p.
- Little, E.L., Jr.; Woodbury, R.O.** 1980. Rare and endemic trees of Puerto Rico and the Virgin Islands. Conservation Research Paper No. 27. Washington, DC: U.S. Department of Agriculture Forest Service. 26 p.
- Lodge, D.J.; Scatena, F.N.; Asbury, C.E.; Sánchez, M.J.** 1991. Fine litterfall and related nutrient inputs resulting from Hurricane Hugo in Subtropical Wet and Lower montane rain forests of Puerto Rico. *Biotropica*. 23(4a): 336-342.
- Longwood, F.R.** 1955. Industrial wood use in Puerto Rico. *Caribbean Forester*. 16(3-4): 64-97.
- Longwood, F.R.** 1961. Puerto Rican woods: their machining, seasoning and related characteristics. Agric. Handb. 205. Washington, DC: U.S. Department of Agriculture Forest Service. 98 p.
- Lugo, A.E.** 1986. Water and the ecosystems of the Luquillo Experimental Forest. GTR-SO-63. New Orleans: U.S. Department of Agriculture Forest Service, Southern Forest Experiment Station. 17 p.
- Lugo, A.E.** 1987. Biosphere Reserves in the tropics: an opportunity for integrating wise use and preservation of biotic resources. In: 4th World Wilderness Congress for worldwide conservation; Proceedings of the symposium on biosphere reserves. Atlanta: U.S. Department of the Interior, National Park Service: 53-61.
- Lugo, A.E.** 1994. Preservation of primary forests in the Luquillo Mountains, Puerto Rico. *Conservation Biology*. 8(4): 1122-1131.
- Lugo, A.E.** 2008. Visible and invisible effects of hurricanes on forest ecosystems: an international review. *Austral Ecology*. 33: 368-398.
- Lugo, A.E.; Brown, S.** 1981. Ecological monitoring in the Luquillo Forest Reserve. *Ambio*. 10(2-3): 102-107.
- Lugo, A.E.; Figueroa, J.** 1985. Performance of *Anthocephalis chinensis* in Puerto Rico. *Canadian Journal of Forest Research*. 15: 577-585.
- Lugo, A.E.; Frangi, J.L.** 1993. Fruit fall in the Luquillo Experimental Forest, Puerto Rico. *Biotropica*. 25(1): 73-84.
- Lugo, A.E.; Frangi, J.L.** 2003. Changes in necromass and nutrients on the forest floor of a palm floodplain forest in the Luquillo Mountains of Puerto Rico. *Caribbean Journal of Science*. 39(3): 265-272.
- Lugo, A.E.; López, T. del M.; Ramos, O.M.** 2000. Zonificación de terrenos en la periferia de El Yunque. GTR-ITF-16. Río Piedras, PR: U.S. Department of Agriculture Forest Service, International Institute of Tropical Forestry. 12 p.
- Lugo, A.E.; López, T. del M.; Ramos González, O.M.; Velez, L.L.** 2004. Urbanización de los terrenos en la periferia de El Yunque. GTR-WO-66. Washington, DC: U.S. Department of Agriculture Forest Service. 29 p.
- Lugo, A.E.; Lowe, C.** 1995. Tropical forests: management and ecology. New York: Springer-Verlag. 461 p.

- Lugo, A.E.; Rivera Batlle, C.T.** 1987. Leaf production, growth rate, and age of the palm *Prestoea montana* in the Luquillo Experimental Forest, Puerto Rico. *Journal of Tropical Ecology*. 3: 151-161.
- Lugo, A.E.; Salgado Herrera, M.; Ramírez, J.; Pérez Castro, I.E.** 1999. Estructura y composición del sotobosque de plantaciones en el arboreto del Bosque Experimental de Luquillo. *Acta Científica*. 13(1-3): 89-105.
- Lugo, A.E.; Wadsworth, F.H.** 1990. *Dacryodes excelsa* Vahl, Tabonuco, Burseraceae, Bursera family. In: Burns, R.M.; Honkala, B.H., tech. coords. *Silvics of North America: 2, Hardwoods*. Agric. Handb. 654. U.S. Department of Agriculture Forest Service. Washington, DC: U.S. Government Printing Office: 284-287. Vol. 2.
- LUQ LTER.** 2011. Publications. luq.lternet.edu/publications/lterpub/peerbib.html. [Date accessed: March 10, 2011].
- Lyford, W.H.** 1969. The ecology of an elfin forest in Puerto Rico, 7. Soil, root, and earthworm relationships. *Journal of the Arnold Arboretum*. 50(2): 210-224.
- Maldonado, E.D.** 1962. Durabilidad de postes tratados para su finca. *Revista de Agricultura de Puerto Rico*. 49(1): 165-168.
- Man and the Biosphere (MAB).** 1975. Biosphere reserves. Paris, France: United Nations Educational, Scientific, and Cultural Organization (UNESCO). *Man and the Biosphere Secretariat*. 1 p. + map.
- March, J.G.; Benstead, J.P.; Pringle, C.M.; Scatena, F.N.** 2003. Damming tropical island streams: problems, solutions, and alternatives. *Bioscience*. 53(11): 1069-1078.
- Marino, J.** 2011. What caused our water shortage? *Caribbean Business*. May 5, 2011: 16-20.
- Marrero, J.** 1947. A survey of the forest plantations in the Caribbean National Forest. Ann Arbor, MI: University of Michigan, School of Forestry and Conservation. 167 p. M.S. thesis.
- Marrero, J.** 1948. Repoblación forestal en el Bosque Nacional del Caribe de Puerto Rico: experiencias en el pasado como guía para el futuro. *Caribbean Forester*. 9: 148-213.
- Marrero, J.** 1950. Reforestation of degraded lands in Puerto Rico. *Caribbean Forester*. 11(1): 3-15.
- Martínez-Fernández, L.** 1998. Puerto Rico in the whirlwind of 1898: conflict, continuity, and change. *OAH Magazine of History*. 12(3): 24-29.
- Martorel, L.F.** 1945. A survey of the forest insects of Puerto Rico. *Journal of Agriculture of the University of Puerto Rico*. 29: 70-608.
- May, D.W.** 1924. La influencia de la luna. *Revista de Agricultura de Puerto Rico*. 12: 233-236.
- McCool, S.F.; Cole, D.N., eds.** 1997. Proceedings—limits of acceptable change and related planning processes: progress and future directions. GTR-INT-371. Ogden, UT: U.S. Department of Agriculture Forest Service, Intermountain Research Station. 84 p.
- McCormick, J.F.** 1995. A review of the population dynamics of selected tree species in the Luquillo Experimental Forest, Puerto Rico. In: Lugo, A.E.; Lowe, C. *Tropical forests: management and ecology*. New York: Springer-Verlag: 224-257.
- Medina, E.; Cuevas, E.; Weaver, P.L.** 1981. Composición foliar y transpiración de especies leñosas de Pico del Este, Sierra de Luquillo, Puerto Rico. *Acta Científica Venezolana*. 32: 159-165.
- Meyerhoff, H.A.** 1933. *Geology of Puerto Rico*. Río Piedras, PR: University of Puerto Rico. 306 p.
- Mitchell, R.C.** 1954. A survey of the geology of Puerto Rico. Tech. Pap. 13. Río Piedras, PR: University of Puerto Rico, Agricultural Station. 167 p.
- Moir, W.H.** 1972. Natural areas. *Science*. 177: 396-400.
- Morán Árce, L.** 1971. *Enciclopedia clásicos de Puerto Rico*, tomo 1. Barcelona, España: Publicaciones Reunidas, S.A. 477 p.
- Mosquera, M.; Fehleley, J.** 1984. *Bibliography of forestry in Puerto Rico*. GTR-SO-51. New Orleans: U.S. Department of Agriculture Forest Service, Southern Forest Experiment Station. 196 p.
- Mowbray, A.** 2008. Roads, radar and research: the U.S. military and the Luquillo Forest Reserve. In: *Annual letter 2003-2004: 100 years of tropical forestry in Puerto Rico and the U.S. Virgin Islands*. San Juan, PR: U.S. Department of Agriculture Forest Service, International Institute of Tropical Forestry: 69-77.
- Muñiz-Meléndez, E.** 1978. Demographic analysis of the life history of *Inga vera* subspecies *vera*. Knoxville, TN: The University of Tennessee. 48 p. M.S. thesis.
- Murphy, L.S.** 1916. *Forests of Porto Rico, past present, and future, and their physical and economic development*. Bull. 354. Washington, DC: Government Printing Office. 99 p.
- Myster, R.W.; Thomlinson, J.R.; Larsen, M.C.** 1997. Predicting landslide vegetation in patches on landscape gradients in Puerto Rico. *Landscape Ecology*. 12: 299-307.
- Myster, R.; Walker, L.R.** 1997. Plant successional pathways on Puerto Rican landslides. *Journal of Tropical Ecology*. 13: 165-173.
- National Oceanic and Atmospheric Administration.** 2002. *Climatology of the United States No. 81. Monthly normals of temperature, precipitation, and heating and cooling degree days, 1971-2000*, Puerto Rico. Asheville, NC: National Oceanic and Atmospheric Administration. 13 p.
- National Park Service.** 2005. Wild and scenic rivers by State. <http://www.nps.gov/rivers/wildriverslist.html>. [Date accessed: December 25, 2007].
- Naumann, M.** 1994. A water use budget for the Caribbean National Forest of Puerto Rico. European Postgraduate Program thesis. Trier, Germany: Universität Trier. 53 p. + appendices.
- Neumann, C.J.; Jarvinen, B.R.; Pike, A.C.** 1988. Tropical cyclones in the north Atlantic Ocean, 1871- 1986. *Historical climatology Series 6-2*. Asheville, NC: National Climatic Data Center; Coral Gables, FL: National Hurricane Center. 186 p.
- Neveling, L.I., Jr.** 1970a. The ecology of an elfin forest in Puerto Rico, 5. Chromosome numbers of some flowering plants. *Journal of the Arnold Arboretum*. 50(1): 99-103.
- Neveling, L.I., Jr.** 1970b. The ecology of an elfin forest in Puerto Rico, 12. A new species of *Gonocalyx* (Ericaceae). *Journal of the Arnold Arboretum*. 51(2): 221-227.
- Neveling, L.I., Jr.** 1971. The ecology of an elfin forest in Puerto Rico, 16. The flowering cycle and an interpretation of its seasonality. *Journal of the Arnold Arboretum*. 52(4): 586-613.
- Nieves, L.O.** 1979. Ecological life history study of *Didymopanax morototoni*. Río Piedras, PR: University of Puerto Rico, Biology Department. 85 p. M.S. thesis.
- Nieves, L.O.** 1998. Ecological study of the freshwater stream fishes of the upper Mameyes River (Bisley) in the Luquillo Mountains of Puerto Rico. Fairfax, VA: George Mason University. 177 p. Ph.D. dissertation.
- Nolla, J.A.B.** 1936. Historia de la agricultura de Puerto Rico. *Revista de Agricultura de Puerto Rico*. 28(2): 215-219.
- Northern Research Station.** 2006. Research Natural Areas. NRS Home/ Research Programs/Research Natural Areas. www.nrs.fs.fed.us/research/lands. [Date accessed: March 22, 2011].
- O'Conner, P.J.; Covich, A.P.; Scatena, F.N.; Loope, L.L.** 2000. Non-indigenous bamboo along headwater streams of the Luquillo Mountains, Puerto Rico: leaf fall, aquatic leaf decay and patterns of invasion. *Journal of Tropical Ecology*. 16: 499-516.

- Odum, H.T.** 1970. Rain forest structure and mineral cycling homeostasis. In: Odum, H.T.; Pigeon, R.F., eds. A tropical rain forest: a study of irradiation and ecology at El Verde, Puerto Rico. Springfield, VA: U.S. Department of Commerce: 3-52. Chapter H-1.
- Odum, H.T.; Drewry, G.; Kline, J.R.** 1970. Climate at El Verde, 1963-1966. In: Odum, H.T.; Pigeon, R.F., eds. A tropical rain forest: a study of irradiation and ecology at El Verde, Puerto Rico. Springfield, VA: U.S. Department of Commerce: 347-418. Chapter B-22.
- Odum, H.T.; Pigeon, R.F., eds.** 1970 A tropical rain forest: a study of irradiation and ecology at El Verde, Puerto Rico. Springfield, VA: U.S. Department of Commerce. 1650 p.
- Olander, L.P.; Scatena, F.N.; Silver, W.L.** 1998. Impacts of disturbance initiated by road construction in a subtropical cloud forest in the Luquillo Experimental Forest, Puerto Rico. *Forest Ecology and Management*. 109: 33-49.
- Oliver, J.R.** 1973. Petroglifos en "La Mina." Boletín Informativo Fundación Arqueológica Antropológica e Histórica de Puerto Rico. 1(6): 1-2.
- Ostertag, R.; Scatena, F.N.; Silver, W.L.** 2003. Forest floor decomposition following hurricane inputs in several Puerto Rican forests. *Ecosystems*. 6: 261-273.
- Parés Arroyo, M.** 2010. Limitarán el acceso vehicular a El Yunque. *El Nuevo Día*. Junio 30, 2010: 18.
- Parresol, B.R.; Alemañy, S.** 1998. Analysis of tree damage from Hurricane Hugo in the Caribbean National Forest, Puerto Rico. In: Waldrop, T.A., ed. Proceedings of the Ninth Biennial Southern Silvicultural Research Conference. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Forest Experiment Station: 599-603.
- Parrotta, J.A.; Lodge, D.J.** 1991. Fine root dynamics in a Subtropical wet forest following Hurricane disturbance in Puerto Rico. *Biotropica*. 23(4a): 343-347.
- Persinos, G.J.; Christie, S.K.; Bidinger, J.M.; Lapiana, M.J.** 1970. The ecology of an elfin forest in Puerto Rico, 13. Phytochemical screening and literature survey. *Journal of the Arnold Arboretum*. 51(4): 540-546.
- Picó, R.** 1974. The geography of Puerto Rico. Chicago, IL: Aldine Publishing Company. 439 p.
- PREPA (Puerto Rico Electric Power Authority).** 1974. Annual Report 1973-74. San Juan, PR: PREPA. [Not paged].
- Raffaele, H.A.** 1983. A guide to the birds of Puerto Rico and the Virgin Islands. San Juan, PR: Fondo Educativo Interamericano. 253 p.
- Ramírez, A.; Meléndez-Colom, E.; González, O.** 2004. Meteorological summary for El Verde Field Station. 13 p. <http://ites.upr.edu/>. [Date accessed: April 28, 2009]
- Ramos González, O.M.** 2001. Assessing vegetation and land cover changes in northeastern Puerto Rico: 1978-1995. *Caribbean Journal of Science*. 37(1-2): 95-106.
- Reagan, D.P.; Waide, R.B., eds.** 1996 The food web of a tropical rain forest. Chicago, IL: University of Chicago Press. 616 p.
- Recher, H.F.; Recher, J.T.** 1966. A contribution to the knowledge of the avifauna of the Sierra de Luquillo, Puerto Rico. *Caribbean Journal of Science*. 6(3-4): 151-161.
- Reyes, G.; Brown, S.; Chapman, J.; Lugo, A.E.** 1992. Wood densities of tropical tree species. Gen. Tech. Rep. SO-88. New Orleans: U.S. Department of Agriculture Forest Service, Southern Forest Experiment Station. 15 p.
- Rice, K.; Brokaw, N.; Thompson, J.** 2004. Liana abundance in a Puerto Rican forest. *Forest Ecology and Management*. 190: 33-41.
- Richardson, B.A.; Richardson, M.J.; Soto-Adames, F.N.** 2005. Separating the effects of forest type and elevation on the diversity of litter invertebrate communities in a humid tropical forest in Puerto Rico. *Journal of Animal Ecology*. 74: 926-936.
- Richardson, B.A.; Richardson, M.J.; González, G. [and others].** 2010. A canopy trimming experiment in Puerto Rico: the response of invertebrate communities to canopy loss and debris deposition in a tropical forest subject to hurricanes. *Ecosystems*. 11: 286-301.
- Rivero, J.A.** 1963. *Eleuthrodactylus hedricki*, a new species of frog from Puerto Rico. *Breviora*. 185: 1-7.
- Rivero, J.A.** 1978. Los anfibios y reptiles de Puerto Rico. Mayagüez, PR: Universidad de Puerto Rico, Editorial Universitaria. 152 p. + laminas 63 p.
- Roberts, R.C.** 1942. Soil survey of Puerto Rico. Washington, DC: U.S. Department of Agriculture, Bureau of Plant Industry; Government Printing Office. 503 p.
- Robles Gil, P.** 2006. El Carmen—first wilderness designation in Latin America. *International Journal of Wilderness*. 12(2): 36-40.
- Robinson, K.** 1997. Where dwarfs reign: a tropical rain forest in Puerto Rico. San Juan, PR: University of Puerto Rico Press. 241 p.
- Rodríguez-Vidal, J.A.** 1959. Puerto Rican Parrot (*Amazona vittata vittata*) study. Monograph No. 1. (Puerto Rico Federal Aid Project W-7-R). San Juan, PR: Department of Agriculture and Commerce, Division of Information. 15 p.
- Rodríguez-Vidal, J.A.** 1962. La Cotorra Puertorriqueña (*Amazona vittata vittata* Boddaert) study. *Revista de Agricultura de Puerto Rico*. 49(2): 67-79.
- Rojas Daporta, M.; Ortiz Otero, B.** 1969. Helicóptero GC sutuá restos. San Juan, PR: El Mundo. March 6, 1969: 1 + 19A.
- Rosario Rivera, R.** 1995. La real Cédula de Gracias de 1815 y sus primeros efectos en Puerto Rico. San Juan, PR: First Book Publishing of P.R. 295 p.
- Ruiz Díaz, B.I.; Flecha, A.; Vilches Norat, M.A. [and others].** 1999. Baúl de actividades sobre bosques tropicales: Palmer, PR: Bosque Nacional el Caribe. U.S. Departamento de Agricultura Servicio Forestal, Bosque Nacional del Caribe. 260 p.
- Russel, K.W.; Miller, H.A.** 1977. The ecology of an elfin forest in Puerto Rico, 17. Epiphytic mossy vegetation of Pico del Oeste. *Journal of the Arnold Arboretum*. 58(1): 1-24.
- Salivia, L.A.** 1972. Historia de los temporales de Puerto Rico y las Antillas, 1542 a 1970. Río Piedras, PR: Editorial Edil., University of Puerto Rico. 385 p.
- Sastre-de Jesús, I.** 1979. Ecological life cycle of *Buchenavia capitata* (Vahl.) Eichl., a late secondary successional species in the rain forest of Puerto Rico. Knoxville, TN: The University of Tennessee. 45 p. M.S. thesis.
- Saunders, D.A.; Hobbs, R.J.; Margules, C.R.** 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology*. 5(1): 18-32.
- Scatena, F.N.** 1989. An introduction to the physiography and history of the Bisley experimental watersheds in the Luquillo Mountains of Puerto Rico. GTR-SO-72. New Orleans: U.S. Department of Agriculture Forest Service, Southern Forest Experiment Station. 22 p.
- Scatena, F.N.** 1990. Watershed scale rainfall interception on two forested watersheds in the Luquillo Mountains of Puerto Rico. *Journal of Hydrology*. 113: 89-102.

- Scatena, F.N.** 1993. The management of Luquillo elfin cloud forest ecosystems: irreversible decisions in a nonsubstitutable ecosystem. In: Hamilton, L.S.; Juvik, J.O.; Scatena, F.N. Tropical montane cloud forests: proceedings of an international symposium. Río Piedras, PR: International Institute of Tropical Forestry: 191-198.
- Scatena, F.N.** 1998a. A comparative ecology of the Bisley biodiversity plot and experimental watersheds, Luquillo Experimental Forest, Puerto Rico. In: Dallmeier, F.; Comiskey, J.A., eds. Forest biodiversity in North, Central and South America, and the Caribbean. Pearl River, NY: Parthenon Publishing Group: 213-230.
- Scatena, F.N.** 1998b. An assessment of climate change in the Luquillo Mountains of Puerto Rico. In: Segarra-Garcá, R.I., ed. Proceedings tropical hydrology and Caribbean water resources, Third international symposium on tropical hydrology and Fifth Caribbean Islands water resources congress. San Juan, PR, Herndon, VA: American Water Resources Association: 193-199.
- Scatena, F.N.** 2002. Ecological rhythms and the management of humid tropical forests: examples from the Caribbean National Forest, Puerto Rico. *Forest Ecology and Management*. 154: 453-464.
- Scatena, F.N.; Larsen, M.C.** 1991. Physical aspects of hurricane Hugo in Puerto Rico. *Biotropica*. 23(4a): 317-323.
- Scatena, F.N.; Lugo, A.E.** 1995. Geomorphology, disturbance, and the soils and vegetation in two subtropical wet steepland watersheds of Puerto Rico. *Geomorphology*. 13: 199-213.
- Scatena, F.N.; Moya, S.; Estrada, C.; Chinea, J.D.** 1995. The first five years in the reorganization of aboveground biomass and nutrient use following Hurricane Hugo in the Bisley Experimental watersheds, Luquillo Experimental Forest, Puerto Rico. *Biotropica*. 28(4a): 424-440.
- Scatena, F.N.; Silver, W.; Siccama, T. [and others].** 1993. Biomass and nutrient content of the Bisley Experimental watersheds, Luquillo Experimental Forest, Puerto Rico, before and after Hurricane Hugo, 1989. *Biotropica*. 25(1): 15-27.
- Schellekens, J.; Bruijnzeel, L.A.; Scatena, F.N. [and others].** 2000. Evaporation from a tropical rain forest, Luquillo Experimental Forest, eastern Puerto Rico. *Water Resources Research*. 36(8): 2183-2196.
- Seiders, V.M.** 1971. Geologic map of the El Yunque quadrangle, Puerto Rico. Miscellaneous Geologic Investigations Map I-658. Washington, DC: U.S. Geological Survey. 1 p. + 1:20,000.
- Seifriz, W.** 1943. The plant life of Cuba. *Ecological Monographs*. 13: 375-426.
- Shaw, J.D.** 2006. Benefits of a strategic national forest inventory to science and society: the USDA Forest Service Inventory and Analysis program. *Forest@* 3(1): 46-53.
- Shiels, A.B.; Zimmerman, J.K.; García-Montiel, D.C. [and others].** 2010. Plant responses to simulated hurricane impacts in a subtropical wet forest, Puerto Rico. *Journal of Ecology*. 98: 659-673.
- Shreve, F.** 1914. A montane rain forest: a contribution to the physiological plant geography of Jamaica. Publication No. 199. Washington, D.C.: Carnegie Institute: 1-110.
- Silander, S.R.** 1979. A study of the ecological life history of *Cecropia peltata* L., an early secondary successional species in the rain forest of Puerto Rico. Knoxville, TN: University Of Tennessee. 94 p. M.S. thesis.
- Silcox, F.A.; Kircher, J.C.** 1936. Caribbean National Forest of Puerto Rico. Washington, DC: Government Printing Office. 29 p + maps.
- Simon, A.; Larsen, M.C.; Hupp, C.R.** 1990. The role of soil process in determining mechanisms of slope failure and hillslope development in a humid-tropical forest, eastern Puerto Rico. In: Kneuper, P.; McFadden, L.D., eds. *Geomorphology*. 3: 263-286.
- Smith, E.E.** 1954. The forests of Cuba. Maria Moors Cabot Foundation. Publ. No. 2. Petersham, MA: Harvard Forest. Cienfuegos, Cuba: Atkins Garden and Research Laboratory. 98 p.
- Smith, R.F.** 1970. The vegetation structure of a Puerto Rican rain forest before and after short-term gamma irradiation. In: Odum, H.T.; Pigeon, R.F. A tropical rain forest: a study of irradiation and ecology at El Verde, Puerto Rico. Springfield, VA: U.S. Department of Commerce: 103-140. Chapter D-3.
- Soil Survey Staff.** 1995. Order 1 soil survey of the Luquillo long-term ecological research grid, Puerto Rico. San Juan, PR: U.S. Department of Agriculture, National Resources Conservation Service; University of Puerto Rico, Terrestrial Ecology Division. U.S. Department of Agriculture Forest Service, International Institute of Tropical Forestry. 92 p. + map.
- Snyder, N.F.R.; Wiley, J.W.; Kepler, C.B.** 1987. The parrots of Luquillo: natural history and conservation of the Puerto Rican Parrot. Los Angeles, CA: The Western Foundation of Vertebrate Zoology. 384 p.
- Stadtmüller, T.** 1986. Cloud forest in the humid tropics. Tokyo, Japan: The United Nations University. Turrialba, Costa Rica: Centro Agronómico de Investigación y Enseñanza (CATIE). 81 p.
- Stewart, G.R.** 1941. Storm. New York: Random House. 349 p.
- Thompson, J.; Brokaw, N.; Zimmerman, J.K. [and others].** 2002. Land use history, environment, and tree composition in a tropical forest. *Ecological Applications*. 12(5): 1344-1363.
- Thompson, J.; Brokaw, N.; Zimmerman, J.K. [and others].** 2004. Luquillo Forest dynamics plot. In: Losos, E.C.; Leigh, Jr., E.G., eds. Tropical forest diversity and dynamism: findings from a long-scale plot network. Chicago, IL: University of Chicago Press: 540-550. Chapter 32.
- Thompson, J.; Lugo, A.E.; Thomlinson, J.** 2007. Land use history, hurricane disturbance, and the fate of introduced species in a subtropical wet forest in Puerto Rico. *Plant Ecology*. 192: 289-301.
- Tomblin, J.** 1981. Earthquakes, volcanoes and hurricanes: a review of natural hazards and vulnerability in the West Indies. *Ambio*. 10(6): 340-345.
- Torres, C.E.** 2002. Mueren cinco al caer una avioneta. San Juan, PR: El Nuevo Día. January 6, 2002: 40.
- Torres, J.A.** 1988. Tropical cyclones effects on insect colonization and abundance in Puerto Rico. *Acta Científica*. 2(1): 40-44.
- Torres, J.A.** 1992. Lepidoptera outbreaks in response to successional changes after the passage of Hurricane Hugo in Puerto Rico. *Journal of Tropical Ecology*. 8: 285-298.
- Tropical Forest Experiment Station.** 1950. 10th Annual report. Caribbean Forester. 11: 59-80.
- UNESCO (United Nations Educational, Scientific and Cultural Organization).** 2011. www.unesco.org/new/en/natural-sciences/environment/. [Date accessed: March 23, 2011].
- Urban, I.** 1903-11. Flora portoricensis. *Symbolae Antillanae*. 4: 1-771.
- Urban, I.** 1924. Apuntes históricos de las investigaciones botánicas de la isla. *Revista de Agricultura de Puerto Rico*. 12(11): 97-107.
- Uriarte, M.; Canham, III, C.D.; Thompson, J. [and others].** 2005. Seedling recruitment in a hurricane-driven tropical forest: light limitation, density-dependence and the spatial distribution of parent trees. *Journal of Ecology*. 93: 291-304.
- U.S. Department of Agriculture, Forest Service.** 1983. The principal laws relating to Forest Service Activities. Agric. Handb. No. 453. Washington, DC: Government Printing Office. 591 p.

- U.S. Department of Agriculture, Forest Service.** 1997a. Revised land use and resource management plan: Caribbean National Forest—Luquillo Experimental Forest, Puerto Rico. Management Bulletin R8-MB 80G. Palmer, PR: Caribbean National Forest. 5 chapters + 3 appendices.
- U.S. Department of Agriculture, Forest Service.** 1997b. Final environmental impact statement for the revised land and resource management plan: Caribbean National Forest—Luquillo Experimental Forest, Puerto Rico. Management Bulletin R8-MB 80F. Palmer, PR: Caribbean National Forest. 5 chapters + 9 appendices.
- U.S. Department of Agriculture, Forest Service.** 2006. National visitor use monitoring results for El Yunque National Forest. Atlanta: Region 8, Forest Service. 60 p.
- U.S. Department of Agriculture, Forest Service.** 2008. International Institute of Tropical Forestry strategic plan for fiscal years 2008-2012. FS-914. Washington, DC: Forest Service. 83 p.
- U.S. Department of Agriculture, Forest Service.** 2009. Interpretive and conservation education master plan: El Yunque National Forest. Palmer, PR: El Yunque National Forest. 92 p.
- U.S. Department of Agriculture, Natural Resources Conservation Service.** 2002. Soil survey of the Caribbean National Forest and Luquillo Experimental Forest, Commonwealth of Puerto Rico. Washington, DC: U.S. Department of Agriculture Natural Resources Conservation Service. 181 p.
- U.S. Department of the Interior, U.S. Fish and Wildlife Service.** 2007. Interior Deputy Secretary Lynn Scarlett joins Fish and Wildlife Service employees and partners for grand opening of the Igauca Aviary. News Release, April 28, 2007. <http://www.fws.gov/southeast/news/2007/r07-066.html>. [Date accessed: June 8, 2010].
- U.S. Geological Survey.** 1999. Puerto Rico: Hurricane Georges. U.S. Geological Service Fact sheet 040-99, April 1999. San Juan, PR: U.S. Department of the Interior, U.S. Geological Survey. 4 p.
- Valdés Pizzini, M.; González Cruz, M.; Martínez Reyes, J.E.** 2011. La transformación del paisaje puertorriqueño y la disciplina del Cuerpo Civil de Conservación, 1933-1942. Río Piedras, PR: Universidad de Puerto Rico, Centro de Investigaciones Sociales. 277 p.
- Van der Molen, M.K.; Dolman, A.J.; Waterloo, M.J.; Bruijnzeel, L.A.** 2006. Climate is affected more by maritime than by continental land use change: a multiple scale analysis. *Global and Planetary Change*. 54: 128-149.
- Van Valen, L.** 1975. Life, death, and energy of a tree. *Biotropica*. 7(4): 260-269.
- Ventosa-Febles, E.A.; Camacho Rodríguez, M.; Chabert Llompart, J.L. [and others].** 2005. Puerto Rico critical wildlife areas. San Juan, PR: Department of Natural and Environmental Resources, U.S. Bureau of Fish and Wildlife, Terrestrial Resources Division. 385 p.
- Vogt, K.A.; Beard, K.H.; Hammann, S. [and others].** 2002. Indigenous knowledge informing management of tropical forests: the link between rhythms in plant secondary chemistry and lunar cycles. *Ambio*. 31(6): 485-490.
- Wadsworth, F.H.** 1947a. Growth in the lower montane forest of Puerto Rico. *Caribbean Forester*. 8: 27-35.
- Wadsworth, F.H.** 1947b. La influencia climatológica e hidrológica de los bosques. *Revista de Agricultura de Puerto Rico*. 38(1): 83-87.
- Wadsworth, F.H.** 1948. The climate of the Luquillo Mountains and its significance to the people of Puerto Rico. *Caribbean Forester*. 9: 321-335.
- Wadsworth, F.H.** 1949. The development of the forest land resources of the Luquillo Mountains, Puerto Rico. Ann Arbor, MI: University of Michigan. 481 p. Ph.D. dissertation.
- Wadsworth, F.H.** 1950. Notes on the climax forests of Puerto Rico and their destruction and conservation prior to 1900. *Caribbean Forester*. 11: 38-47.
- Wadsworth, F.H.** 1951. Forest management in the Luquillo Mountains, I. The setting *Caribbean Forester*. 12(3): 93-114.
- Wadsworth, F.H.** 1952a. Forest management in the Luquillo Mountains, II. Planning and multiple use. *Caribbean Forester*. 13(1): 49-61.
- Wadsworth, F.H.** 1952b. Forest management in the Luquillo Mountains, III. Selection of products and silvicultural policies. *Caribbean Forester*. 13(3): 93-119.
- Wadsworth, F.H.** 1953. New observations of tree growth in tabonuco forest. *Caribbean Forester*. 14: 106-111.
- Wadsworth, F.H.** 1970. Review of past research in the Luquillo Mountains of Puerto Rico. In: Odum, H.T.; Pigeon, R.F. A tropical rain forest: a study of irradiation and ecology at El Verde, Puerto Rico. Springfield, VA: U.S. Department of Commerce: 33-46. Chapter B-2.
- Wadsworth, F.H.** 2000. Producción forestal para América Tropical. Manual de Agricultura 710-S. Washington, DC: Departamento de Agricultura de los EE.UU. Servicio Forestal. 603 p.
- Wadsworth, F.H.; Bonnet, J.A.** 1951. Soil as a factor in the occurrence of two types of montane forest in Puerto Rico. *Caribbean Forester*. 12: 67-70.
- Wadsworth, F.H.; Bryan, B.; Figueroa-Colón, J.** 2010. Cutover tropical forest productivity potential merits assessment, Puerto Rico. *Bois et Forêts des Tropiques*. 305(3): 33-41.
- Wadsworth, F.H.; Englerth, G.H.** 1959. Effects of the 1956 hurricane on forests of Puerto Rico. *Caribbean Forester*. 20: 38-51.
- Wadsworth, F.H.; Huckenpahler, B.J.; Erelebe, C.F.** 1955. A report on the tropical forestry short course held in Puerto Rico, March 1 to May 29, 1955. *Caribbean Forester*. 16(1-2): 12-23.
- Wadsworth, R.K.** 1977. A study of diameter distributions of an uneven aged tropical forest by means of a transition matrix model. Seattle, WA: University of Washington, College of Forest Resources. 153 p. Ph.D. dissertation.
- Wagner, R.J.; Wagner, A.B.; Howard, R.A.** 1970. The ecology of an elfin forest in Puerto Rico, 9. Chemical studies of colored leaves. *Journal of the Arnold Arboretum*. 50 (4): 556-565.
- Waide, R.B.; Zimmerman, J.K.; Scatena, F.N.** 1998. Controls of primary productivity: lessons from the Luquillo Mountains in Puerto Rico. *Ecology*. 79(1): 31-37.
- Walker, L.R.** 1991. Tree damage and recovery from Hurricane Hugo in Luquillo Experimental Forest, Puerto Rico. *Biotropica*. 23(4a): 379-385.
- Walker, L.R.** 1994. Effects of fern thickets on woodland development on landslides in Puerto Rico. *Journal of Vegetation Science*. 5: 525-532.
- Walker, L.R.** 1995. Timing of post-hurricane tree mortality in Puerto Rico. *Journal of Tropical Ecology*. 11: 315-320.
- Walker, L.R.** 2000. Seedling and sapling dynamics of treefall pits in Puerto Rico. *Biotropica*. 32(2): 262-275.
- Walker, L.R.; Brokaw, N.L.V.; Lodge, D.J.; Waide, R.B.** 1991. Ecosystem, plant, and animal responses to hurricanes in the Caribbean. *Biotropica*. 23(4): 313-521.
- Walker, L.R.; Lodge, D.J.; Brokaw, N.V.L.; Waide, R.B.** 1991. An introduction to hurricanes in the Caribbean. *Biotropica*. 23(4a): 313-316.
- Walker, L.R.; Neris, L.E.** 1993. Posthurricane seed rain dynamics in Puerto Rico. *Biotropica*. 25(4): 408-418.
- Walker, L.R.; Silver, W.L.; Willig, M.R.; Zimmerman, J.K.** 1996. Long term responses of Caribbean ecosystems to disturbance. *Biotropica*. 28(4a): 414-614.

- Walker, L.R.; Voltzow, J.; Ackerman, J.D. [and others]. 1992. Immediate impact of Hurricane Hugo on a Puerto Rican rain forest. *Ecology*. 73(2): 691-694.
- Walker, L.R.; Whiteaker, L.D. 1988. Crown shyness in a tropical cloud forest. *Biotropica*. 20(4): 338-339.
- Walker, L.R.; Zimmerman, J.K.; Lodge, D.J.; Guzmán-Grajales, S. 1996. An altitudinal comparison of growth and species composition in hurricane-damaged forests in Puerto Rico. *Journal of Ecology*. 84: 877-889.
- Ward, S.E.; Lugo, A.E. 2003. Twenty mahogany provenances under different conditions in Puerto Rico and the U.S. Virgin Islands. In: Lugo, A.E.; Figueroa Colón, J.; Alayón, M., eds., *Big-leaf mahogany: genetics, ecology and management*. New York: Springer: 29-93.
- Watlington, F. 2008. Parrots in peril, squirrels in Central Park: a proposition for El Yunque neotropical bioreserve forest. Gen.Tech. Rep. IITF-GTR-37. In: Annual letter 2003-2004: 100 years of tropical forestry in Puerto Rico and the U.S. Virgin Islands. San Juan, PR: U.S. Department of Agriculture Forest Service, International Institute of Tropical Forestry: 78-79.
- Watson, A.E. 2004. Human relationships with wilderness: the fundamental definition of wilderness character. *International Journal of Wilderness* 10(3): 4-7.
- Weaver, P.L. 1972. Cloud moisture interception in the Luquillo Mountains of Puerto Rico. *Caribbean Journal of Science*. 12(3-4): 129-144.
- Weaver, P.L. 1983. Tree growth and stand changes in the subtropical life zones of the Luquillo Mountains of Puerto Rico. Res. Pap. SO-190. New Orleans: U.S. Department of Agriculture Forest Service, Southern Forest Experiment Station. 24 p.
- Weaver, P.L. 1986a. Hurricane damage and recovery in the montane forests of the Luquillo Mountains of Puerto Rico. *Caribbean Journal of Science*. 22: 53-70.
- Weaver, P.L. 1986b. Growth and age of *Cyrilla racemiflora* L. in montane forests of Puerto Rico. *Interciencia*. 11(5): 221-228.
- Weaver, P.L. 1987a. Structure and dynamics in the Colorado forest of the Luquillo Mountains of Puerto Rico. East Lansing, MI: Michigan State University, Department of Botany and Plant Pathology. 296 p. Ph.D. dissertation.
- Weaver, P.L. 1987b. Ecological observations on *Magnolia splendens* Urban in the Luquillo Mountains of Puerto Rico. *Caribbean Journal of Science*. 23(3-4): 340-351.
- Weaver, P.L. 1987c. Enrichment plantings in tropical America. In: Figueroa, J.C.; Wadsworth, F.H.; Branahan, S., eds. *Management of the forests of tropical America: prospects and technologies*. San Juan, PR: Institute of Tropical Forestry: 259-276.
- Weaver, P.L. 1989a. Taungya plantings in Puerto Rico. *Journal of Forestry*. 87(3): 37-41.
- Weaver, P.L. 1989b. Forest changes after hurricanes in Puerto Rico's Luquillo Mountains. *Interciencia*. 14(4): 181-192.
- Weaver, P.L. 1989c. Rare trees in the Colorado forest of Puerto Rico's Luquillo Mountains. *Natural Areas Journal*. 9(3): 169-173.
- Weaver, P.L. 1990. Succession in the elfin woodland of the Luquillo Mountains of Puerto Rico. *Biotropica*. 22(1): 83-89.
- Weaver, P.L. 1991. Environmental gradients affect forest composition in the Luquillo Mountains of Puerto Rico. *Interciencia*. 16(3): 142-151.
- Weaver, P.L. 1992. An ecological comparison of canopy trees in the montane rain forest of Puerto Rico's Luquillo Mountains. *Caribbean Journal of Science*. 28(1-2): 62-69.
- Weaver, P.L. 1994. Baño de Oro Natural Area, Luquillo Mountains, Puerto Rico. GTR-SO-111. New Orleans: U.S. Department of Agriculture Forest Service, Institute of Tropical Forestry. 55 p.
- Weaver, P.L. 1995. The Colorado and dwarf forests of Puerto Rico's Luquillo Mountains. In: Lugo, A.E.; Lowe, C., eds., *Tropical forests: management and ecology*. New York: Springer-Verlag: 109-141. Chapter 5.
- Weaver, P.L. 1998. Hurricane effects and long-term recovery in a subtropical rain forest. In: Dallmeier, F.; Comiskey, J.A., eds. *Forest biodiversity in North, Central and South America, and the Caribbean*. Pearl River, NY: Parthenon Publishing Group: 249-270.
- Weaver, P.L. 1999. Impacts of Hurricane Hugo on the dwarf cloud forest of Puerto Rico's Luquillo Mountains. *Caribbean Journal of Science*. 35(1-2): 101-111.
- Weaver, P.L. 2000a. Environmental gradients affect forest structure in Puerto Rico's Luquillo Mountains. *Interciencia*. 25(4): 254-259.
- Weaver, P.L. 2000b. Elfin woodland recovery 30 years after a plane wreck in Puerto Rico's Luquillo Mountains. *Caribbean Journal of Science*. 36(1-2): 1-9.
- Weaver, P.L. 2001. Thinning and regeneration in Puerto Rico's Colorado forest, with comments about their effect on the Puerto Rican Parrot. *Caribbean Journal of Science*. 37(3-4): 252-258.
- Weaver, P.L. 2002a. The importance of forest cover for water supplies in mountainous Caribbean islands. *International Forestry Review*. 4(4): 310-312.
- Weaver, P.L. 2002b. A chronology of hurricane induced changes in Puerto Rico's lower montane rain forest. *Interciencia*. 27(5): 252-258.
- Weaver, P.L. 2006. Estate Thomas Experimental Forest, St. Croix, U.S. Virgin Islands: research history and potential. Gen. Tech. Rep. IITF-30. Río Piedras, PR: U.S. Department of Agriculture Forest Service, International Institute of Tropical Forestry. 62 p.
- Weaver, P.L. 2008. Dwarf forest recovery after disturbances in the Luquillo Mountains of Puerto Rico. *Caribbean Journal of Science*. 44(2): 150-163.
- Weaver, P.L. 2010a. Forest structure and composition in the Lower montane rain forest of the Luquillo Mountains in Puerto Rico. *Interciencia*. 35(9): 35(9): 640-656.
- Weaver, P.L. 2010b. Tree species distribution and forest structure along environmental gradients in the dwarf forest of the Luquillo Mountains of Puerto Rico. *Bois et Forêts des Tropiques*. 306(4): 33-44.
- Weaver, P.L. 2011. El Toro Wilderness, Luquillo Experimental Forest, Puerto Rico. In: Watson, A.; Murrieta-Saldivar, J.; McBride, B., comps. 2011. *Science and Stewardship to Protect and Sustain Wilderness Values: Ninth World Wilderness Congress symposium. Proceedings RMRS-P-000*. Fort Collins, CO: U.S. Department of Agriculture Forest Service, Rocky Mountain Research Station: 95-108.
- Weaver, P.L.; Bauer, G.P. 1986. Growth, survival and shoot borer damage in mahogany plantings in the Luquillo Forest in Puerto Rico. *Turrialba*. 36(4): 509-522.
- Weaver, P.L.; Byer, M.D.; Brook, D. 1973. Transpiration rates in the Luquillo Mountains of Puerto Rico. *Biotropica*. 5(2): 123-133.
- Weaver, P.L.; Francis, J.K. 1990. The performance of *Tectona grandis* in Puerto Rico. *Commonwealth Forestry Review*. 69(4): 313-323.
- Weaver, P.L.; Gillespie, A.J.R. 1992. Tree biomass equations for the forests of the Luquillo Mountains, Puerto Rico. *Commonwealth Forestry Review*. 71(1): 35-39.
- Weaver, P.L.; Medina, E.; Pool, D. [and others]. 1986. Ecological observations in the dwarf cloud forest of the Luquillo Mountains in Puerto Rico. *Biotropica*. 18(1): 79-85.

- Weaver, P.L.; Murphy, P.G. 1990. Forest structure and productivity in Puerto Rico's Luquillo Mountains. *Biotropica*. 22(1): 69-82.
- Weaver, P.L.; Ramírez, J.L.; Coll Rivera, J.L. 1999. Las Cabezas de San Juan Nature Reserve (El Faro). GTR IITF-5. Río Piedras, PR: U.S. Department of Agriculture Forest Service, International Institute of Tropical Forestry. 58 p.
- Weaver, P.L.; Schwagerl, J. 2009. U.S. Fish and Wildlife Service refuges and other nearby reserves in southwestern Puerto Rico. GTR--IITF-40. Río Piedras, PR: U.S. Department of Agriculture Forest Service, International Institute of Tropical Forestry. 110 p.
- Wellcok, T.R. 2010. The dickey bird scientists take charge: science, policy, and the spotted owl. *Environmental History*. 15: 381-414.
- Wetmore, A. 1916. Birds of Porto Rico. U.S. Department of Agriculture Bulletin No. 326. Washington, DC: Government Printing Office. 139 p.
- Wetmore, A. 1927. Birds of Porto Rico and the Virgin Islands. Scientific Survey of Porto Rico and the U.S. Virgin Islands. New York: New York Academy of Sciences. 9(3-4): 245-571.
- White, H.H., Jr. 1963. Variation of stand structure correlated with altitude in the Luquillo Mountains. *Caribbean Forester*. 24(1): 46-52.
- White, T.H. Jr.; Collazo, J.A.; Vilella, F.J. 2005. Survival of captive-reared Puerto Rican parrots released in the Caribbean National Forest. *The Condor*. 107: 424-432.
- Wilderness.net 2011. About wilderness, fast facts: creation and growth of the National Wilderness Preservation System. [Date accessed: March 22, 2011].
- Wiley, J.W.; Bauer, G.P. 1985. Caribbean National Forest, Puerto Rico. *American Birds*. 39(1): 12-18.
- Wiley, J.W.; Wunderle, J.M., Jr. 1993. The effects of hurricanes on birds, with special reference to Caribbean islands. *Bird Conservation International*. 3: 319-349.
- Willig, M.R.; Bauman, A. 1984. Notes on bats from the Luquillo Mountains of Puerto Rico. CEER-T-194. San Juan, PR: Center for Energy and Environment Research, University of Puerto Rico; U.S. Department of Energy. 12 p.
- Willig, M.R.; Gannon, M.R. 1991. The effect of Hurricane Hugo on bat ecology with emphasis on an endemic Puerto Rican bat (*Stenoderma rufum*) in the Luquillo Experimental Forest. Research report. Lubbock, TX: Texas Technical University, Department of Biological Science. 30 p.
- Wolcott, G.N. 1924. The food of Porto Rican lizards. *The Journal of Agriculture of the University of Porto Rico*. 7(4): 5-37.
- Wolcott, G.N. 1946. A list of woods arranged according to their resistance to the attack of the West Indian dry-wood termite, *Cryptotermes brevis* (Walker). *Caribbean Forester*. 9(1): 329-336.
- Wolcott, G.N. 1948. The insects of Puerto Rico. *The Journal of Agriculture of the University of Puerto Rico*. 32(4): 749-871.
- Wolcott, G.N. 1950. An index to the termite-resistance of woods. Bulletin No. 85. Río Piedras, PR: University of Puerto Rico Agricultural Experiment Station. 26 p.
- Wolcott, G.N. 1953. The food of the mongoose (*Herpestes javanicus auropunctatus* Hodgson) in St. Croix and Puerto Rico. *Journal of Agriculture of the University of Puerto Rico*. 37(3): 241-247.
- Woodbury, R.; Raffaele, H.; Fram, M. [and others]. 1975. Rare and endangered plants of Puerto Rico: a committee report. San Juan, PR: U.S. Department of Agriculture, Soil Conservation Service; Commonwealth of Puerto Rico Department of Natural Resources. 85 p.
- Woolbright, L.L. 1996. Disturbance influences long-term population patterns in the Puerto Rican frog, *Eleutherodactylus coqui* (Anura: Leptodactylidae). *Biotropica*. 28(4a): 493-501.
- Woolbright, L.L. 1997. Local extinctions of anuran amphibians in the Luquillo Experimental Forest of northeastern Puerto Rico. *Journal of Herpetology*. 31(4): 572-576.
- Wunderle, J.M., Jr. 1995. Responses of bird populations in a Puerto Rican forest to Hurricane Hugo: the first 18 months. *The Condor*. 97: 879-896.
- Wunderle, J.M., Jr.; Arendt, W.J. 2011. Avian studies and research opportunities in the Luquillo Experimental Forest: a tropical rain forest in Puerto Rico. *Forest Ecology and Management*. 262: 33-48.
- Wunderle, J.M., Jr.; Mercado, J.E.; Parresol, B.; Terranova, E. 2004. Spatial ecology of Puerto Rican boas (*Epicrates inornatus*) in a hurricane impacted forest. *Biotropica*. 36(4): 555-571.
- Wunderle, J.M., Jr.; Snyder, N.F.R.; Muiznieks, B. [and others]. 2003. Histories of Puerto Rican Parrot nests in the Caribbean National/Luquillo Experimental Forest, 1973-2000. Gen. Tech. Rep. IITF-GTR-21. San Juan, PR: U.S. Department of Agriculture Forest Service, International Institute of Tropical Forestry. 28 p.
- You, C. 1991. Population dynamics of *Manilkara bidentata* (A. DC.) Cher. in the Luquillo Experimental Forest, Puerto Rico. Knoxville, TN: University of Tennessee. 175 p. Ph.D. dissertation.
- You, C.; Petty, W.H. 1991. Effects of Hurricane Hugo on *Manilkara bidentata*, a primary tree species in the Luquillo Experimental Forest of Puerto Rico. *Biotropica*. 23(4a): 400-406.
- Zimmerman, J.K.; Aide, T.M.; Rosario, M. [and others]. 1995. Effects of land management and a recent hurricane on forest structure and composition in the Luquillo Experimental Forest, Puerto Rico. *Forest Ecology and Management*. 77: 65-76.
- Zimmerman, J.K.; Everham, III, E.M.; Waide, R.B. [and others]. 1994. Responses of tree species to hurricane winds in subtropical wet forest in Puerto Rico: implications for tropical tree life histories. *Journal of Ecology*. 82: 911-922.
- Zou, X.; Zucca, C.P.; Waide, R.B.; McDowell, W.H. 1995. Long-term influence of deforestation on tree species composition and litter dynamics of a tropical rain forest in Puerto Rico. *Forest Ecology and Management*. 78: 147-157.
- Zwank, P.J.; Layton, B.W. 1989. Black rats as potential Puerto Rican parrot nest predators. *Caribbean Journal of Science*. 25(1-2): 13-20.

APPENDIX A

Appendix A— Chronology of critical activities, events, important documents and laws, and little known facts influencing the environment of the Luquillo Mountains and its flora and fauna. Related activities and events with multiple occasions (e.g., mining) are entered once or twice at the most appropriate dates^{a, b}

Date	Topic
~3000–1493	Several cultural groups occupy Puerto Rico at different times, including Archaic, Igneri, Ostiones, Tainos, and Caribs. The pre-Columbian groups inhabit small villages surrounding the Luquillo Mountains where they subsist on tropical crops and seafood, and occasionally venture into the forest for construction materials and other purposes (Dominguez Cristóbal 1997a, 1997b, 1997c; Robinson 1997; Wadsworth 1970).
1493	Columbus sails along Puerto Rico's south coast during his second voyage most likely viewing the Luquillo Mountains on November 17 (Dominguez Cristóbal 1997a, Moran Arce 1971). On November 19 (discovery day), the Spanish land in western Puerto Rico. Some claim that the Spanish discovery of Puerto Rico was during November 1492 by Martín Alonso Pinzón (Hueriga 2004).
1508–09	Spanish colonization begins in river valleys flowing out of the Luquillo Mountains (Wadsworth 1949).
1508–1946	Placer gold mining begins in Puerto Rico in the valleys of the Río Blanco and Río Fajardo, and continues at different sites and times within the Luquillo Mountains, including the Río de la Mina, Río Espíritu Santo, Río Mameyes, Río Prieto, and Río Sabana, through the mid-20th century (Cardona 1984, Wadsworth 1949). Some examples are: the upper Río Mameyes valley in 1870 and 1903, and the upper Río Blanco valley in 1903 (Scatena 1989); and a large scale operation just below the Puente Roto bridge on the Sabana Road (PR route 988), abandoned in 1946 (Wadsworth 1970).
1511–15	Tainos living in the Luquillo Mountains rebel against Spanish colonists (Dominguez Cristóbal 1997a, Wadsworth 1970).
1513	Spanish Crown grants settlers title to about 70 ha of land if they comply with requirements for residence and cultivation (Wadsworth 1949).
1529–30	Natives attack miners and burn their houses. Gold mining operations decline as colonists substitute agriculture for mining (Cardona 1984).
1550	Island native population devastated by introduced diseases and forced labor (Anderson-Córdova 2005).
1582	Spanish settlements on lower slopes of the Espíritu Santo and Sabana watersheds are abandoned due to indigenous attacks from their stronghold located within the mountains (Wadsworth 1949, 1970).
1500s	Spanish use resin from <i>Dacryodes excelsa</i> (tabonuco tree) to caulk ship timbers (Dominguez Cristóbal 1997a).
1500s	A Spanish explorer discards an olive jar, which is found nearly 400 years later (Jeffrey Walker 2009, see endnotes).
1600s	Puerto Rico, with only three populated areas (San Germán, San Juan, and Coamo), remains isolated and residents live by contraband. Timber exports are negligible (Alegría and Rivera Quiñones 1999, Wadsworth 1949).
1736–1899	Coffee, introduced from the Dominican Republic, is later grown on the lower slopes of the Luquillo Mountains through the end of the 19th century when cultivation is ended by a major hurricane (Nolla 1936, Scatena 1989, Wadsworth 1949).
1772–1880	The island population increases and towns surround the Luquillo Mountains—Fajardo (1772), Las Piedras (1773), Naguabo (1794), Luquillo and Juncos (1797), Gurabo (1815), Ceiba (1836), and Río Grande (1880)—placing a demand on forest resources (Dominguez Cristóbal 1997a, Wadsworth 1949).
1797–98	French botanist Pierre Ledru explores northeastern Puerto Rico and collects plant specimens (Liogier 1996, Urban 1924).
1815	The “Cédula de Gracia” cedes Crown lands to the public for agricultural use, mandates that boundaries be planted with trees, and stimulates the local economy with new farms, equipment, and industry, including sawmills (Rosario Rivera 1995).
1820–90	Spanish Crown makes land concessions at the base of the Luquillo Mountains (Scatena 1989, Wadsworth 1949).
1827	Swiss botanist Heinrich Wydler visits Luquillo Mountains during travels to the West Indies (Urban 1903-11, 1924).
1837–95	Timber is cut and exported from the Luquillo Mountains through the port of Luquillo (Wadsworth 1949, 1970).

continued

Appendix A— (continued) Chronology of critical activities, events, important documents and laws, and little known facts influencing the environment of the Luquillo Mountains and its flora and fauna. Related activities and events with multiple occasions (e.g., mining) are entered once or twice at the most appropriate dates^{a, b}

Date	Topic
1839	Spanish Crown orders the establishment of a board to protect forests, fish, and wildlife. The board recommends that no cutting be allowed along streams or headwaters of rivers (Scatena 1989).
1853	By royal decree, two Spanish foresters survey and manage Crown forests, including the Luquillo Forest (Wadsworth 1970). subsistence crops are planted on farms in the area (Scatena 1989).
1857	A tract in the Bisley area is cut for <i>Dacryodes excelsa</i> , <i>Manilkara bidentata</i> , and firewood. Coffee, bananas, and subsistence crops are planted on farms in the area (Scatena 1989).
1860	Spanish records indicate that 7850 ha of crown lands remained in the Luquillo Mountains, declining to 6190 ha in 1880, and to about 5040 ha in 1898 (Snyder and others 1987).
1867	Hurricane San Narciso passes over the Luquillo Mountains. Subsequently, five other major hurricanes would impact the Luquillo Mountains: San Ciriaco in 1899, San Felipe in 1928, San Cipriano in 1932, Hugo in 1989, and Georges in 1998 (Salivia 1972, Weaver 2002b).
1876	Spanish King Alphonso XII proclaims forest reserves in Puerto Rico, including 10 000 ha in the Luquillo Mountains, making it one of the oldest in the Western Hemisphere (Domínguez Cristóbal 1997a).
1877	<i>Herpess auropunctatus</i> (mongoose) is introduced to Puerto Rico with negative impacts on native wildlife throughout the island, including the Luquillo Mountains (Raffaele 1983).
1880–81	Illicit timber felling, carried out intermittently during Spanish times in the Jiménez and Mameyes valleys, is discontinued (Wadsworth 1949). The “Sierra de Luquillo” (Luquillo Mountains) forest reserve is named (Domínguez Cristóbal 1997a).
1883	Henrik F.A. Baron von Eggers (1844-1903), Danish soldier and botanist, collects plant samples from the northwestern slopes of the Luquillo Mountains and notes farming within the Mameyes drainage (Eggers 1883).
1885	German botanist Paul Ernst Emil Sintenis (1847-1907) visits the Luquillo Mountains and collects several plant specimens recorded for the first time (Wadsworth 1970).
1885	A forest guard assigned to patrol the Luquillo Forest presents numerous trespass cases to authorities in the town of Luquillo. Transportation difficulties remain a major deterrent to timber extraction (Wadsworth 1949).
1891–97	The U.S. Land Revision Act and the Organic Administrative Act allow the President of the United States to set aside forest lands from the public domain (U.S. Department of Agriculture, Forest Service 1983).
1898	Augustin Stahl (1842-1917), botanist and ethnologist in Puerto Rico, collects in the Luquillo Mountains (Liogier 1996, Wadsworth 1970).
1898	The Treaty of Paris cedes Spanish Crown lands to the United States at the end of the Spanish-American War, with about 5040 ha situated in the Luquillo Mountains (Wadsworth 1949).
1898	Puerto Rico is designated as Porto Rico from July 16, 1898 until May 17, 1932 purportedly because it was easier to pronounce in English (Martínez-Fernández 1998).
1899	About 16 000 ha of forest and brushlands remain in the Luquillo Mountains, including 2270 ha of virgin forest (Hill 1899, Wadsworth 1970).
1902	Percy Wilson (1879-1944), botanist working with the New York Botanical Garden, collects 3,000 plant specimens between the foothills and summits of the Luquillo Mountains (Britton and Wilson 1923-30, Wadsworth 1970).
1903	Under authority of a 1902 Act of Congress, President Theodore Roosevelt proclaims the Luquillo Forest Reserve (Wadsworth 1949).
1903	Proclamation boundary - all land with an area of 9 by 11 miles (i.e., ~25 650 ha) is classified for reservation as public forest as soon as it might be acquired by the government (Wadsworth 1949). Subsequently, the boundary is modified (fig. 4).
1903–11	Ignatz Urban (1848-1930), a German botanist, classifies plants from Puerto Rico, including the national forest, and publishes “Flora Portoricensis” (Liogier 1996, Urban 1903-11, Wadsworth 1970).
1905	A narrow, infrequently used trail exists to El Yunque and across the mountains to the south, possibly for hiking or hunting parrots and pigeons (Wadsworth 1949).

continued

Appendix A— (continued) Chronology of critical activities, events, important documents and laws, and little known facts influencing the environment of the Luquillo Mountains and its flora and fauna. Related activities and events with multiple occasions (e.g., mining) are entered once or twice at the most appropriate dates^{a, b}

Date	Topic
1905	A report on the Luquillo Forest Reserve discusses climate, forest resources, forest industry, and related topics, including the general lack of valuable timber species, and the sale of torches made from tabonuco resin (Gifford 1905).
1907	The Luquillo Forest Reserve (1903-1907) becomes the Luquillo National Forest (1907-1935). Subsequently, other forest designations are used: Caribbean National Forest or CNF (1935-2007); Luquillo Experimental Forest or LEF (1956-present); and El Yunque National Forest or EYNF (2007-present) (Silcox and Kircher 1936, Wadsworth 1970).
1908	The Preservation of American Antiquities Act protects ruins situated on government lands (U.S. Department of Agriculture, Forest Service 1983).
1908	The Luquillo National Forest proclamation boundaries are located and marked with concrete markers by the U.S. Coast and Geodetic Survey (Wadsworth 1970).
1908–09	Trails into the Espíritu Santo and Jiménez watersheds are used to illicitly cut timber. Trespass by charcoal cutters to high elevations within the mountains leads the Commissioner of Agriculture to request forest guards (Domínguez Cristóbal 1997c, Wadsworth 1949).
1910	Surveys determine that El Toro, and not El Yunque, is the highest peak in the Luquillo Mountains (Wadsworth 1970).
1910–11	Property ownership records for the Luquillo Mountains are in chaos. The Governor of the Insular government persuades the U.S. Forest Service to survey the land (Murphy 1916, Wadsworth 1970).
1911	The U.S. Weeks Act allows the Secretary of Agriculture to acquire forested, cutover, or denuded lands in the watersheds of navigable rivers by purchase or exchange (U.S. Department of Agriculture, Forest Service 1983).
1912	Beginning in 1912, water from the Luquillo Mountains is tapped for several towns and cities: from the Río Fajardo for Fajardo (1912), from Río Gurabo for Juncos (1914), from Quebrada Grande for Naguabo (1922), again from Quebrada Grande for Río Grande (1924), from the Río Canovanas for Canovanas (1925), from Río Cristal for Luquillo (1926), from the Río Blanco and nearby streams for hydropower (1928), and from the Río Gurabo (stored in the reservoir on Río Loíza) for San Juan (1950) (Wadsworth 1970). During the 1970s, water from the Río Blanco was supplied to Roosevelt Roads and Vieques (PREPA 1974). Water extraction projects continue today with the Valenciano and Río Blanco reservoirs in the Juncos and Fajardo areas, respectively (Marino 2011).
1912–16	The forest boundary survey of the proclaimed Luquillo National Forest is completed and shows about 5040 ha. Persons farming within the boundaries are allowed to continue by permit (Bruner 1923; Wadsworth 1949, 1970).
1913–17	Nathaniel Britton and co-workers of the the New York Botanical Garden conduct a scientific survey of the physical and natural history of Puerto Rico and the Virgin Islands, including the Luquillo Mountains, and summarize their work in several volumes (Britton and Wilson 1923-30, Cook 1928, Gleason and Cook 1927).
<1914	Logging on 160 ha is carried out between Quebrada Grande and the Río Espíritu Santo (Wadsworth 1949).
1914	Uncontrolled cutting of timber is reported on the north slopes of the Luquillo Mountains (Wadsworth 1970).
1916	Three types of mountain forest—rain forest, hurricane hardwoods, and palm—are described for the Luquillo Mountains. An appendix of 170 tree species is included (Murphy 1916).
1916	The Puerto Rican government turns over 1200 ha adjacent to the Luquillo National Forest to the federal government (Bruner 1919).
1916–27	The birds of Puerto Rico, about 40 of which nest in the Luquillo Mountains, are described (Wetmore 1916, 1927).
1917	The first forest supervisor is appointed and the U.S. Forest Service begins management of the Luquillo Forest Reserve. The supervisor helps draft the first forest law after departure of the Spanish. The law foresees the creation of a Forest Service (Bruner 1923, Kramer 1928, Wadsworth 1970).
1918	Forest guards are appointed to work in the Luquillo National Forest. Also, agriculture is underway at Bisley and along the southern forest border up to 550 m in elevation (Bruner 1923, Wadsworth 1949).

continued

Appendix A—(continued) Chronology of critical activities, events, important documents and laws, and little known facts influencing the environment of the Luquillo Mountains and its flora and fauna. Related activities and events with multiple occasions (e.g., mining) are entered once or twice at the most appropriate dates^{a, b}

Date	Topic
1919	The first description of four basic forest types is provided for the Luquillo Mountains—cove, slope or lower slope, upper slope or sierra palm, and ridge or dwarf forest (Bruner 1918, see endnotes).
1919–26	About 50 km of horse trails are built to patrol forest boundaries, including along the Río Sabana in the northeast, from Palmer to Río Blanco via the Río Mameyes valley and from Catalina to El Yunque in the north, and along the western boundary of the forest. One trail traverses the mountains. Another 10 km of trails are built by 1926 (Kramer 1928, Wadsworth 1949).
1919–50s	One family lives within the forest boundary in 1919, increasing to 220 families in 1940, then decreasing to 60 by 1949. By 1953, all families are relocated outside of forest boundaries (Wadsworth 1949, 2009, see endnotes).
1920–43	Three sawmills operate at low elevations in the Río Sabana and Río Espíritu Santo river valleys near forest boundary, and remain operational for up to 15 years (Scatena 1989, Wadsworth 1949).
1924	The U.S. Clarke-McNary Act allows the Forest Service to support local tree production (U.S. Department of Agriculture, Forest Service 1983).
1925–26	The mammals of Puerto Rico are described, including native bats in the Luquillo Mountains (Anthony 1925, 1926).
1926–42	Construction begins on the Mameyes-Río Blanco highway (PR Route 191) to traverse the Luquillo Mountains. The first section from Palmer to Catalina is completed by 1929. The road is finished in 1942 (Bagué 1962, Wadsworth 1970). Subsequently, another 15 roads are built entirely or partially within or bordering the forest (table 3).
1927	Ecological descriptions of four distinct forest associations are provided for the Luquillo Mountains (Gleason and Cook 1927).
1928	The U.S. McSweeney-McNary Act authorizes a Federal forest research station in Puerto Rico (U.S. Department of Agriculture, Forest Service 1983).
1928	A narrow gauge cable railway is built from the lower Río Blanco valley to 430 m elevation then westward (i.e., below the forest boundary) on the south slope to facilitate the construction of water control structures on the Río Icacos and other streams flowing out of the Luquillo Mountains (Krug 1930).
1928–32	Three hurricanes cause considerable damage to the Luquillo Forest and flood lands in eastern Puerto Rico. Salvage use of timber is authorized under the Free Use Provision Act for rural reconstruction after San Felipe in 1928, the island's legendary storm (Crow 1980, Synder and others 1987).
1930–62	Four systematic forest surveys are carried out: stocking in 1930; sawtimber, saplings, and reproduction in 1937; sawtimber in 1948; and a resample of the most accessible saw timber areas in 1962 (Wadsworth 1951, 1970).
1930s	Stands of exotic bamboo are planted within the national forest to stabilize soils along PR Route 191 (Blundell and others 2003).
1931	First <i>Swietenia macrophylla</i> x <i>mahagoni</i> (hybrid mahogany) plantations are established on the Harvey tract and and experimental plantings at Del Valle (Marrero 1948, Wadsworth 1970).
1931–39	Leslie R. Holdridge, the author of life zone ecology, begins a herbarium collection. By 1948, it contains 3,000 specimens, including many trees in the Luquillo National Forest (Wadsworth 1970). In the early 1980s, the collection is donated to the herbarium at University of Puerto Rico Agricultural Experiment Station.
1931–49	Reforestation, mainly between 1935 and 1945, results in the planting of nearly 1600 ha (Wadsworth 1949, 1970).
1931–49	The Forest Service authorizes the sale of timber which begins the following year (Wadsworth 1949). Timber sales, >80 percent fuelwood (i.e., 3.25 million board feet), take place on the most accessible 2150 ha. Supervision of tree cutting assures the release of desirable timber species. The charcoal market collapses in 1949 with the importation of kerosene stoves (Snyder and others 1987; Wadsworth 2009, see endnotes).
1932	The forest supervisor completes a policy statement for the Luquillo National Forest, which calls for forest protection and wood production, and allows post-hurricane salvage (Kramer 1932, see endnotes; Wadsworth 1949).
1932	The Forest Service builds overnight cabins on the north and south slopes of the Luquillo Mountains to facilitate patrol and protection of the national forest (Wadsworth 1949).

continued

Appendix A—(continued) Chronology of critical activities, events, important documents and laws, and little known facts influencing the environment of the Luquillo Mountains and its flora and fauna. Related activities and events with multiple occasions (e.g., mining) are entered once or twice at the most appropriate dates^{a, b}

Date	Topic
1933	The geology of Puerto Rico is described, including the Luquillo Mountains (Meyerhoff 1933).
1933–34	The Civilian Conservation Corps (CCC) is created in the United States to carry out emergency conservation work (Lavandero 1998). The U.S. Congress enacts the Emergency Public Works Program for Puerto Rico. U.S. Army reserve officers temporarily take charge of the camps to construct buildings and trails (Mowbray 2008).
1933–49	The area of the Luquillo National Forest increases by nearly one-half of its current size of 11 310 ha (figs. 1 and 4).
1934–37	Troughs and rearing pools for a trout nursery are built near the La Mina Recreation Area. Trout eggs are introduced from United States but national forest waters are too warm for reproduction (Domínguez Cristóbal 1997c; Gerhart 1936, see endnotes).
1934	The La Mina area first opens to the public and attracts 2,200 visitors on a single day (Gerhart 1936, see endnotes).
1934–51	A sawmill is established at Sabana to cut <i>Dacryodes excelsa</i> and build houses for temporary forest residents (i.e., parceleros) (Holdridge 1940, Wadsworth 1949).
1935–39	Small scale timber stand improvement on an experimental basis is carried out in 55 ha of Lower Montane rain forest in the Río Espíritu Santo and Río Mameyes Valleys. Study plots are established in 1938 (Wadsworth 1949).
1935–43	The CCC builds 100 km of roads and 80 km of trails along with two picnic areas, cabins, a fish hatchery, two swimming pools and a restaurant (closed in 1989). Subsequently in 1939, the La Mina Recreation Area is built. The trails extend from the La Mina Recreation Area to La Mina Falls and Baño de Oro, and from PR route 191 to Mt. Britton, El Yunque, Los Picachos, and the summits of Pico del Este, Pico del Oeste, and El Toro. Also, the CCC carries out extensive reforestation within the mountains (Domínguez Cristóbal 1997a, 1997c; Gerhart 1936a, 1936b; Wadsworth 1949).
1937	A 6 percent timber cruise of 6900 ha is carried out within the forest (Wadsworth 1970).
1937	The Pittman-Robinson Act expands government involvement in wildlife conservation by providing funds to acquire lands, restore habitat, and conduct research (Snyder and others 1987).
1937–39	The Puerto Rico Reconstruction Administration builds the El Verde Field Station at 350 m elevation (Odum and Pigeon 1970; Wadsworth 1970). The station is renovated in early 1960s and laboratory facilities are added in 1963 and 1977. Later, a 22-m walk-up tower and canopy walkway are built in the vicinity. In 2005, a dormitory is added.
1938	The El Yunque and Mt. Britton towers are built (El Yunque National Forest 2009, see endnotes; Walker and others 1999, see endnotes).
1938–40s	Spur roads for summer homes are built near La Mina Recreation Area (e.g., Molindero Road) (Gerhart 1936, see endnotes). Lack of use or maintenance results in their loss (U.S. Department of Agriculture, Forest Service 1997b).
1939	Silviculture is first practiced in the forest by removing vines and poor trees to favor desirable saplings (Wadsworth 1970).
1939	The Tropical Forest Experiment Station (today the International Institute of Tropical Forestry) begins to operate. Site adaptability testing for more than 100 native and 350 introduced tree species commences. The staff also starts publication of the Caribbean Forester, organizes the Institute's library, and develops a system of research files. Much of the research is carried out in the Luquillo Mountains (Anonymous 1939, Francis 1989, Marrero 1948).
1940s	About 220 families resident on acquired tracts of land within the Caribbean National Forest intercrop trees with their subsistence crops (i.e., agroforestry), gradually reforesting the land (Holdridge 1940).
1940s	Parts of the Bisley watersheds are logged (Scatena 1989)
1940s–2008	A plane crashes in Lower montane forest near the Bisley watersheds, possibly during World War II. Subsequently, crashes occur in 1968 on Pico del Este, in 1969 on Cacique, in 2002 near the restaurants on PR route 191, and in 2008 in the El Toro Wilderness Area (Hernández Pérez 2008, Rojas Daporta and Ortiz Otero 1969, Torres 2002, Weaver 2000).
1942	The U.S. Geological Survey completes Luquillo Mountains topographic maps at 1/30,000 scale, with revisions in 1952 and 1958 at 1/20,000 scale (Wadsworth 1970).

continued

Appendix A— (continued) Chronology of critical activities, events, important documents and laws, and little known facts influencing the environment of the Luquillo Mountains and its flora and fauna. Related activities and events with multiple occasions (e.g., mining) are entered once or twice at the most appropriate dates^{a, b}

Date	Topic
1942	The U.S. Army builds access road FS-10 from PR route 191 to El Yunque peak for an early warning radar post to detect enemy aircraft; also, barracks on FS-10 are constructed for off-duty radar crews (Mombrey 2008).
1942–55	Stream gauging stations are maintained on the Río Icacos and Río Espíritu Santo from 1942 to 1955 (Wadsworth 1970).
1943	Long-term research begins with the 0.72-ha El Verde plot. Today, plots to determine tree growth number about 450 and are located in all forest types. Some are still monitored (Crow 1980, Weaver 1983) (table 7).
1945	Puerto Rican forest insects are described, including species from the Luquillo Mountains (Martorel 1945).
1945	Timber stand improvement on 1620 ha in the Río Grande, Río Icacos, and Río Sabana watersheds is used to alleviate a post-war energy crisis and provide employment (Snyder and others 1987).
1945–57	The U.S. military carries out maneuvers under permit within the national forest (Wadsworth 2009, see endnotes).
1945–74	A tree nursery at Catalina is established and within 2 years has the capacity to produce 6 million trees and ornamentals. The nursery continues to operate until 1974 (Domínguez Cristóbal 1997c).
1946	All Puerto Rican public forests, including the Luquillo Mountains, are designated as wildlife refuges (Wadsworth 1970).
1946–48	A 2-percent timber cruise is carried out on 4550 ha in Lower Montane and Montane rain forests to help prepare a multiple use forest management plan (Wadsworth 1951, 1952a, 1952b).
1948	Climatic data from 1935 to 1948 are reported for the La Mina Station at 720 m elevation in the Luquillo Mountains (Wadsworth 1948).
1948	An assessment of 4 million seedlings of 27 tree species planted on nearly 1600 ha of abandoned farm land in the Luquillo Mountains shows generally poor survival and growth (Marrero 1948).
1948–63	Multi-species volume tables are derived for the Lower montane and Montane rain forests, and later a combined regression equation is derived to estimate tree volumes (Wadsworth 1949, 1970).
1949	The Baño de Oro Natural Area is established on 745 ha in the Mameyes watershed. The area contains each of four forest types (Lower montane, Montane, Palm, and Dwarf forests) in pristine condition (Weaver 1994).
1949	The natural vegetation of the Windward and Leeward Islands is described using a forest classification system still employed widely in the Caribbean Islands, including the Luquillo Mountains (Beard 1949).
1950	The 5-ha Elizabeth Colberg Girl Scout Camp is established along PR route 186 near El Verde. The camp sign reads—Marzo 12, 1950 campamento “Eliza Colberg” ninas escuchas—indicating a March 1950 commemorative date.
1950	A Luquillo Forest multiple use and timber management plan calls for reservation of uplands, parrot habitat, watershed conservation, and research. A forest type map is produced and timber species in the forest are classified according to utility. About 2270 ha of virgin forest remains. Subsequent timber plans for sustainable harvest are revised in mid-1960s (Muñoz 1965, see endnotes; Wadsworth 1951, 1952a, 1952b, 1970).
1950	Resistance of Puerto Rican woods to attack by dry wood termites is summarized and indexed by species (Wolcott 1950).
1953	First of 16 international tropical forestry short courses begins with field activities in the Luquillo Mountains. The courses emphasize multiple use planning, tree identification, forest mensuration, timber production, silviculture, and public forest administration (Anonymous 1954, Barres 1963, Lamb 1959, Wadsworth and others 1955).
1953–56	With support from the Pittman-Robinson Program, the Puerto Rican parrot population in the mid-1950s is estimated at 200 birds within the forest. Other estimates were: 1864, abundant in the eastern lowlands; 1931, about 2,000 in the Luquillo Mountains; 1963, about 120 in the LEF; 1972, only 13 birds (Rodríguez-Vidal 1959, Snyder and others 1987).
1955	<i>Swietenia macrophylla</i> and <i>Khaya nyasica</i> are planted in gaps and openings in the Bisley area (Scatena 1989).
1955	All logging with oxen ceases within the forest due mahogany imports (i.e., demand for local timber is depressed). Harvest and pit sawing of <i>Magnolia splendens</i> for furniture terminates (Wadsworth 1970).

continued

Appendix A— (continued) Chronology of critical activities, events, important documents and laws, and little known facts influencing the environment of the Luquillo Mountains and its flora and fauna. Related activities and events with multiple occasions (e.g., mining) are entered once or twice at the most appropriate dates^{a, b}

Date	Topic
1955–61	Information on industrial wood use in Puerto Rico, and on the machining, seasoning, and related characteristics of 60 Puerto Rican timbers, many found in the Luquillo Mountains, are published (Longwood 1955, 1961).
1956	A pilot management program begins on slightly more than 3200 ha of land designated for timber production. It includes the liberation of promising crop trees and timber plantations (Anonymous 1957, 1958).
1958	Timber access roads to Bisley, Espíritu Santo, Jiménez, and Sabana working areas are completed (Anonymous 1958).
1958–62	Weather (rainfall, temperature, humidity, wind velocity, solar radiation) are continuously recorded for 4 years at El Yunque Peak. Eight other sites at lower elevations provide comparative data (Briscoe 1966).
1958–62	The 5-km FS-27 (Pico del Este) road and radar facilities are built (Mowbray 2008, Scatena 1993) (table 3).
1959	<i>Pinus caribaea</i> is successfully introduced to Puerto Rico with some plantings in the Luquillo Mountains (Mosquera and Feheley 1984)
1960	The U.S. Multiple-Use Sustained Yield Act establishes that national forests be managed for outdoor recreation, range, timber, watershed, and wildlife and fish purposes (U.S. Department of Agriculture, Forest Service 1983).
1960	An arboretum is established at 625 m elevation on the lower western slope of the LEF along PR route 186 where more than 80 native and exotic species are maintained (Francis 1989).
1961–65	The Atomic Energy Commission experiments with the effects of gamma radiation on tropical vegetation as part of the “Atoms for Peace” program and proposed sea-level Panama Canal project (Mowbray 2008). The University of Puerto Rico runs the Verde field station under Forest Service permit. Studies culminate in “A Tropical Rain Forest” (Odum and Pigeon 1970).
1962	A cottage on the Molindero Road is made available to the University of Puerto Rico as a biological research station (Wadsworth 1970).
1962–63	Summer courses in tropical silviculture are offered for forestry students from the United States (Anonymous 1963).
1962–63	Yokahú Tower is built (Dominguez Cristóbal 1997b).
1963	A major <i>Swietenia</i> hybrid line planting program establishes 1275 ha of plantings by 1981 (Weaver and Bauer 1986).
1963	A new species, tree frog (<i>Eleutherodactylus hedricki</i>), is discovered in the LEF (Joglar 1998, Rivero 1963).
1963	<i>Corvus leucognathus</i> (White-necked crow) is last seen within the LEF (Raffaele 1983).
1963	The U.S. Army carries out herbicide research (i.e., Picloram or Agent White) on 0.4 ha in the LEF (Mowbray 2008).
1963–2003	U.S. Navy operates an electronic site at Pico del Este for tracking missiles on Vieques and joint surveillance activities for three agencies, including the Federal Aviation Administration (FAA). Navy use discontinues in 2003 but FAA activities remain through a special use permit with the USDA Forest Service (Mowbray 2008).
1964	The Wilderness Act establishes a national wilderness system (U.S. Department of Agriculture, Forest Service 1983).
1964–74	Foresters and plant taxonomists describe and illustrate in two volumes of all known tree species in Puerto Rico and the U.S. Virgin Islands, including those in the Luquillo Mountains (Little and Wadsworth 1964; Little and others 1974).
1965	The LEF timber management plan is drafted (Muñoz 1965, see endnotes).
1965–77	The Arnold Arboretum initiates research in the Dwarf forest on Pico del Oeste. Ultimately, 17 research papers are published dealing with the climate, soils, and vegetation on the Luquillo Mountain summits (Howard 1968).
1968	The U.S. Wild and Scenic Rivers Act is passed (U.S. Department of Agriculture, Forest Service 1983).
1968–87	Puerto Rican parrot occupies the LEF as a last refuge and is designated an endangered species. The parrot recovery program begins with cooperation from the U.S. Fish and Wildlife Service, the Puerto Rico Department of Natural Resources, and the World Wildlife Fund. The parrot program work is summarized in a book and in 2000 the first parrots reared in captivity are released into the wild (Snyder and others 1987, White and others 2005).

continued

Appendix A—(continued) Chronology of critical activities, events, important documents and laws, and little known facts influencing the environment of the Luquillo Mountains and its flora and fauna. Related activities and events with multiple occasions (e.g., mining) are entered once or twice at the most appropriate dates^{a, b}

Date	Topic
1969	The National Environmental Policy Act states that systematic, interdisciplinary approaches be employed for environmental planning and decisionmaking, and that environmental impact statements with alternatives be presented for proposed actions (U.S. Department of Agriculture, Forest Service 1983).
1970	The Toro Negro forest is transferred to the Commonwealth of Puerto Rico Forest Reserve System in exchange for forest lands added to the LEF in the Luquillo Mountains (Wadsworth 1970).
1970–92	P.R. route 191 near the LEF's south border is closed by a landslide and by 1992 efforts to reopen it are abandoned. The highway remains closed between km 13 and 21 (Domínguez Cristóbal 1997c; U.S. Department of Agriculture, Forest Service 1997a).
1971	<i>Dendroica angelae</i> (Elfin woods warbler), an endemic, is discovered within the LEF (Kepler and Parkes 1972).
1972	The first Puerto Rican Parrot aviary is established in the LEF's old army barracks (Snyder and others 1987).
1973	The U.S. Endangered Species Act authorizes the government to designate a species as endangered or threatened, and to indicate its critical habitat (U.S. Department of Agriculture, Forest Service 1983).
1973	Life zones are described for Puerto Rico and the U.S. Virgin Islands (Ewel and Whitmore 1973).
1974–76	The U.S. Forest and Rangeland Renewable Resources Planning Act and the U.S. National Forest Management Act establish a periodic review of programs for administration and management of the National Forest System, including research and cooperation with State and Private Forest Service programs (U.S. Department of Agriculture, Forest Service 1983).
1974–91	The El Yunque Electronics site consolidation plan is implemented, eliminating 23 buildings and reducing permittees from > 200 to 9 (U.S. Department of Agriculture, Forest Service 1991). In 1981, the Puerto Rican Telephone Company Communications Tower on El Yunque is completed, culminating > 30 years of construction and modification of facilities.
1975	A book on the common ferns in the Luquillo Forest is published (Kepler 1975).
1976	The LEF is designated as part of the international network of Biosphere Reserves (Domínguez Cristóbal 1997b).
1976	The Youth Conservation Corps (YCC) program begins in the LEF based on the 1970 U.S. YCC Act. The Act implements needed conservation work, provides gainful employment, and educates the island's youth on nature conservation and heritage (U.S. Department of Agriculture, Forest Service 1983).
1982	The Catalina Service Center, formerly the district ranger office, serves as a new office complex for the CNF (Luis Rivera 2010, see endnotes).
~1982	A parked crane falls off FS-27 road and damages 0.3 ha of Montane rain forest below Pico del Oeste (Weaver, pers. obs).
1984	Mineral resources, the location of > 20 mining sites, and mining history are described for the forest (Cardona 1984).
1985	U.S. Congress authorizes watershed research in the Bisley watersheds where work begins on the Long Term Ecological Research (LTER) program in 1987 (Scatena 1989).
1985	Two books describe vines and climbing plants in Puerto Rico, including those in the LEF (Acevedo-Rodríguez 2005; Acevedo-Rodríguez and Woodbury 1985).
1985–97	The descriptive treatment of the flora of Puerto Rico is completed, including all species in the Luquillo Mountains (Liogier 1985-97).
1986–97	The land and resource management plan for the CNF (also LEF) is reviewed by the public, revised through amendments, and finally adopted (U.S. Department of Agriculture, Forest Service 1997a, 1997b).
1989	The Institute celebrates 50 years (1939-89) of research, much of it carried out in the LEF (Lugo and Lowe 1995).
1990	Long-term Ecological Research Grid is established in Lower montane rain forest near El Verde (Soil Survey Staff 1995).
1992	The first visitor interpretative plan is completed for the LEF (Vélez and others 1992, see endnotes).

continued

Appendix A— (continued) Chronology of critical activities, events, important documents and laws, and little known facts influencing the environment of the Luquillo Mountains and its flora and fauna. Related activities and events with multiple occasions (e.g., mining) are entered once or twice at the most appropriate dates^{a, b}

Date	Topic
1994	A drought emergency plan is drafted to supply 3 million liters from forest streams to surrounding communities during major water shortages (Caribbean National Forest 1994, see endnotes).
1996	El Portal Tropical Forest Center opens with 3000 m ² of exhibition space, offering educational opportunities for the public. The interpretation program highlights an introduction to tropical forests, benefits of forests to humans, and future forest conservation and management (U.S. Department of Agriculture, Forest Service 1997a).
1999	An environmental education program for teachers is developed to complement tours in the LEF (Ruiz Díaz and others 1999).
2000	A silvics manual is published and includes many tree species that grow in the LEF (Francis and Lowe 2000).
2000	Forest inventory sampling, first carried out in 1980, is expanded to the Luquillo Mountains (Birdsey and Weaver 1982, Brandeis and others 2003).
2002	The Caribbean National Forest Wild and Scenic Rivers Act of 2002 (P.L. 107-365 as amended) designates the Río Icacos, Río Mameyes, and Río de la Mina, totaling 15.2 km in length (El Yunque National Forest 2009).
2002	The soil survey of the Luquillo Experimental Forest is published (U.S. Department of Agriculture, Natural Resources Conservation Service 2002).
2005	H.R. 539, the Caribbean National Forest Act (P.L. 109-118) designates 10,000 acres (about 4050 ha) of National Forest land in Puerto Rico as the El Toro Wilderness (El Yunque National Forest 2009).
2007	A forest transportation study concludes that a mass transit system be implemented for PR 191 (U.S. Department of Agriculture, Forest Service 2009).
2007	U.S. Fish and Wildlife Service officially opens the new Iguaca (Puerto Rican Parrot) aviary along PR route 9966 (U.S. Department of the Interior, U.S. Fish and Wildlife Service 2007).
2009	An interpretation and conservation education master plan is produced for El Yunque (El Yunque National Forest 2009).

^aMain and related topics (e.g., gold mining, hurricanes, and others) are presented on one date for convenience.

^bAdditional sources: Mosquera and Feheley (1984); also, information derived from IITF archives and notes compiled by Frank H. Wadsworth, Institute of Tropical Forestry director from 1956 to 1979 (Wadsworth 2009, see endnotes); and El Yunque National Forest 2011.

APPENDIX B

Appendix B—Forest supervisors of the National Forest^a

Years	Names (titles) ^b
1917	Emory M. Bruner, Forest Supervisor, Superintendent General of the Forests of Puerto Rico (Department of Agriculture and Labor)
1923	William P. Kramer, Forest Supervisor, Superintendent General of the Forests of Puerto Rico (Department of Agriculture and Labor)
1931	Thomas R. Barbour, Forest Supervisor, Superintendent General of the Forests of Puerto Rico (Department of Agriculture and Labor)
1935	Evan Worth Hadley, Forest Supervisor, Superintendent General of the Forests of Puerto Rico (Department of Agriculture and Labor)
1943	Arthur T. Upson, Forest Supervisor/Tropical Forest Experiment Station Director ^b
1949	Henry B. Bosworth, Forest Supervisor/Tropical Forest Experiment Station Director ^b
1951	Irvin P. Murray, Forest Supervisor
1956	Frank H. Wadsworth, Forest Supervisor and Tropical Forest Research Center Project Leader (later called Institute of Tropical Forestry) ^c
1963	Lawrence W. Hill, Forest Supervisor at the Institute of Tropical Forestry
1974	Leonard A. Linquist, Forest Supervisor ^d
1976	Juan E. Muñoz, Forest Supervisor
1986	Bernie Ríos, Forest Supervisor
1989	José Salinas, Forest Supervisor
1993	Pablo Cruz, Forest Supervisor

^aThe name of the National Forest changed several times during the period 1903-2007; also, the name of the current International Institute of Tropical Forestry changed several times between 1939 and 1992 (see Introduction).

^bSource: Bagué 1962.

^cThe Caribbean National Forest and the Tropical Forest Experiment Station were combined into a unit called the Tropical Region.

^dThe administration of the Caribbean National Forest was separated from the Institute of Tropical Forestry.

APPENDIX C

Appendix C—Gradient sampling tally—occurrence of 105 tree species, mostly natives, by environmental factors within the Luquillo Experimental Forest

Species name	Type ^a	Stems		Elevation ^b	Occurrence of species										
					Forest type ^c				Topography ^d						
					LM	MO	PA	DW	R	S	V	Total	R	S	V
		total	%	m	--- stems (no.) ---				--- plots (no.) ---				--- stems (no.) ---		
<i>Alchornea latifolia</i> Sw.		64	0.486	350-915	7	47	10		12	7	6	25	31	14	19
<i>Alchorneopsis portoricensis</i> Urban		3	0.023	380-630	1	2			0	1	1	2	0	1	2
<i>Andira inermis</i> (W. Wright) DC.		2	0.015	350-380	2				0	1	1	2	0	1	1
<i>Antirhea obtusifolia</i> Urb.	LEF	10	0.076	350-760	5	5			1	6	3	10	1	6	3
<i>Ardisia luquillensis</i> (Britton) Alain	LEF	22	0.167	640-990		12		10	6	5	2	13	8	12	2
<i>Brunfelsia lactea</i> Krug & Urban	LEF	1	0.007	860			1		1	0	0	1	1	0	0
<i>Buchenavia tetraphylla</i> (Aublet) R. Howard		15	0.114	350-780	6	9			5	5	2	12	7	5	3
<i>Byrsonima spicata</i> (Cav.) HBK		2	0.015	560-650	1	1			1	1	0	2	1	1	0
<i>Byrsonima wadsworthii</i> Little	PR	74	0.562	350-950	3	69		2	16	9	5	30	46	21	7
<i>Calyptranthes krugii</i> Kiaersk.	PR	99	0.752	640-1000		37	1	61	14	8	6	28	60	23	16
<i>Calyptropsidium sintensis</i> Kiaersk.		7	0.053	820			7		0	0	1	1	0	0	7
<i>Casearia arborea</i> (L.C. Rich) Urban		7	0.053	560-800	6	1			2	1	0	3	6	1	0
<i>Casearia decandra</i> Jacq.		3	0.023	740-750		3			0	1	2	3	0	1	2
<i>Casearia sylvestris</i> Sw.		2	0.015	460	2				0	0	1	1	0	0	2
<i>Cassipourea guianensis</i> Aubl.		13	0.099	350-700	4	9			6	3	0	9	10	3	0
<i>Cecropia schreberiana</i> Mig.		237	1.801	350-950	48	54	130	5	9	13	25	47	66	73	98
<i>Cestrum macrophyllum</i> Vent.		3	0.023	650		3			1	0	0	1	3	0	0
<i>Chionanthus domingensis</i> Lam.		3	0.023	650-920		1		2	1	1	0	2	1	2	0
<i>Citharexylum caudatum</i> L.		34	0.258	645-960		31		3	3	1	11	15	7	1	26
<i>Cleyera albo-punctata</i> (Griseb.) Krug & Urban		2	0.015	820-850		2			2	0	0	2	2	0	0
<i>Clibadeum erosum</i> (Sw.) DC.		13	0.099	730-880			13		1	1	2	4	5	2	6
<i>Clusia clusioides</i> (Griseb.) D'Arcy		220	1.671	450-1000	7	136	1	76	19	17	6	42	91	109	20
<i>Coccoloba swartzii</i> Meisner		2	0.015	670		2			1	0	0	1	2	0	0
<i>Cordia borinquensis</i> Urban	PR	432	3.281	350-960	23	347	37	25	25	28	28	81	153	144	135
<i>Cordia sulcata</i> DC.		4	0.03	380-460	4				0	1	2	3	0	1	3
<i>Croton poecilanthus</i> Urban	LEF	393	2.985	360-960	51	313	18	11	8	13	29	50	30	84	279
<i>Cyathea arborea</i> (L.) J.E. Smith		121	0.919	460-970	5	70	3	43	7	7	11	25	40	53	28
<i>Cyathea bryophila</i> (R. Tryon) Proctor	PR	435	3.304	850-1000		12	2	421	6	8	9	23	47	176	212
<i>Cyathea portoricensis</i> Spreng ex Kuhn	PR	13	0.099	720-870			13		0	1	3	4	0	8	5
<i>Cybianthus sintensisii</i> Mart.	LEF	3	0.023	680-950		2		1	1	2	0	3	1	2	0
<i>Cyrilla racemiflora</i> L.		274	2.081	450-970	36	206	2	30	20	18	7	45	154	107	13
<i>Dacryodes excelsa</i> Vahl		192	1.458	350-850	150	41	1		10	10	4	24	104	81	7
<i>Daphnopsis philippiana</i> Krug & Urban	PR	234	1.777	450-970	49	140	2	43	19	23	13	55	83	120	31
<i>Dendropanax arboreus</i> (L.) Decne & Planch.		2	0.015	750		2			0	0	1	1	0	0	2
<i>Dendropanax laurifolius</i> (E. March.) Decne & Planch.	PR	3	0.023	860-915		1	2		2	0	0	2	3	0	0

continued

Appendix C—(continued) Gradient sampling tally—occurrence of 105 tree species, mostly natives, by environmental factors within the Luquillo Experimental Forest

Species name	Type ^a	Occurrence of species													
		Stems	Elevation ^b	Forest type ^c				Topography ^d							
				LM	MO	PA	DW	R	S	V	Total	R	S	V	
		<i>total</i>	<i>%</i>	<i>m</i>	--- stems (no.) ---				--- plots (no.) ---				--- stems (no.) ---		
<i>Ditta myricoides</i> Griseb.		79	0.601	450-950	2	60	12	5	10	11	12	33	23	27	29
<i>Drypetes glauca</i> Vahl		103	0.782	350-800	55	48			4	8	7	19	20	58	25
<i>Eugenia borinquensis</i> Britton	LEF	572	4.345	550-1000	1	115	24	432	20	18	20	58	258	204	110
<i>Eugenia eggersii</i> Kiaersk.	PR	8	0.061	660-750		4	4		2	1	1	4	4	1	3
<i>Eugenia stahlII</i> (Kiaersk.) Krug & Urban	PR	41	0.311	380-850	4	37			6	9	3	18	13	24	4
<i>Ficus citrifolia</i> P. Miller		3	0.023	640-760		3			0	2	1	3	0	2	1
<i>Ficus crassinervia</i> Desf.		3	0.023	760-890		3			1	2	0	3	1	2	0
<i>Ficus sintenisii</i> Warb.		3	0.023	460-750	1	2			2	1	0	3	2	1	0
<i>Guarea glabra</i> Vahl		13	0.099	450-780	1	12			0	3	5	8	0	6	7
<i>Guarea guidonia</i> (L.) Sleumer		13	0.099	350-730	12		1		3	3	4	10	3	3	7
<i>Guatteria caribaea</i> Urban		8	0.061	350-470	8				2	2	0	4	6	2	0
<i>Guettarda valenzuelana</i> A. Rich.		32	0.243	380-750	4	28			4	4	3	11	7	8	17
<i>Haenianthus salicifolius</i> Griseb.		231	1.755	350-1000	3	172	8	48	20	20	12	52	110	88	33
<i>Hedyosmum arborescens</i> Sw.		25	0.189	550-1050	1	17		7	7	2	4	13	11	4	10
<i>Henriettea macfadyenii</i> (Triana) Alain		2	0.015	820			2		0	0	1	1	0	0	2
<i>Henriettea squamulosa</i> (Cogn.) Judd.	PR	1401	10.642	350-1000	34	925	85	357	32	35	32	99	476	594	331
<i>Hirtella rugosa</i> Pers.	PR	134	1.018	360-860	10	124			11	9	2	22	89	43	2
<i>Hirtella triandra</i> Sw.		6	0.045	350	6				1	0	0	1	6	0	0
<i>Homalium racemosum</i> Jacq.		14	0.106	350-700	3	11			3	2	2	7	6	6	2
<i>Ilex nitida</i> (Vahl) Maxim.		16	0.122	650-920		13		3	5	6	0	11	9	7	0
<i>Ilex sideroxyloides</i> (Sw.) Griseb.		3	0.023	470-835	2		1		1	2	0	3	1	2	0
<i>Ilex sintenisii</i> (Urban) Britton	LEF	4	0.031	1050				4	1	0	0	1	4	0	0
<i>Inga laurina</i> (Sw.) Willd.		37	0.281	350-680	9	28			2	2	3	7	28	6	3
<i>Inga vera</i> Willd. Ex L.		14	0.106	370-780	4	10			2	2	3	7	2	2	10
<i>Ixora ferrea</i> (Jacq.) Benth.		26	0.197	350-780	8	18			7	3	0	10	18	8	0
<i>Laetia procera</i> (Poeppig) Eichl.		1	0.008	370	1				1	0	0	1	1	0	0
<i>Laplacea portoricensis</i> (Krug & Urban) Dyer	LEF	2	0.015	350	2				1	0	0	1	2	0	0
<i>Magnolia splendens</i> Urban	LEF	88	0.668	350-990	7	59		22	16	14	12	42	40	34	14
<i>Manilkara bidentata</i> (A.DC.) Chev.		82	0.623	350-650	79	3			5	4	3	12	32	38	12
<i>Margaritaria nobilis</i> L. f.		1	0.008	350	1				1	0	0	1	1	0	0
<i>Marliera sintenisii</i> Kiaersk.	LEF	25	0.189	640-990		25			5	5	0	10	13	12	0
<i>Matayba domingensis</i> (DC.) Radlk.		122	0.927	370-875	17	105			12	10	3	25	68	48	6
<i>Mecranium latifolium</i> (Cogn.) Skean		6	0.046	630-960		5		1	1	1	4	6	1	1	4
<i>Meliosma herbertii</i> Rolfe		30	0.228	350-800	13	17			4	3	0	7	21	9	0
<i>Menendezia urbanii</i> Cogn.		25	0.191	350-750	15	10			3	3	1	7	15	7	3
<i>Miconia laevigata</i> (L.) DC.		42	0.319	640-920		40		2	4	8	2	14	10	30	2
<i>Miconia pachyphylla</i> Cogn.	PR	12	0.091	680-1000		4		8	3	2	1	6	5	5	2
<i>Miconia prasina</i> (Sw.) DC.		1	0.007	680		1			0	1	0	1	0	1	0
<i>Miconia sintenisii</i> Cogn.	PR	9	0.068	720-950		1	3	5	1	1	4	6	1	1	7
<i>Miconia tetrandra</i> D. Don		147	1.116	450-915	8	138		1	13	9	10	32	74	32	41
<i>Micropholis garciniifolia</i> Pierre	LEF	1097	8.333	350-1000	83	642	10	362	38	36	15	89	499	539	59

continued

Appendix C— (continued) Gradient sampling tally—occurrence of 105 tree species, mostly natives, by environmental factors within the Luquillo Experimental Forest

Species name	Type ^a	Stems		Elevation ^b	Occurrence of species											
					Forest type ^c				Topography ^d							
					LM	MO	PA	DW	R	S	V	Total	R	S	V	
		total	%	m	--- stems (no.) ---				--- plots (no.) ---				--- stems (no.) ---			
<i>Micropholis guyanensis</i> (A. DC.) Pierre		369	2.803	370-900	19	349		1	14	11	8	33	206	130	33	
<i>Myrcia deflexa</i> (Poir.) DC.		13	0.099	450-880	1	11		1	2	1	2	5	4	1	8	
<i>Myrcia fallax</i> (A. Rich) DC.		104	0.791	470-970	3	97	1	3	22	10	2	34	80	21	3	
<i>Myrcia leptoclada</i> DC.		20	0.152	380-560	20				1	3	1	5	7	12	1	
<i>Myrcia splendens</i> (Sw.) DC.		1	0.007	660		1			0	0	1	1	0	0	1	
<i>Myrcine coriacea</i> (Sw.) R. Br. Ex Roem. & Schult.		1	0.007	850		1			0	0	1	1	0	0	1	
<i>Ocotea leucoxylon</i> (Sw.) Mez		75	0.571	350-970	13	46	6	10	20	11	10	41	49	15	11	
<i>Ocotea moschata</i> (Meisn.) Mez	PR	8	0.061	450-790	1	7			1	2	2	5	1	5	2	
<i>Ocotea portoricensis</i> Mez	PR	5	0.038	650-915		3		2	3	0	1	4	4	0	1	
<i>Ocotea spathulata</i> Mez		931	7.072	350-1000	19	338	9	565	35	30	19	84	528	326	77	
<i>Ormosia krugii</i> Urban		27	0.205	380-780	9	18			5	3	0	8	21	6	0	
<i>Palicourea croceoides</i> W. Hamilton		38	0.289	450-940	4	1		33	3	1	2	6	25	11	2	
<i>Prestoea montana</i> (R. Grah.) Nichols		2366	17.972	350-970	285	1296	650	135	26	28	43	97	468	503	1395	
<i>Psychotria berteriana</i> DC.		108	0.82	450-970	21	56	19	12	16	14	15	45	48	22	38	
<i>Pterocarpus officinalis</i> Jacq.		1	0.007	350	1				0	0	1	1	0	0	1	
<i>Rheedia portoricensis</i> (Urban) Alain	PR	60	0.456	350-750	5	55			4	3	1	8	48	10	2	
<i>Rondeletia portoricensis</i> Krug & Urban	PR	10	0.076	450-915	1	9			1	1	3	5	2	1	7	
<i>Sapium laurocerasus</i> Desf.	PR	50	0.381	450-950	5	30	13	2	5	7	13	25	7	10	33	
<i>Schefflera morototoni</i> (Aubl.) Mcguire		42	0.319	350-790	23	14	5		8	6	4	18	26	12	4	
<i>Sloanea berteriana</i> Choisy		90	0.684	350-890	60	28	2		8	8	13	29	30	25	35	
<i>Syzygium jambos</i> (L.) Alston	EXO	5	0.038	730-760		4	1		1	1	0	2	1	4	0	
<i>Tabebuia heterophylla</i> (DC.) Britton		14	0.106	350-740	7	7			2	1	5	8	5	1	8	
<i>Tabebuia rigida</i> Urban	LEF	1303	9.897	450-1000	32	391	36	844	30	26	13	69	606	578	119	
<i>Ternstroemia luquillensis</i> Krug & Urban	LEF	2	0.015	1050				2	1	0	0	1	2	0	0	
<i>Tetragastris balsamifera</i> (Sw.) Kuntze		53	0.402	360-780	52	1			4	3	2	9	33	17	3	
<i>Torrabasia cuneifolia</i> (C. Wright) Krug & Urban		29	0.221	620-1000		15		14	10	3	0	13	25	4	0	
<i>Trichilia pallida</i> Sw.		5	0.038	360-460	5				0	0	2	2	0	0	5	
<i>Vitex divaricata</i> Sw.		2	0.015	615-960		2			0	1	1	2	0	1	1	
<i>Xylosma schwaneckeanum</i> Krug & Urban	LEF	8	0.061	710-970		5		3	3	1	1	5	6	1	1	
Total (105 species)		13165	100	350-1000	1390	7023	1135	3617	44	44	44	132	5075	4623	3467	

^aType: PR = endemic to Puerto Rico; LEF = endemic to Luquillo Experimental Forest; EXO = exotic; blank = non-endemic native species.

^bElevational range for species tallied in the gradient sampling.

^cSampling by forest type varied. Total number of plots = 132 in LEF (5.77 ha), including 18 in LM (0.90 ha), 69 in MO (3.45 ha), 12 in PA (0.60 ha), and 33 in DW (0.82 ha).

^dOccurrence by topography—R = ridge (44 plots), S = slope (44 plots), and V = ravine (44 plots). Stem numbers are absolute values (i.e., not converted to a hectare basis).

continued

APPENDIX D

Appendix D—Tentative successional classification of some tree species within the Luquillo Experimental Forest and notes on where they regenerate^a

Species ^b	Forest type ^c				Regeneration category ^d			
	LM	MO	PM	DF	Open areas	Gaps	Shade	Landslides
<i>Acnistis arborescens</i> (L.) Schlecht.								3
<i>Alchornea latifolia</i> Sw.	8		P		W	X		1,2,3
<i>Alchorneopsis floribunda</i> (Benth.) Muell. Arg.	4				X	X		2
<i>Antirhea coriacea</i> (Vahl.) Urban								1
<i>Bambusa vulgaris</i> Schrad. ^e								3
<i>Buchenavia tetraphylla</i> (Aublet) R. Howard	16					X		1,2
<i>Byrsonima spicata</i> (Cav.) HBK	17					X		
<i>Byrsonima wadsworthii</i> Little		14				X	X	
<i>Calophyllum calaba</i> L.								2
<i>Calyptanthes krugii</i> Kiaersk.				D	W			1
<i>Casearia arborea</i> (L.C. Rich) Urban								2
<i>Casearia decandra</i> Jacq.	5					X		
<i>Casearia sylvestris</i> Sw.								2
<i>Cecropia schreberiana</i> Miq	1	1	P		HX	XH		1,2,3
<i>Cestrum macrophyllum</i> Vent.								2,3
<i>Chionanthus domingensis</i> Lam.	24					X	X	2,3
<i>Citharexylum caudatum</i> L.								3
<i>Citharexylum fruticosum</i> L.								1
<i>Cleyera albo-punctata</i> (Griseb.) Krug & Urban								1
<i>Clibadium erosum</i> (Sw.) DC.			P		X	X		2,3
<i>Clusia clusioides</i> (Griseb.) D'Arcy		6		D	TWX	XT		
<i>Coccoloba schwartzii</i> Meisner								3
<i>Coffea arabica</i> L. ^{e, f}								2
<i>Cordia borinquensis</i> Urban			P	D				1,2
<i>Cordia sulcata</i> DC.	6					X		3
<i>Croton poecilanthus</i> Urban	11	16	P	D		X	X	1,2
<i>Cyathea arborea</i> (L.) J.E. Smith				D	WX	X		1,3
<i>Cyathea bryophila</i> (R. Tryon) Proctor				D	WX	X		
<i>Cyathea portoricensis</i> Spreng ex Kuhn			P					
<i>Cyrilla racemiflora</i> L.	3	3		D		XT		1,2,3
<i>Dacryodes excelsa</i> Vahl	19						X	2
<i>Daphnopsis philippiana</i> Krug & Urban				D				1
<i>Dittha myricoides</i> Griseb.			P					1
<i>Eugenia borinquensis</i> Britton		20	P	D	W	X	X	1
<i>Eugenia stahlii</i> (Kiaersk.) Krug & Urban	28	19					X	2
<i>Eupatorium portoricense</i> Urban								2
<i>Ficus citrifolia</i> P. Miller								1
<i>Ficus sintenisii</i> Warb.								2
<i>Guarea glabra</i> Vahl								1
<i>Guarea guidonia</i> (L.) Sleumer ^l	25					X	X	2,3
<i>Guettarda valenzuelana</i> A. Rich.								2
<i>Haenianthus salicifolius</i> Griseb.		17		D		XT	XT	1

Appendix D— (continued) Tentative successional classification of some tree species within the Luquillo Experimental Forest and notes on where they regenerate^a

Species ^b	Forest type ^c				Regeneration category ^d			
	LM	MO	PM	DF	Open areas	Gaps	Shade	Landslides
<i>Hedyosmum arborescens</i> Sw.								1
<i>Henriettea squamulosa</i> (Cogn.) Judd.	12	15	P	D	W	X	X	1
<i>Heterotrichum cymosum</i> (Wendl.) Urban								2,3
<i>Hirtella rugosa</i> Pers.						X	X	1,2,4
<i>Homalium racemosum</i> Jacq.	9					X		3
<i>Inga laurina</i> (Sw.) Willd. ^f	22					X	X	2,3
<i>Inga vera</i> Willd. ex L. ^f	13					X		2,3
<i>Lonchocarpus latifolius</i> (Willd.) H.B.K.								3
<i>Magnolia splendens</i> Urban		4		D		XT		1
<i>Manilkara bidentata</i> (A.DC.) Chev.	15					XH	X	4
<i>Margaritaria nobilis</i> L. ^f								2,3
<i>Matayba domingensis</i> (DC.) Radlk.	20	7				X	X	2
<i>Mecranium latifolium</i> (Cogn.) Skee								1,2
<i>Miconia faveolata</i> Cogn.					XHW	XH		3
<i>Miconia impetolaris</i> (Sw.) D. Don.								2
<i>Miconia laevigata</i> (L.) DC.						XT		
<i>Miconia mirabilis</i> (Aubl.) L.O. Williams								2
<i>Miconia pachyphylla</i> Cogn.					W			2
<i>Miconia prasina</i> (Sw.) DC.								2,3
<i>Miconia racemosa</i> (Aubl.) DC.								1,2,3
<i>Miconia serrulata</i> (DC.) Naud.								2,3
<i>Miconia sintenisii</i> Cogn.					W			1,3
<i>Miconia tetrandra</i> D. Don	2				W	X		1,2,3
<i>Micropholis garciniifolia</i> Pierre	21	12	P	D	W		X	1
<i>Micropholis guyanensis</i> (A. DC.) Pierre		10				X	X	1,3
<i>Myrcia citrifolia</i> (Aubl.) Urban								2
<i>Myrcia deflexa</i> (Poir.) DC.							X	2,3,4
<i>Myrcia fallax</i> (A. Rich) DC.		13				X	X	2
<i>Myrcia leptoclada</i> DC.							X	2
<i>Myrcia splendens</i> (Sw.) DC.							X	2,4
<i>Myrcine coriacea</i> (Sw.) R. Br. ex Roem. & Schult.								2
<i>Ocotea leucoxydon</i> (Sw.) Mez				D				1,2,3
<i>Ocotea moschata</i> (Meisn.) Mez	26	11					X	
<i>Ocotea sintenisii</i> (Mez) Alain								2
<i>Ocotea spathulata</i> Mez		18		D	W	X	X	1,2
<i>Ochroma pyradimale</i> (Cav. ex Lamb) Urban ^e								2
<i>Ormosia krugii</i> Urban	23					X	X	
<i>Palicourea croceoides</i> W. Hamilton				D			X	1,4
<i>Palicourea riparia</i> Benth.							X	2,3,4
<i>Pinus caribaea</i> Morelete								3
<i>Piper aduncum</i> L.								1,2,3
<i>Piper amalago</i> L.								2
<i>Prestoea montana</i> (R. Grah.) Nichols	18	9	P	D		X	X	1,2,3
<i>Psidium guajava</i> L. ^e								3
<i>Psychotria berteriana</i> DC.			P	D	WX	X		1,2,3

continued

Appendix D— (continued) Tentative successional classification of some tree species within the Luquillo Experimental Forest and notes on where they regenerate^a

Species ^b	Forest type ^c				Regeneration category ^d			
	LM	MO	PM	DF	Open areas	Gaps	Shade	Landslides
<i>Rheedia portoricensis</i> (Urban) Alain								1,2,3
<i>Roystonea borinquena</i> O.F. Cook								3
<i>Sapium laurocerasus</i> Desf.	7	5	P			X		1,2,3
<i>Samyda dodecandra</i> Jacq.								2
<i>Schefflera morototoni</i> (Aubl.) Mcguire	14	2			X	X		1,2,3
<i>Sloanea berteriana</i> Choisy	27						XH	1,3
<i>Solanum torvum</i> Sw.								2
<i>Swietenia macrophylla</i> G. King ^e						X	X	2,4
<i>Syzygium jambos</i> (L.) Alston ^e							X	2,4
<i>Tabebuia heterophylla</i> (DC.) Britton	10				X	X		1,2,3
<i>Tabebuia rigida</i> Urban		8	P	D	W	XT		1,3
<i>Tetragastris balsamifera</i> (Sw.) Kuntze	29						X	1
<i>Tetrazygia urbanii</i> Cogn.								1,3
<i>Trema lamarckiana</i> (R.&S.) Blume								2
<i>Trema micrantha</i> (L.) Blume								2
<i>Trichilia hirta</i> L.								1
<i>Trichilia pallida</i> Sw.					W			
<i>Urera baccifera</i> (L.) Gaud.-Bapre								2

^aSources: Byer and Weaver (1977); Devoe (1989); Guariguata (1990); Myster and Walker (1997); Shiels (2010); Smith (1970); Wadsworth (2009), see endnotes; Weaver (1990, 1992, 2000, 2002).

^bSpecies included represent: (a) 34 species that were previously ranked on a successional scale in Lower montane rain forest and/or Montane rain forest; (b) species that were tallied in the gradient study; or (c) species that were encountered by authors cited in footnote a. Species taxonomy (Liogier 1985, 1997).

^cForest type: LM = Lower montane; MO = Montane; PM = Palm; DF = Dwarf. Numbers indicate ranking of species from 1 = most secondary to 29 = most primary in LM (Smith 1970), and 1 = most secondary to 20 = most primary in MO (Weaver 1999). Species lacking numbers were not ranked. Gradient study: P = species with ≥10 individuals recorded in Palm brake; D = species with ≥10 individuals recorded in Dwarf forest.

^dRegeneration category is based on Lower montane and Montane rankings and other observations. X = regeneration as indicated (i.e., open, gap, or shade), H = regeneration after hurricanes, T = regeneration after thinnings, W = regeneration on plane wreck site in dwarf forest. Regeneration after landslides according to study: 1 (Guariguata 1990); 2 (Myster and Walker 1997); 3 (landslide on PR route 191 at km 21, this study); 4 (Wadsworth 2009, see endnotes).

^eExotic species.

^fCoffee and tree species used for coffee shade.

APPENDIX E

Appendix E—Tree species planted within the Luquillo Experimental Forest^a

Species	Purpose of planting ^b				Origin ^c	Percent area ^d
	AR	AG	OR	PL		
<i>Acrocarpus franinifolius</i> Arn.	AR				E	
<i>Agathis robusta</i> (C. Moore) F.M. Bailey ^e	AR			PL	ENS	
<i>Albizia lebbbeck</i> (L.) Benth.				PL	EN	1.1
<i>Aleurites moluccana</i> (L.) Willd. ^e	AR				ENS	
<i>Alstonia macrophylla</i> Wall.	AR				E	
<i>Andira inermis</i> (W. Wright) DC.				PL	NA	<0.1
<i>Annona muricata</i> L.		AG			NI	
<i>Annona reticulata</i> L.		AG			NI	
<i>Annona squamosa</i> L.	AR				NI	
<i>Anthocephalis chinensis</i> (Lam.) A. Rich. ex Walp. ^e	AR			PL	ES	
<i>Araucaria angustifolia</i> (Bertol.) O. Kuntze	AR				E	
<i>Araucaria cunninghamii</i> Aiton ex D. Don. ^e	AR				ES	
<i>Artocarpus altilis</i> (Parkinson) Fosberg ^e		AG			ENS	
<i>Bambusa gigantochloa</i> ^f				SS	E	
<i>Bambusa longispiculata</i> Gamble ex Brandis				SS	E	
<i>Bambusa textilis</i> McClure				SS	E	
<i>Bambusa tulda</i> Roxb.				SS	E	
<i>Bambusa tuldoidea</i> Munro.				SS	E	
<i>Bambusa vulgaris</i> Schrad. ^e				PL	ENS	
<i>Brunfelsia americana</i> L.			OR		NA	
<i>Byrsonima spicata</i> (Cav.) HBK				PL	NA	0.5
<i>Callitris glauca</i> R. Br. ex Mirb.	AR				E	
<i>Callitris intratropica</i> R.T. Baker & H.G. Smith	AR				E	
<i>Calophyllum calaba</i> L.			OR	PL	NI	
<i>Carapa guianensis</i> Aubl. ^e	AR			PL	ENS	
<i>Castanospermum australe</i> A. Cunn. & C. Fraser ex Hook	AR				E	
<i>Castilla elastica</i> Cervantes ^g			OR		EN	
<i>Casuarina equisetifolia</i> L.	AR			PL	EN	3.0
<i>Catalpa longissima</i> (Jacq.) Sims			OR	PL	E	
<i>Cecropia schreberiana</i> Miq.	AR			PL	NA	
<i>Cedrela odorata</i> L.				PL	NI	13.0
<i>Ceiba pentandra</i> (L.) Gaertn.				PL	NA	0.1
<i>Chrysophyllum cainito</i> L.		AG			?	
<i>Chukrasia tabularis</i> A. Juss.	AR				E	
<i>Cibistax donnell-smithii</i> Rose	AR			PL	E	
<i>Citrus aurantifolia</i> (L.) Swingle		AG			E	
<i>Citrus aurantium</i> L.		AG			EN	
<i>Citrus limon</i> (L.) Burm. F.		AG			EN	
<i>Citrus sinensis</i> (L.) Osbeck		AG			EN	
<i>Clitoria racemosa</i> G. Don. ^e	AR				ES	
<i>Coccoloba krugii</i> Lindau.				PL	NA	
<i>Cocos nucifera</i> L.		AG	OR		EN	

continued

Appendix E— (continued) Tree species planted within the Luquillo Experimental Forest^a

Species	Purpose of planting ^b				Origin ^c	Percent area ^d
	AR	AG	OR	PL		
<i>Coffea arabica</i> L.		AG			EN	
<i>Cordia alliodora</i> Ruiz & Pav.	AR			PL	NA	8.5
<i>Cryptomeria japonica</i> (L. f.) D. Don.	AR				E	
<i>Cunninghamia lanceolata</i> (Lamb.) Hook. ^e	AR				ES	
<i>Cupressus lusitanica</i> Mill. Cv. <i>Bentharii</i> ^e	AR			PL	ENS	
<i>Dacryodes excelsa</i> Vahl				PL	NA	
<i>Dalbergia sissoo</i> Roxb.				PL	EN	1.5
<i>Delonix regia</i> (Bojer) Raf. ^e			OR		ENS	
<i>Dendrocalamus strictus</i> Nees				SS	E	
<i>Entandophragma angolensis</i> C. DC.	AR				E	
<i>Eucalyptus maculata</i> Hook	AR				E	
<i>Eucalyptus alba</i> Reinw. ex Blum ^e				PL	E	
<i>Eucalyptus botryoides</i> Sm.				PL	E	
<i>Eucalyptus camaldulensis</i> Dehnh.				PL	E	
<i>Eucalyptus citriodora</i> Hook	AR			PL	E	<0.1
<i>Eucalyptus crebra</i> F. Muell.	AR				E	
<i>Eucalyptus grandis</i> Hill ex Maiden ^e	AR				ES	
<i>Eucalyptus kirtoniana</i> F. Muell				PL	E	
<i>Eucalyptus maidenii</i> F. Muell.	AR				E	
<i>Eucalyptus mysore-bangalore</i> (hybrid) ^f	AR				E	
<i>Eucalyptus paniculata</i> Sm.	AR				E	
<i>Eucalyptus patentinervis</i> R.T. Bak. ^e	AR				ES	
<i>Eucalyptus resinifera</i> J.E. Smith				PL	E	
<i>Eucalyptus robusta</i> J.E. Smith ^e	AR			PL	ENS	0.4
<i>Eucalyptus rostrata</i> Schl. ^e				PL	ES	
<i>Eucalyptus saligna</i> Sm. ^e	AR			PL	ES	
<i>Eucalyptus</i> spp.				PL	E	0.1
<i>Eucalyptus tereticornis</i> Sm.				PL	E	
<i>Eugenia jambolana</i> Lam.				PL	E	
<i>Eugenia stahlia</i> (Kiaersk.) Krug & Urban				PL	N	
<i>Fraxinus uhdei</i> (Wenzig) Lingelsh. ^e	AR			PL	ENS	
<i>Gliricidia sepium</i> (Jacq.) Kunth ex Griseb.		AG			EN	
<i>Gmelina arborea</i> Roxb. ^e					ES	
<i>Goetzia elegans</i> Wydler	AR				N	
<i>Guarea guidonia</i> (L.) Sleumer				PL	N	1.6
<i>Gyranthera caribensis</i> Pittier	AR				E	
<i>Hernandia sonora</i> L.	AR				NA	
<i>Hibiscus elatus</i> Sw. ^e	AR		OR	PL	ENS	
<i>Hibiscus rosa-sinensis</i> L.			OR		E	
<i>Hibiscus tiliaceus</i> L. ^e			OR		ES	
<i>Hymenaea courbaril</i> L.				PL	NA	0.1
<i>Inga vera</i> Willd.	AR				NA	
<i>Jatropha multifida</i> L.			OR		NA	
<i>Khaya grandifoliola</i> C. DC. ^e	AR				ES	
<i>Khaya nyasica</i> Stapf. ex Baker ^e	AR			PL	ENS	
<i>Khaya senegalensis</i> (Desr.) A. Juss. ^e	AR				ENS	

continued

Appendix E— (continued) Tree species planted within the Luquillo Experimental Forest^a

Species	Purpose of planting ^b				Origin ^c	Percent area ^d
	AR	AG	OR	PL		
<i>Lagerstroemia speciosa</i> (L.) Pers.			OR		E	
<i>Maesopsis eminii</i> Engler ^e	AR				ENS	
<i>Mammea americana</i> L.		AG			NA	
<i>Mangifera indica</i> L. ^e		AG			ENS	
<i>Manilkara bidentata</i> (A. DC.) Chev.				PL	NA	0.5
<i>Matayba domingensis</i> (DC.) Radlk.				PL	NA	
<i>Montezuma speciosissima</i> Sesse & Moc.			OR	PL	NI	5.1
<i>Myroxylon balsamum</i> (L.) Harms	AR				EN	
<i>Ochroma pyramidale</i> (Cav.) Urban				PL	E	
<i>Ocotea moschata</i> (Meisn.) Mez	AR				NA	
<i>Olea</i> sp.	AR				E	
<i>Parkia timoriana</i> (DC.) Merr.	AR				EN	
<i>Peltophorum inerme</i> (Roxb.) Naves				PL	E	
<i>Persea americana</i> Mill.		AG			EN	
<i>Petitia dominguensis</i> Jacq.				PL	NA	4.7
<i>Pinus ayacahuite</i> Ehrenb. ex Schldl.	AR				E	
<i>Pinus caribaea</i> Morelet ^{e, h}	AR			PL	ENS	
<i>Pinus chiapensis</i> (Martínez) Andresen ^e	AR				ES	
<i>Pinus devoniana</i> Lund ⁱ	AR				E	
<i>Pinus douglasiana</i> Martínez	AR				E	
<i>Pinus echinata</i> Mill.	AR				E	
<i>Pinus ellioti</i> var. <i>densa</i> Engelm. ^e	AR				ES	
<i>Pinus kesiya</i> Royle ex Gordon ⁱ	AR				E	
<i>Pinus massoniana</i> Lamb.	AR				E	
<i>Pinus montezumae</i> Lamb.	AR				E	
<i>Pinus occidentalis</i> Sw.	AR				E	
<i>Pinus oocarpa</i> Schiede ex Schldl. ^e	AR				ES	
<i>Pinus patula</i> Schiede ex Schldl. & Cham.	AR				E	
<i>Pinus pseudostrobus</i> Lindl.	AR				E	
<i>Pinus taeda</i> L.	AR				E	
<i>Plumeria rubra</i> L.			OR		E	
<i>Pouteria multiflora</i> (A. DC.) Eyma				PL	NA	
<i>Psidium guajava</i> L.		AG			E	
<i>Pterocarpus indicus</i> Willd.	AR			PL	EN	
<i>Pterocarpus macrocarpus</i> Kurz	AR				EN	
<i>Sabinea florida</i> (Vahl.) DC.			OR		NI	
<i>Sambucus simpsonii</i> (Rehd.)			OR		E	
<i>Schizolobium parahybum</i> (Vell.) Blake	AR				EN	
<i>Senna siamea</i> (Lam.) Irwin			OR	PL	EN	1.1
<i>Sequoia sempervirens</i> (D. Don.) Endl.	AR				E	
<i>Sideroxylon foetidissimum</i> Jacq.				PL	NI	
<i>Simarouba amara</i> Aubl.	AR				EN	
<i>Sloanea berteriana</i> Choisey				PL	NA	
<i>Spathodea campanulata</i> Beauv. ^e			OR		ENS	
<i>Swietenia macrophylla</i> King ^e	AR			PL	ENS	27.3
<i>Swietenia mahagoni</i> Jacq.	AR			PL	EN	23.8

continued

Appendix E— (continued) Tree species planted within the Luquillo Experimental Forest^a

Species	Purpose of planting ^b				Origin ^c	Percent area ^d
	AR	AG	OR	PL		
<i>Swietenia hybrid</i> (macrophylla x mahagoni) ^e				PL	ENS	
<i>Syzygium jambos</i> (L.) Alston ^e		AG		PL	ENS	<0.1
<i>Tabebuia heterophylla</i> (DC.) Britton	AR			PL	NA	5.7
<i>Taxodium mucronatum</i> Tenore	AR				E	
<i>Tectona grandis</i> L.				PL	EN	1.6
<i>Terminalia catappa</i> L.	AR		OR		EN	
<i>Terminalia ivorensis</i> A. Chev. ^e	AR				ENS	
<i>Theobroma cacao</i> L.		AG			EN	
<i>Toona ciliata</i> Roem. ^e	AR			PL	ES	
<i>Toona sureni</i> (Blume) Merr.	AR				E	
<i>Vitex divaricata</i> Sw.				PL	NA	0.2
<i>Widdringtonia whytei</i> Rendle	AR				E	
Total	75	17	18	61	144	100.0

^aSources: Francis (1987, 1989); Francis and Liogier (1991); Little (1976); Marrero (1947, 1948, 1950). Some species listed as planted also grow naturally in the mountains.

^bAR = arboretum; AG = agriculture; OR = ornamental; PL = forest plantations; SS = soil stabilization along roadsides.

^cOrigin: E = exotic; EN = naturalized exotic; ES or ENS = exotic adapted for planting in the LEF; NA = native to Puerto Rico, NI = native but introduced to the Luquillo Mountains; ? = uncertain.

^dTotal area in forest before 1950 plantations is about 1600 ha, estimated from seedlings planted. Precise areas of other species not known (i.e., agricultural, ornamental, or roadside stabilization). Most arboretum species were planted in small blocks of 50 trees.

^eAdapted to conditions in the LEF (Francis 1987).

^fNomenclature and authorities from 70 year-old records are uncertain (e.g., *Bambusa* and *Gigantochloa* are currently both genus names).

^gObserved in Mameyes valley near Bisley during the 1990s.

^h*Pinus caribaea* has three varieties planted in the LEF: *bahamensis*, *caribaea*, and *hondurensis*.

ⁱFormerly *Pinus insularis* and *P. michoacana*, respectively.

APPENDIX F

Appendix F—Available wood specific gravities for 87 tree species native to the Luquillo Experimental Forest^a

Tree species Density by decimal group	Specific gravity	Tree species Alphabetical	Specific gravity
	<i>g cm⁻³</i>		<i>g cm⁻³</i>
<i>Ochroma pyramiale</i>	0.22	<i>Alchornea latifolia</i>	0.39
<i>Prestoea montana</i>	0.26	<i>Andira inermis</i>	0.63
<i>Cecropia schreberiana</i>	0.29	<i>Antirhea obtusifolia</i>	0.73
<i>Pterocarpus officinalis</i>	0.32	<i>Ardisia luquillensis</i>	0.70
<i>Hedyosmum arborescens</i>	0.33	<i>Beilschmiedia pendula</i>	0.54
<i>Simarouba amara</i>	0.34	<i>Buchenavia tetraphylla</i>	0.61
<i>Schefflera morototoni</i>	0.36	<i>Byrsonima spicata</i>	0.64
<i>Sapium laurocerasus</i>	0.38	<i>Byrsonima wadsworthii</i>	0.54
<i>Alchornea latifolia</i>	0.39	<i>Calyptanthes krugii</i>	0.78
<i>Daphnopsis philippiana</i>	0.40	<i>Cassipourea guianensis</i>	0.70
<i>Ficus citrifolia</i>	0.40	<i>Cecropia schreberiana</i>	0.29
<i>Meliosma herbertii</i>	0.42	<i>Chionanthes domingensis</i>	0.81
<i>Ocotea leucoxylon</i>	0.45	<i>Citharexylum caudatum</i>	0.57
<i>Ormosia krugii</i>	0.50	<i>Clusia clusioides</i>	0.90
<i>Nectandra coriacea</i>	0.51	<i>Clusia rosea</i>	0.67
<i>Palicourea riparia</i>	0.51	<i>Cordia borinquensis</i>	0.70
<i>Psychotria berteriana</i>	0.51	<i>Cordia sulcata</i>	0.60
<i>Guarea guidonia</i>	0.52	<i>Croton poecilanthus</i>	0.60
<i>Cyrilla racemiflora</i>	0.53	<i>Cyathea arborea</i>	0.70
<i>Dacryodes excelsa</i>	0.53	<i>Cyrilla racemiflora</i>	0.53
<i>Beilschmiedia pendula</i>	0.54	<i>Dacryodes excelsa</i>	0.53
<i>Byrsonima wadsworthii</i>	0.54	<i>Daphnopsis philippiana</i>	0.40
<i>Guarea glabra</i>	0.54	<i>Ditta myricoides</i>	0.57
<i>Mecranium amygdalinum</i>	0.55	<i>Drypetes glauca</i>	0.67
<i>Miconia pachyphylla</i>	0.55	<i>Eugenia borinquensis</i>	0.70
<i>Tetrazygia urbanii</i>	0.55	<i>Eugenia eggersii</i>	0.75
<i>Miconia laevigata</i>	0.56	<i>Eugenia stahlii</i>	0.73
<i>Citharexylum caudatum</i>	0.57	<i>Ficus citrifolia</i>	0.40
<i>Ditta myricoides</i>	0.57	<i>Garcinia portoricensis</i>	0.90
<i>Tabebuia rigida</i>	0.57	<i>Grammadenia sintenisii</i>	0.70
<i>Tabebuia heterophylla</i>	0.58	<i>Guarea glabra</i>	0.54
<i>Tabebuia heterophylla</i>	0.58	<i>Guarea guidonia</i>	0.52
<i>Torrabasia cuneifolia</i>	0.58	<i>Guatteria caribaea</i>	0.80
<i>Inga vera</i>	0.59	<i>Guettarda scabra</i>	0.65
<i>Magnolia splendens</i>	0.59	<i>Haenianthus salicifolius</i>	0.81
<i>Ocotea moschata</i>	0.59	<i>Hedyosmum arborescens</i>	0.33
<i>Cordia sulcata</i>	0.60	<i>Henriettea squamulosa</i>	0.74
<i>Croton poecilanthus</i>	0.60	<i>Hirtella rugosa</i>	0.90
<i>Laplacea portoricensis</i>	0.60	<i>Homalium racemosum</i>	0.77
<i>Rondeletia portoricensis</i>	0.60	<i>Hymenaea courbaril</i>	0.76
<i>Buchenavia tetraphylla</i>	0.61	<i>Ilex sideroxyloides</i>	0.77
<i>Inga laurina</i>	0.62	<i>Inga laurina</i>	0.62

continued

Appendix F— (continued) Available wood specific gravities for 87 tree species native to the Luquillo Experimental Forest^a

Tree species Density by decimal group	Specific gravity	Tree species Alphabetical	Specific gravity
	<i>g cm⁻³</i>		<i>g cm⁻³</i>
<i>Mammea americana</i>	0.62	<i>Inga vera</i>	0.59
<i>Ocotea spathulata</i>	0.62	<i>Ixora ferrea</i>	0.73
<i>Andira inermis</i>	0.63	<i>Laetia procera</i>	0.68
<i>Tetragastris balsamifera</i>	0.63	<i>Laplacea portoricensis</i>	0.60
<i>Byrsonima spicata</i>	0.64	<i>Magnolia splendens</i>	0.59
<i>Micropholis garciniifolia</i>	0.64	<i>Mammea americana</i>	0.62
<i>Guettarda scabra</i>	0.65	<i>Manilkara bidentata</i>	0.82
<i>Ternstroemia luquillensis</i>	0.65	<i>Margaritaria nobilis</i>	0.90
<i>Clusia rosea</i>	0.67	<i>Marliera sintenisii</i>	0.75
<i>Drypetes glauca</i>	0.67	<i>Matayba domingensis</i>	0.70
<i>Laetia procera</i>	0.68	<i>Mecranium amygdalinum</i>	0.55
<i>Micropholis guyanensis</i>	0.68	<i>Meliosma herbertii</i>	0.42
<i>Ardisia luquillensis</i>	0.70	<i>Miconia laevigata</i>	0.56
<i>Cassipourea guianensis</i>	0.70	<i>Miconia pachyphylla</i>	0.55
<i>Cordia borinquensis</i>	0.70	<i>Miconia prasina</i>	0.70
<i>Cyathea arborea</i>	0.70	<i>Miconia sintenisii</i>	0.70
<i>Eugenia borinquensis</i>	0.70	<i>Miconia tetrandra</i>	0.70
<i>Grammadenia sintenisii</i>	0.70	<i>Micropholis garciniifolia</i>	0.64
<i>Matayba domingensis</i>	0.70	<i>Micropholis guyanensis</i>	0.68
<i>Miconia prasina</i>	0.70	<i>Myrcia deflexa</i>	0.80
<i>Miconia sintenisii</i>	0.70	<i>Myrcia fallax</i>	0.75
<i>Miconia tetrandra</i>	0.70	<i>Myrcia splendens</i>	0.80
<i>Antirhea obtusifolia</i>	0.73	<i>Nectandra coriacea</i>	0.51
<i>Eugenia stahlii</i>	0.73	<i>Ochroma pyramiale</i>	0.22
<i>Ixora ferrea</i>	0.73	<i>Ocotea leucoxylon</i>	0.45
<i>Henriettea squamulosa</i>	0.74	<i>Ocotea moschata</i>	0.59
<i>Eugenia eggersii</i>	0.75	<i>Ocotea spathulata</i>	0.62
<i>Marliera sintenisii</i>	0.75	<i>Ormosia krugii</i>	0.50
<i>Myrcia fallax</i>	0.75	<i>Palicourea riparia</i>	0.51
<i>Xylosma schwaneckeanum</i>	0.75	<i>Prestoea montana</i>	0.26
<i>Hymenaea courbaril</i>	0.76	<i>Psychotria berteriana</i>	0.51
<i>Homalium racemosum</i>	0.77	<i>Pterocarpus officinalis</i>	0.32
<i>Ilex sideroxyloides</i>	0.77	<i>Rondeletia portoricensis</i>	0.60
<i>Calyptanthus krugii</i>	0.78	<i>Sapium laurocerasus</i>	0.38
<i>Guatteria caribaea</i>	0.80	<i>Schefflera morototoni</i>	0.36
<i>Myrcia deflexa</i>	0.80	<i>Simarouba amara</i>	0.34
<i>Myrcia splendens</i>	0.80	<i>Sloanea berteriana</i>	0.80
<i>Sloanea berteriana</i>	0.80	<i>Tabebuia heterophylla</i>	0.58
<i>Chionanthus domingensis</i>	0.81	<i>Tabebuia heterophylla</i>	0.58
<i>Haenianthus salicifolius</i>	0.81	<i>Tabebuia rigida</i>	0.57
<i>Manilkara bidentata</i>	0.82	<i>Ternstroemia luquillensis</i>	0.65
<i>Clusia clusioides</i>	0.90	<i>Tetragastris balsamifera</i>	0.63
<i>Garcinia portoricensis</i>	0.90	<i>Tetrazygia urbanii</i>	0.55
<i>Hirtella rugosa</i>	0.90	<i>Torralsbasia cuneifolia</i>	0.58
<i>Margaritaria nobilis</i>	0.90	<i>Xylosma schwaneckeanum</i>	0.75

^aSources: Reyes and others (1992); Little and Wadsworth (1964); Little and others (1974).

Peter L. Weaver. 2012. The Luquillo Mountains: Forest Resources and Their History. Gen. Tech. Rep. IITF-44. San Juan, PR: U.S. Department of Agriculture, Forest Service, International Institute of Tropical Forestry. 159 p.

This report presents an overview of the El Yunque National Forest, which is also designated as Luquillo Experimental Forest, in northeastern Puerto Rico. The principal topics include the environmental setting (geology, soils, and climate), environmental gradients, arborescent flora, vertebrate fauna, and forest management (i.e., plantations, silvicultural operations, planning, research, and designated land uses). A chronology from the time of European discovery to the present outlines major events in the Luquillo Experimental Forest, including an early presence of indigenous peoples, exploration for gold, timber extraction, farming, trail and road construction, and recreational developments.

Keywords: Disturbances, forest resources, gradients, history, Luquillo Mountains of Puerto Rico, management, research.



The Forest Service, United States Department of Agriculture (USDA), is dedicated to the principle of multiple use management of the Nation's forest resources for sustained yields of wood, water, forage, wildlife, and recreation. Through forestry research, cooperation with the States and private forest owners, and management of the National Forests and National Grasslands, it strives—as directed by Congress—to provide increasingly greater service to a growing Nation.

The USDA prohibits discrimination in all its programs and activities on the basis of race, color, national origin, age, disability, and where applicable, sex, marital status, familial status, parental status, religion, sexual orientation, genetic information, political beliefs, reprisal, or because all or part of an individual's income is derived from any public assistance program. (Not all prohibited bases apply to all programs.) Persons with disabilities who require alternative means for communication of program information (Braille, large print, audiotape, etc.) should contact USDA's TARGET Center at (202) 720-2600 (voice and TDD).

To file a complaint of discrimination, write to USDA, Director, Office of Civil Rights, 1400 Independence Avenue, SW, Washington, D.C. 20250-9410, or call (800) 795-3272 (voice) or (202) 720-6382 (TDD). USDA is an equal opportunity provider and employer.