

11. Vegetation

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The first forest supervisor and chief forester of the then Luquillo National Forest and eventual Luquillo Experimental Forest (LEF) recognized four forest types in the national forest. These forest types were based on the “nature, circumstance, and elevation of the vegetation” for “convenience in description and to aid in preparation of management plans” (Bruner 1919). The four forest types are riparian, slope, sierra palm, and elfin forests. Bruner’s classification formed the basis for the forest “sites” or “areas of distinct productivity,” as later renamed by Wadsworth (1951), and this nomenclature is presently in common usage: tabonuco, palo colorado, palm, and elfin (also termed dwarf, cloud, or mossy forest) forest types. We don’t recommend the use of dwarf or cloud forest to identify elfin forests because these elfin or mossy forests (*sensu* Howard 1968) are not dwarfed *sensu stricto* nor are they uniquely cloud forests. All forests above the cloud condensation level at the LEF are cloud forests, including the elfin forests. Elfin forests have the highest concentration of epiphytic mosses and other plants along the elevation gradient of the LEF, thus the name mossy forest. The height of elfin forests ranges from 1 to 5 meters (m) depending on their aspect or local hydrologic conditions.

Brown et al. (1983) described Wadsworth’s four forest types according to their spatial distribution, species composition, and structural attributes. Since the publication of Brown et al. (1983), a key realization of many researchers has been that the vegetation of the LEF is distributed along both longitudinal (elevation) and lateral (topographical) gradients. Although the four-forest-types model has served well to describe general patterns at a coarse scale, the tradeoff is the simplification of vegetation patterns observed at finer scales. Advances in the way researchers analyze and understand data on vegetation distribution and patterns signal a need to develop a new paradigm of vegetation associations in the LEF. Therefore, the gradient concept has replaced the four-forest-types model and presents a more thorough view of vegetation associations within the LEF. The section below organizes vegetation types by elevation range and by the topographic gradients that occur within the elevation ranges. Finally, the section reviews some species of concern within the LEF. This section does not address plantation forests or the effects on vegetation of past land use or hurricanes or other disturbances because these topics are covered elsewhere in the text.

Factors Influencing Species Distribution Patterns

A panoramic view of the forested LEF landscape reveals a continuous canopy (fig. 62), but, upon closer examination, the codominance of various tree species at different elevations begins to emerge. Although specks of silvery white (*Cecropia schreberiana*) and dark yellow (*Schefflera morototoni*) can be seen on days with strong winds, most apparent are the conspicuous patches of light-green fronds that comprise the palm forest,



Figure 62.—Landscape view from the west of the Luquillo Experimental Forest. Note *Cyathea arborea* and *Cecropia schreberiana* in the foreground. Photo by T. Heartsill Scalley.

breaking up an otherwise darker green canopy. In fact, the most widespread and abundant canopy-forming species—the sierra palm, *Prestoea montana*—occurs from the lowest elevations of the LEF to elevations of more than 1,000 m above sea level.

What factors control the distribution of plant species in the LEF? Vegetation patterns along environmental gradients historically have been described using individualistic-continuum models in which the vegetation present at any particular site is the result of the co-occurrence of species with similar habitat requirements (Gleason 1926, Austin and Smith 1989, Collins et al. 1993, Hoagland and Collins 1997). Most studies of tropical montane vegetation along elevation gradients, however, tend to describe vegetation as discrete (*sensu* Clements 1936) community types (Gleason and Cook 1927, Weaver and Murphy 1990, Waide et al. 1998). A recent community-level study (Barone et al. 2008) focused on species distribution and species turnover variance along the LEF’s elevation gradient. The study’s results indicate a more complex framework of vegetation communities and metacommunities, forest types, associations, and individual species distribution dynamics than the Clementian model or the four-forest type paradigm would suggest. As described previously (Brown et al. 1983, Weaver and Murphy 1990, Waide et al. 1998), a pattern of decreasing species richness with increasing elevation is apparent, but individual tree species also respond to environmental conditions such as rainfall, soil moisture, and geomorphic position (Frangi 1983, Weaver 1991, Lugo et al. 1995, Lugo and Scatena 1995, Scatena and Lugo 1995, Heartsill Scalley 2005, Barone et al. 2008). The Barone et al. (2008) data set clearly shows that species occurrence and distribution conform to the continuum models, but also shows that species groups tend to form discrete community units (fig. 63). Tree species along the Sonadora stream elevation gradient in the LEF have various distribution patterns (fig. 64), with species such as *Prestoea montana* and *Psychotria berteriana* occurring in great abundance at all elevations, while others such

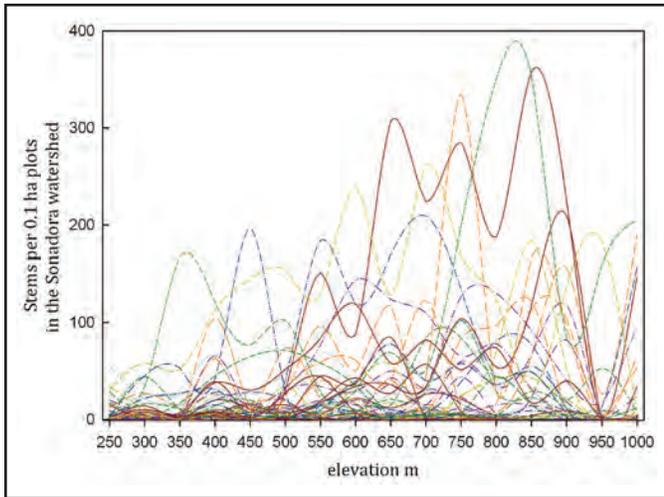


Figure 63.—Total number of stems of all tree species measured in 0.1 hectare plots across an elevation gradient in the Sonadora watershed. Luquillo Long Term Ecological Research data set Iterdb123, compiled by T. Heartsill Scalley.

as *Dacryodes excelsa* and *Manilkara bidentata* occur exclusively at lower elevations. From mid-elevations to higher elevations, *Rhedia portoricensis* and *Magnolia splendens* are more abundant, while *Cyathea bryophylla* and *Lobelia portoricensis* are found only in the highest elevation sites. The intensively sampled elevation transects of Barone et al. (2008) demonstrate that boundaries of vegetation associations are not as clear as boundaries in surrounding palm forests.

Community types are influenced by environmental factors that vary along the elevation gradient (referred to here as “longitudinal” gradients), but riparian to upland gradients (i.e., “lateral” gradients) also influence vegetation characteristics as a result of fine-scale variations in soil moisture and the accumulation of nutrients and organic materials from litterfall and woody debris. Changes in most species associations are subtle and gradual, with each species honing in on specific habitat requirements, such as the documented differences in tree species distributions in ridges, slopes, upland areas, and riparian valleys within sites at various elevations in the LEF (Weaver

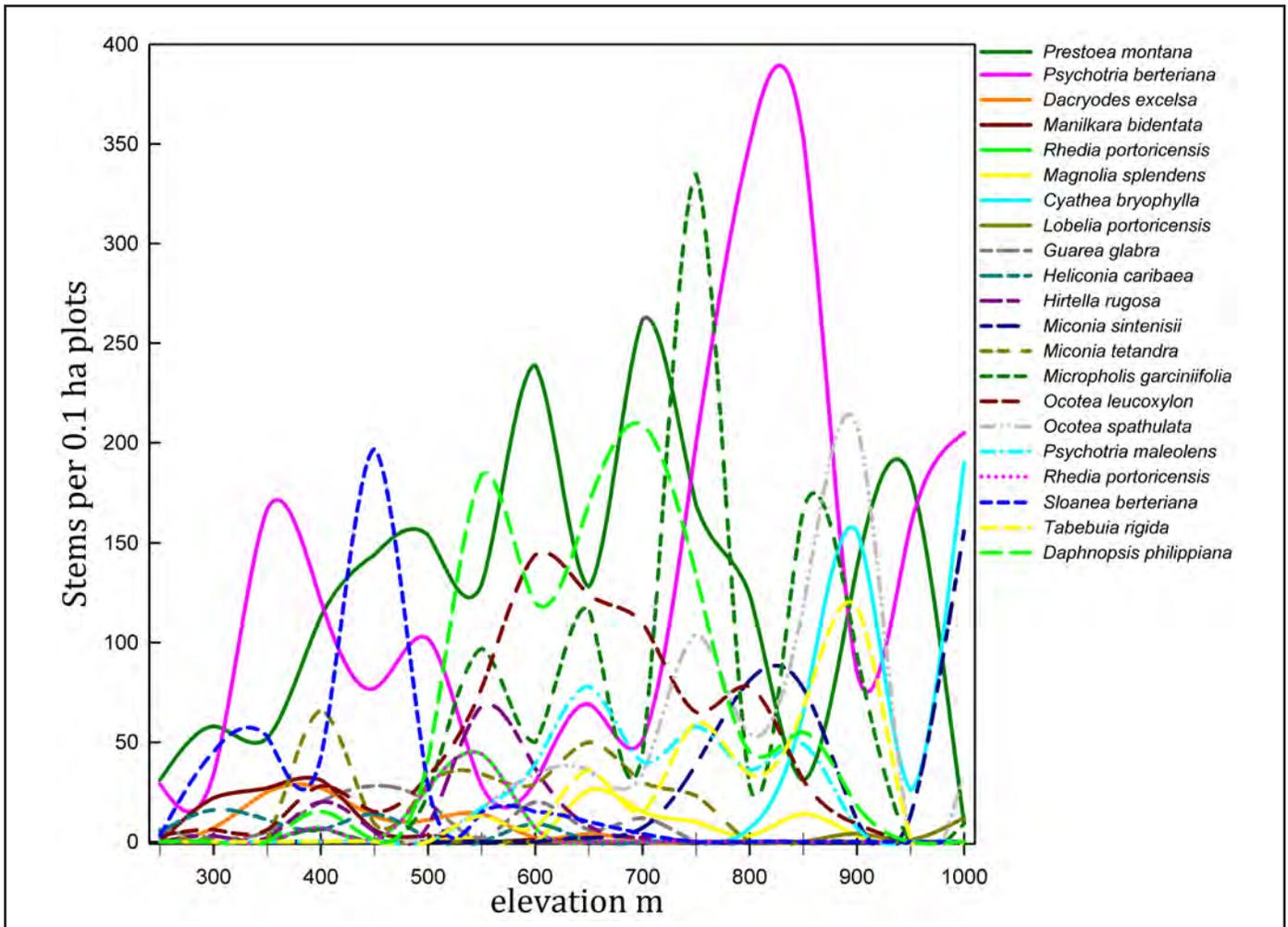


Figure 64.—Total number of stems of dominant tree species measured in 0.1 hectare plots across an elevation gradient in the Sonadora watershed. Luquillo Long Term Ecological Research data set Iterdb123, compiled by T. Heartsill Scalley.

1991; Scatena and Lugo 1995; Lugo and Scatena 1995; Weaver 2000; Heartsill Scalley et al. 2009b).

The vegetation communities in the LEF are also associated with periodic disturbances, including treefalls, landslides, and hurricanes (Scatena and Larsen 1991, Weaver 1991, Scatena and Lugo 1995, Zimmerman et al. 1995, Reagan and Waide 1996, Lugo 2008). An additional factor that influences vegetation community structure is the *massenerhebung*, or mountain mass elevation, effect. The mountainous terrain of the LEF rises steeply and abruptly to above 1,000 m in elevation over a linear distance of 8 kilometer (km) from the coast, resulting in distinctive changes in vegetation structure (fig. 65a) and composition (such as the presence of the cloud forest types) at a relatively low elevation (Grubb 1971, Weaver 1991). The observations of Barone et al. (2008) suggest that the extent of cloud cover is an important factor that influences species distribution along the LEF elevation gradient. Although no experimental evidence is currently available, they proposed that the observed decrease in species richness at mid-elevations of the LEF (fig. 65b) could be related to the lower boundary of the cloud cover base in the LEF, as other studies have connected the frequency of fog with the transitions among different forest types on tropical mountains (Grubb 1971).

Silver et al. (1999) documented a soil O₂ (oxygen) concentration gradient with elevation and along topography at the LEF (see section on nutrient fluxes) and found that tree species density decreased as the average soil O₂ concentration declined along a ridge, slope, valley catena (their table 1). It appears from this study and the observations of Frangi (1983) that all plant communities above the cloud condensation level are wetland communities (fig. 66a). Above this level, soil O₂ concentrations decrease, soil saturation increases, and plant species density and distributions are affected.

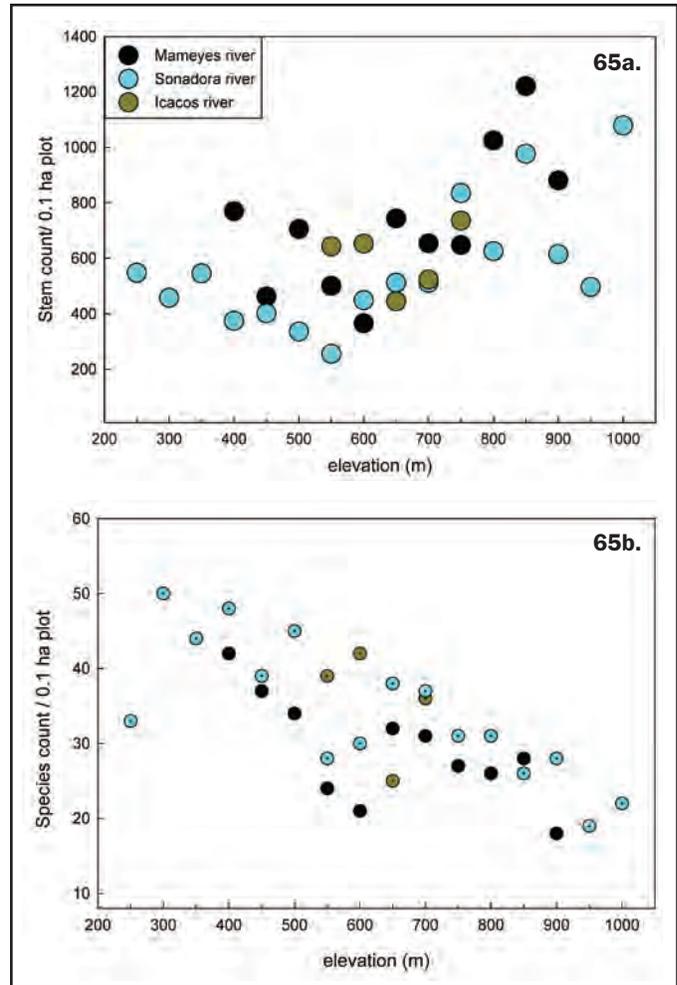


Figure 65.—Stem (a) and species (b) density versus elevation in the Mameyes and Sonadora watersheds of the Luquillo Experimental Forest. From Luquillo Long Term Ecological Research data set Iterdb123, compiled by T. Heartsill Scalley.

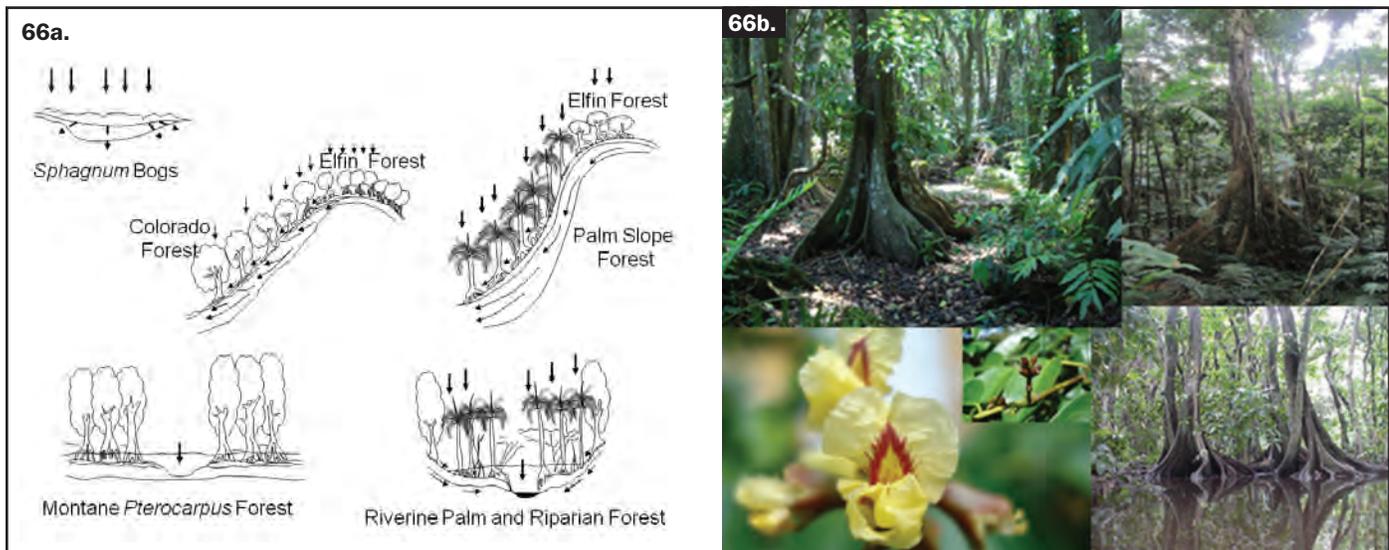


Figure 66.—(a) Conceptual model of wetland ecosystems in the Luquillo Experimental Forest. Arrows indicate movement of water flow. From Frangi (1983). (b) *Pterocarpus* forest, one of the wetland ecosystems of the Luquillo Experimental Forest. Photos by Neftalí Ríos and Samuel Moya.

Low-Elevation Vegetation Below the Cloud Condensation Level

Tall trees with canopy heights extending up to ~30 m along with lianas (i.e., woody vines) dominate low elevations (<600 m) of the LEF and are abundant and important structural elements of these forest communities. Dominant tree species at low elevations—*Dacryodes excelsa* (tabonuco) and *Sloanea berteriana* (motillo)—are distributed primarily as a function of the geomorphology of the underlying terrain (lateral gradients), as these species tend to occupy ridges and ridge tops (Basnet et al. 1993). Other common emergent trees at low elevations in the LEF include *Manilkara bidentata* (ausubo), *Guarea guidonia* (guaraguao), *Buchenavia capitata* (granadillo), and *Ocotea leucoxydon* (laurel geo) (table 21). This tree community, referred to commonly as the tabonuco forest, ranges in elevation from approximately 200 to 600 m above sea level. Younger successional forest stands are observed commonly at the periphery of the LEF, ranging from low to mid elevations, and

include tree species such as *Tabebuia heterophylla*, *C. schreberiana*, *S. morototoni*, and the shrub *Miconia prasina*. Animals disperse the seeds of most of these tree species—*M. prasina* and *S. morototoni* by birds and *C. schreberiana* by bats—while only the *T. heterophylla* seeds are dispersed by wind. Landscape views of the western periphery of the LEF at low elevations are particularly identifiable by *Tabebuia heterophylla* during its flowering periods (fig. 67).

The most abundant lianas in the low-elevation forests are *Marcgravia* spp., *Rourea surinamensis*, *Schlegia brachyata*, and *Paullinia pinnata* (Rice et al. 2004). Two of these lianas, *R. surinamensis* and *S. brachyata*, contribute nearly 5 percent of annual litterfall (Zalamea and González 2008). Epiphytes that rely on other vegetation for structural support—such as bromeliads and ferns—are also present in both upland and riparian areas, but are much more abundant in riparian areas (Sharpe 1997). Ferns also tend to dominate the forest

Table 21. Stem density and biomass of various species of the tabonuco forest in the Bisley watersheds. Data from (Heartsill Scalley et al. 2010). In **bold** low light/primary forest species, underlined high light/secondary forest species, other species are intermediary in their successional status and light requirements. *C. portorricensis* = *Cyathea portorricensis*, *A. floribunda* = *Alchorneopsis floribunda*.

a. Stems ha⁻¹

Pre Hugo	1989	Post Hugo	1989	1994	1999	2004			
<i>Sloanea berteriana</i>	92.87	<i>Sloanea berteriana</i>	76.72	<u><i>Cecropia schreberiana</i></u>	104.4	<u><i>Cecropia schreberiana</i></u>	107.3	<u><i>Cecropia schreberiana</i></u>	103.3
<i>Prestoea montana</i>	71.90	<i>Prestoea montana</i>	55.50	<i>Prestoea montana</i>	61.52	<u><i>Psychotria berteriana</i></u>	95.85	<i>Prestoea montana</i>	100.4
<i>Dacryodes excelsa</i>	61.41	<i>Dacryodes excelsa</i>	45.70	<i>Sloanea berteriana</i>	60.09	<i>Prestoea montana</i>	94.42	<i>Sloanea berteriana</i>	76.39
<u><i>Inga laurina</i></u>	40.44	<u><i>Inga laurina</i></u>	26.11	<i>Dacryodes excelsa</i>	37.2	<i>Sloanea berteriana</i>	84.41	<u><i>Psychotria berteriana</i></u>	76.39
<i>Ocotea leucoxydon</i>	38.94	<u><i>Casearea arborea</i></u>	19.58	<u><i>Inga laurina</i></u>	27.18	<i>Dacryodes excelsa</i>	48.64	<i>Dacryodes excelsa</i>	52.34
<i>C. portorricensis</i>	35.92	<i>C. portorricensis</i>	17.95	<u><i>Casearea arborea</i></u>	24.32	<u><i>Sapium laurocerasus</i></u>	41.49	<i>C. portorricensis</i>	42.44
<i>Guarea glabra</i>	28.46	<i>Guarea guidonia</i>	16.32	<i>Guarea guidonia</i>	18.6	<i>C. portorricensis</i>	37.2	<i>Ocotea leucoxydon</i>	38.2
<i>Guarea guidonia</i>	25.46	<i>Cordia borinquensis</i>	14.69	<u><i>Sapium laurocerasus</i></u>	18.6	<u><i>Inga laurina</i></u>	34.33	<u><i>Sapium laurocerasus</i></u>	35.37
<u><i>Casearea arborea</i></u>	25.46	<i>Ocotea leucoxydon</i>	14.69	<i>C. portorricensis</i>	17.17	<i>Ocotea leucoxydon</i>	34.33	<u><i>Inga laurina</i></u>	32.54
<u><i>Psychotria berteriana</i></u>	25.46	<i>Guarea glabra</i>	13.05	<i>Cordia borinquensis</i>	12.88	<u><i>Casearea arborea</i></u>	32.9	<u><i>Casearea arborea</i></u>	32.54

b. Percent Biomass

Pre Hugo	1989	Post Hugo	1989	1994	1999	2004			
<i>Dacryodes excelsa</i>	39.87	<i>Dacryodes excelsa</i>	43.88	<i>Dacryodes excelsa</i>	39.39	<i>Dacryodes excelsa</i>	34.99	<i>Dacryodes excelsa</i>	33.06
<i>Guarea guidonia</i>	16.38	<i>Guarea guidonia</i>	11.39	<u><i>Cecropia schreberiana</i></u>	14.14	<u><i>Cecropia schreberiana</i></u>	18.68	<u><i>Cecropia schreberiana</i></u>	18.82
<i>Sloanea berteriana</i>	8.85	<i>A. floribunda</i>	8.26	<i>Guarea guidonia</i>	12.53	<i>Guarea guidonia</i>	9.23	<i>Guarea guidonia</i>	13.94
<i>A. floribunda</i>	4.27	<i>Buchenavia capitata</i>	6.96	<i>Guarea guidonia</i>	5.48	<i>Prestoea montana</i>	7.76	<i>Prestoea montana</i>	8.10
<i>Ormosia krugii</i>	3.77	<i>Ormosia krugii</i>	4.21	<i>Prestoea montana</i>	4.72	<i>Sloanea berteriana</i>	5.64	<i>Sloanea berteriana</i>	3.60
<i>Buchenavia capitata</i>	3.48	<u><i>Inga laurina</i></u>	3.86	<u><i>Inga laurina</i></u>	4.58	<u><i>Inga laurina</i></u>	4.04	<i>Alchornea latifolia</i>	2.63
<u><i>Schefflera morototoni</i></u>	2.62	<i>Prestoea montana</i>	2.79	<i>A. floribunda</i>	3.11	<i>Buchenavia capitata</i>	2.64	<i>Buchenavia capitata</i>	2.22
<u><i>Cecropia schreberiana</i></u>	2.49	<i>Sloanea berteriana</i>	2.71	<i>Buchenavia capitata</i>	2.72	<i>A. floribunda</i>	2.13	<i>Manilkara bidentata</i>	1.78
<i>Prestoea montana</i>	2.44	<i>Alchornea latifolia</i>	2.61	<i>Ormosia krugii</i>	2.26	<i>Laetia procera</i>	1.81	<i>Laetia procera</i>	1.70
<u><i>Sapium laurocerasus</i></u>	2.09	<i>Laetia procera</i>	1.93	<i>Alchornea latifolia</i>	2.02	<i>Alchornea latifolia</i>	1.67	<u><i>Inga laurina</i></u>	1.47

understory, however, and have been shown to constitute up to 34 percent of the total vegetation (China 1999). Another epiphyte seen commonly on large trees in open canopy areas of the low-elevation forest is the cactus known as the “tree beard” (*Rhipsalis baccifera*). This species has long, thornless stems that hang from tree trunks and branches, and birds readily consume its fruits (Santiago 2008). It is the only member of the cactus family that grows in the LEF (fig. 68).

Orchids (both epiphytic and terrestrial) are also present in low-elevation forests, with epiphytic orchids present typically above the first branch of larger diameter trees (>16.5 cm DBH [diameter at breast height]) (Migenis and Ackerman 1993). *Guarea guidonia* and *Dacryodes excelsa* are the two tree species that have been observed to host the most epiphytic orchids (such as *Maxillaria coccinea*, *Pleurothallis ruscifolia*, and *Jaquiniella globosa*) within the tabonuco forest type (Migenis and Ackerman 1993). The spatial distribution of terrestrial orchids in the tabonuco forest type has been related to disturbances and past land use (Bergman et al. 2006). This is the case of *Wulfschlaegelia calcarata*, the acolorophyllous, saprophytic (nonphotosynthetic) orchid found in primary, closed canopy forests and absent from areas with past land use history and natural disturbances such as canopy gaps. There were positive associations of *W. calcarata* and *D. excelsa* and a negative association of *W. calcarata* and *C. schreberiana*, a light-demander pioneer (early successional) tree. Another positive relationship was found with *W. calcarata* and leaf litter abundance (but not basal area) of *Buchenavia tetraphylla*, a deciduous tree species with a unimodal (March and April) leaf fall pattern. Previous land use effects on the soils and the fungal leaf litter symbionts of *W. calcarata* may be part of the complex environmental requirements of this orchid’s distribution. Other easily observed orchids are those occurring along riparian zones on streamside boulders and stems, in particular the various species of the endemic genus *Lepanthes* (fig. 69).

In addition to the tabonuco-dominated, low-elevation forests, wetlands in the LEF found below the cloud condensation level include riparian forests (fig. 66a). In the lower elevations of the Mameyes river watershed, the wetland tree *P. officinalis* (Álvarez López 1990) forms stands along riparian areas. This tree, with its characteristic massive buttress roots and floating seeds, has leaves that are readily consumed by stream fauna (Crowl et al. 2006, Welsh et al. unpublished data). Buttress roots up to 8 m in width and 5 m in height have been recorded, and root color varies with age such that younger roots are yellow and change to reddish and dark gray as they age. A *P. officinalis* stand of approximately 3.7 hectares occurs at 500 m above sea level in the LEF; it is described as a montane riverine forest system with organic soil over clay (Álvarez López 1990). Other species within this rare wetland forest type include *Casearia arborea*, *Cordia borinquensis*, *Inga laurina*, *Manilkara bidentata*, the tree fern *Nephelea portoricensis*, and the palm *Prestoea montana*. The



Figure 67.—*Tabebuia heterophylla*, a common tree species that inhabits low elevations of the Luquillo Experimental Forest, during a flowering period. Photo by T. Heartsill Scalley.

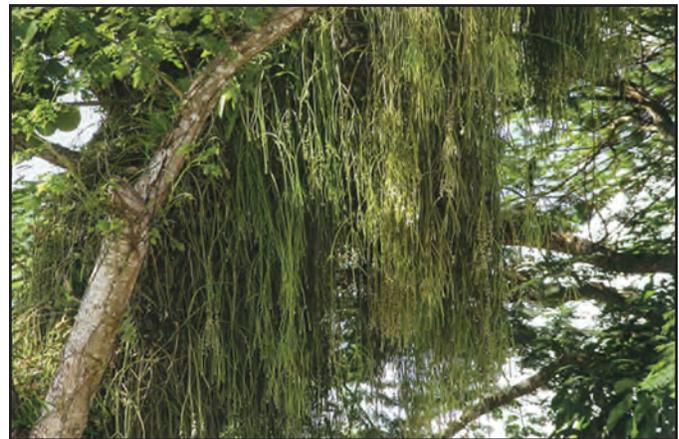


Figure 68.—*Rhipsalis baccifera*, or “tree beard,” a common epiphyte of the tabonuco forest type. Photo by Eugenio Santiago Valentín.



Figure 69.—Orchid of the genus *Lepanthes*, which is seen commonly on streamside boulders and in adjacent riparian areas. Photo by T. Heartsill Scalley.

upper canopy is 25 to 30 m in height, and a second canopy layer is found at 15 m, with abundant epiphytes and woody vines. *Pterocarpus officinalis*, a species with a wide Caribbean distribution (Rivera Ocasio et al. 2006), also occurs in small groups of individuals along streambanks at elevations below the LEF boundary (fig. 66b).

More diverse riparian communities dominate other low-elevation wetland areas. In the Luquillo Forest Dynamics Plot along the Prieta and Toronja streams, Heartsill Scalley et al. (2009b) calculated the minimum distance of individual stems (>10 cm DBH) to the nearest of the two streams. The species with stems in close proximity to streams were *Clusia rosea*, *Coccoloba diversifolia*, *Margaritaria nobilis*, *Ixora ferrea*, *Trichilia pallida*, and *Guettarda valenzuelana*, with a median distance to streams between 21 and 29 m. *Margaritaria nobilis* and *C. diversifolia*, however, were most abundant closer to the streams, with 75 percent of their stems within 30 to 40 m of the stream. Other species had 75 percent of their stems within 40 to 50 m from the stream and included *C. rosea*, *Guatteria caribaea*, *G. valenzuelana*, *Byrsonima wadsworthii*, and *Eugenia stablii* (fig. 70).

Cloud and Wetland Forests Above the Cloud Condensation Level

As rainfall increases toward higher elevations of the LEF as a result of adiabatic cooling, forest structure shifts to an increased presence of epiphytes and to a higher density of shorter and smaller trees and shrubs. The lifting condensation level, which occurs typically around 600 m above sea level, determines where clouds will form and, thus, where the cloud forest community begins. The lower elevation cloud forest (~600 to 800 m) is characterized by the late successional species *Cyrilla racemiflora* (palo colorado) but is dominated on a stem density basis by *Prestoea montana*, *Micropholis garciniifolia*, and *Calycogonium squamulosum*. Bromeliads are common on the forest floor in the palo colorado forest particularly those of the genus *Guzmania*. Weaver (1991, 2000) has described the tree species in this vegetation association in great detail and discussed lateral gradients in relation to aspect (leeward versus windward) observed regarding both composition and structure. Lateral gradients in vegetation structure and community characteristics described for forests below the cloud condensation level are also observed in higher elevation cloud forests, with higher stem density, species richness, and aboveground biomass on ridges versus slopes and riparian valleys.

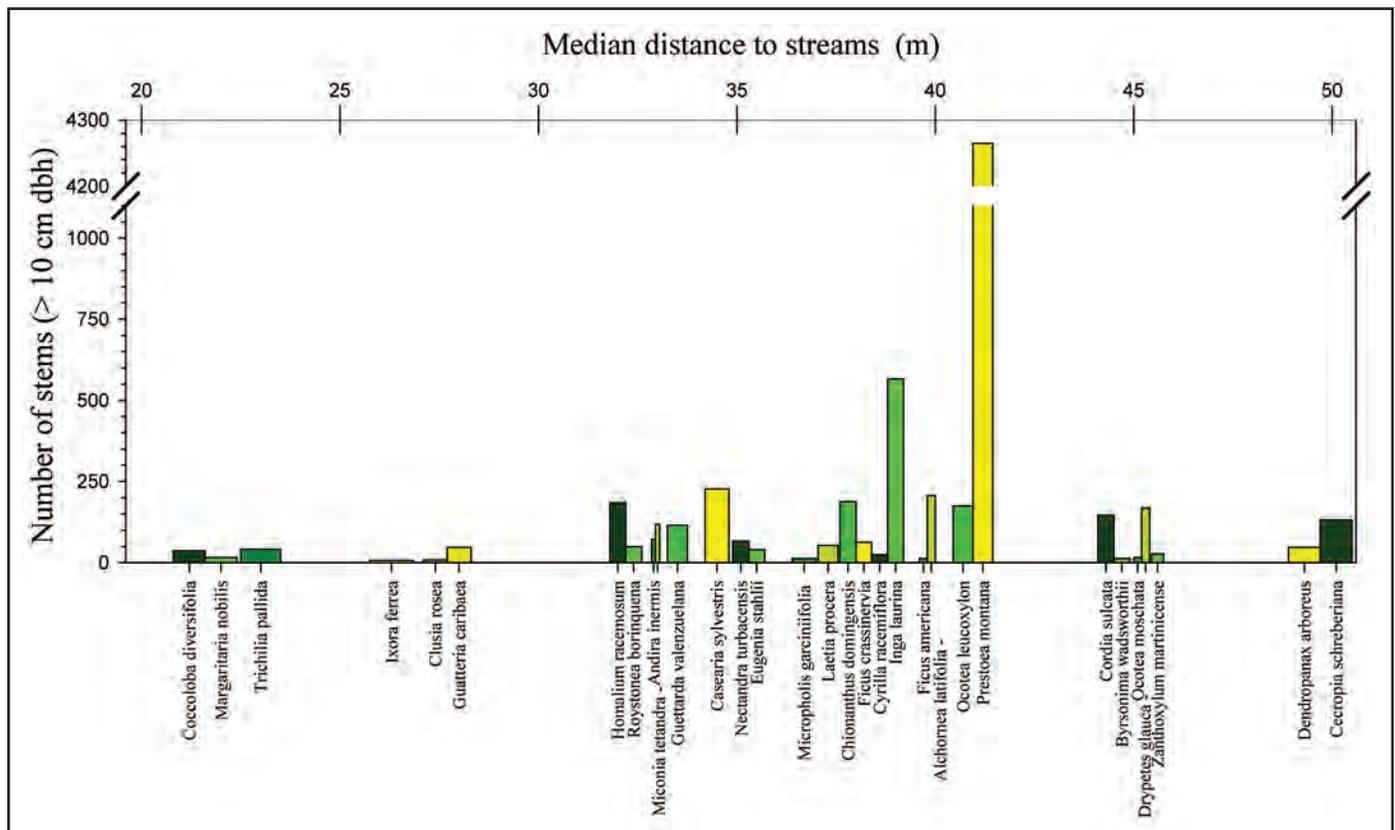


Figure 70.—Tree species distribution in relation to distance from streams. From Heartsill Scalley et al. (2009b).

Large stands of the sierra palm (*Prestoea montana*) begin to occur at approximately 500-m elevation—at the intersection of premontane wet and rain forest life zones—and extend up to the mountain peaks on steep slopes and ravines adjacent to elfin cloud forests (Brown et al. 1983, Weaver and Murphy 1990, Lugo et al. 1995). Palm forests are generally classified as either palm brake (i.e., palm slope) or palm floodplain forest, depending on the specific environmental and geomorphic conditions present. Palm brake forests are found on steep slopes where soils undergo long periods of saturation, while floodplain forests are periodically inundated with water (Brown et al. 1983, Frangi and Lugo 1985, Lugo et al. 1995). Common tree species in the palm brake forest include *Daphnopsis philippiana* and *Calycogonium squamulosum* in addition to the palm *P. montana*, a species that is found in all LEF elevation gradients (Barone et al. 2008).

Lugo et al. (1995) found that the species composition and species density of palm brakes varied with aspect. More species occur on leeward slopes than windward slopes, presumably due to greater rainfall and soil saturation in the windward slopes. Long-term records of species density changes in these palm brakes also showed that after the 1932 hurricane and the initial enrichment of sites due to pioneer species, the number of species decreased over the next 40 years in the windward slopes, while in the leeward slopes species continued to accumulate. Apparently differences in the long-term patterns of soil saturation determined the number of tree species capable of surviving in these contrasting palm brakes. Lugo and Scatena (1995) observed that the length of successional sequences after disturbances were shorter above the cloud condensation level when compared to communities below the cloud condensation level (their fig. 4.8).

The most common trees based on stem density in the palm floodplain forest include *Croton poecilanthus*, *Micropholis crysophylloides*, and *Eugenia eggersii*, but the trees with the highest aboveground biomass are *M. splendens* and *S. berteriana*. In contrast to the adjacent palo colorado and elfin forest types, the most abundant bromeliad in the palm floodplain forest, *Guzmania berteriana*, is found more commonly along canopy tree trunks than on the forest floor, whereas *Selaginella* spp. and other bryophytes cover the ground at various distances from the river floodplain (Frangi and Lugo 1985). In a study relating *P. montana* fecundity to hurricane disturbance, Gregory and Sabat (1996) found that palms with more fronds in exposed areas produced more fruit than palms in less disturbed sites, and that hurricane effects on the canopy opening resulted in increased palm seed production. Therefore, one can conclude that palm forest areas subjected to hurricane effects will grow and reproduce more than those in undisturbed areas. The peak timing time for the palm fruit to fall in the palm floodplain forest occurs between May and June (Lugo and Frangi 1993), and fruit production of *P. montana* individuals in the palm

floodplain forest is an order of magnitude higher than that in the tabonuco forest (Bannister 1970, Lugo and Frangi 1993).

All vegetation above the cloud condensation level is classified as wetlands (Frangi 1983, Scatena 1993, Heartsill Scalley 2005). Many environmental gradients reach their extreme values at the mountain peaks (e.g., highest wind speeds, lowest air temperatures, lowest incoming sunlight, highest rainfall, lowest soil O₂ concentrations, etc.). The vegetation responds in unique ways including unique vegetation structures, unique even between the forests of East Peak and West Peak (Howard 1968). Most notable is the woody vegetation of the elfin forest with an abundance of vascular flowering plants that adopt an epiphytic habit, particularly in the seedling and immature stages. At elevations above ~800 m, the elfin cloud forest is characterized by abundant stems of the tree fern *Cyathea bryophylla*, stunted individuals of the tree species *Ocotea spathulata* and *Tabebuia rigida*, and an abundance of epiphytes, of which the most striking and abundant is the small red bromeliad *Werahuia sintenisii* (fig. 71). This bromeliad is so common that it can be found in densities of up to 32,000 individuals per hectare (Lasso 2001) and contributes 12 percent of the net primary productivity of this forest type. It can also hold up to 3.3 tons of water per hectare and accumulate 25 percent of the phosphorus and K rainfall inputs (Richardson et al. 2000a).



Figure 71.—The most abundant epiphyte of the elfin cloud forest in the Luquillo Experimental Forest, the bromeliad *Werahuia sintenisii*. Photo by Alexis Molinares.

The elfin cloud forest's narrow ranges of temperature, precipitation, and cloud cover make this forest particularly vulnerable to changes in environmental factors, such as those changes proposed to occur as a result of global climate change. In particular, the epiphytic vegetation in the cloud forests may serve as indicators of climate change. For example, Lasso and Ackerman (2003 and 2004) observed an earlier flowering period for the elfin forest bromeliad *W. sintenisii* and showed that monthly mean minimum temperatures and monthly mean irradiance in the months leading up to flowering events explained 66 percent of the variation in the number of open flowers per month. It seems that *W. sintenisii* is responding to changes in the elfin cloud forests' environment by timing its flowering correspond to the cues of the nocturnal minimum temperatures and to the changes in cloud cover as measured indirectly by increases in solar irradiance.

Another distinction of the cloud forests when compared with the lower elevation forest types is the abundance of epiphytes, including liverworts and mosses (Bryophyta). The LEF contains more than one-half of Puerto Rico's moss flora (Sastre De Jesús and Tan 1995). One characteristic bryophyte is *Sphagnum portoricense* (fig. 72), whose presence has been identified as an indicator of the striking differences in ecosystem conditions existing between cloud forests and lower elevation tabonuco forests (Wadsworth 1951, Wadsworth and Bonnet 1951). With a very low tolerance for desiccation, *S. portoricense* is found next to open water in coastal areas, rivers, or wet banks throughout the rest of its geographical range (from the eastern coast of the United States to Venezuela). Throughout most of the LEF, *S. portoricense* is present as forest floor mats and surrounding the base of trees and shrubs where stem flow accumulates. However, it is also abundant next to disturbed roadsides and trails in saturated cloud forest soils. This species occasionally forms small bogs over exposed soil surfaces of uprooted trees or other small soil surface depressions (Karlin 2006). Within the LEF elfin cloud forests, Karlin (2006) describes the distribution of *S. portoricense* as "patchy"; it has been observed more commonly on the easternmost mountain summits (e.g., along the road to and at Pico del Este) while not observed along the trails to El Yunque and El Toro Peaks. The ecology of *S. portoricense* has not been studied extensively, however, and limited information is available regarding the threshold conditions that limit its distribution, growth, reproduction, survival, and roles in succession and competition in the forest types where it occurs. Also, very few notes exist on the distribution of *S. portoricense* before anthropogenic disturbances occurred in the cloud forests of the LEF; one hypothesis is that its present distribution may reflect its ability to colonize after disturbance.

Herbaceous and sphagnum bogs, riparian vegetation, and palm floodplain forests (Frangi 1983, Frangi and Lugo 1985, Lugo

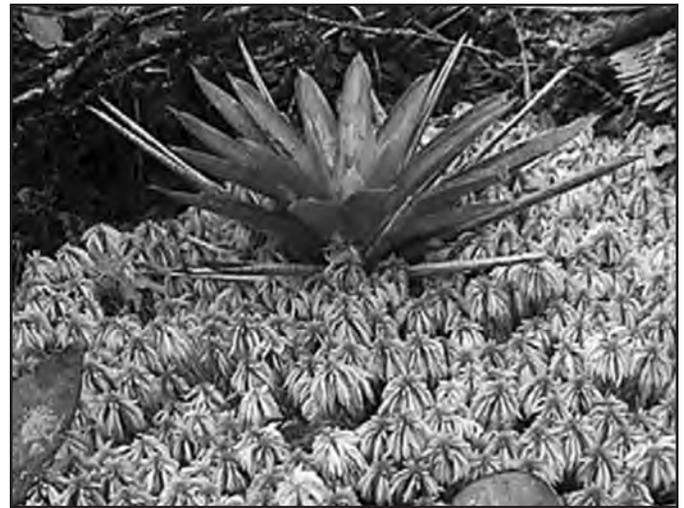


Figure 72.—*Sphagnum portoricense* mat surrounding a terrestrial bromeliad in cloud forest near the summit of Pico del Este, Puerto Rico. Photo by E.F. Karlin, from Karlin (2006).

et al. 1990) also occur above the cloud condensation level. The functioning of floodplain palm forests is discussed below in the nutrient cycling section. In environments with high light levels, one can observe herbaceous bog areas that include clumps of *Carex polystachya*, *Eleocharis* spp., large masses of *Sphagnum*, and other wetland vegetation (Howard 1968, Karlin 2006).

Although the LEF supports most of the moss flora found across the island of Puerto Rico, 19 percent of the moss species found in the LEF are endemic. It is estimated, however, that the cloud forests have lost many more moss species than the lowland and mid-elevation forests; one-half of the moss species originally observed in cloud forests have not been observed again since their initial reporting (Sastre De Jesús and Tan 1995, Sastre De Jesús and Santiago Valentín 1996). One hypothesis for the loss of species, such as *Thamniopsis incurve*, *Bryoerythrophyllum recurvirostre*, *Squamidium isocladum*, *Cyrtohypnum minutulum*, *Schoenobryum concavifolium*, and *Breutelia scoparia*, from the cloud forests is the loss of suitable habitat resulting from disturbances related to the establishment of a communications infrastructure and road construction in the elfin cloud forests (Sastre De Jesús and Tan 1995). Although the opening of canopy structure and a resulting loss of forest cover are considered to be the main factors leading to the decline of most moss species, the role of climate change, changes in air quality, and other factors associated with land use change and pollution may also contribute to the decline. One species, *S. portoricense*, seems to be able to occupy disturbed areas in the elfin cloud forest. The distribution, physiology, and ecology of bryophytes in the LEF remain to be further described and studied particularly in the elfin cloud forest.

Species of Concern

Tree species found in the LEF that are listed as endangered include *Ilex sintenisii* (Sintenis' holly), *Styrax portoricensis* (jazmin tree), *Ternstroemia luquillensis* (colorado), and *Ternstroemia subsessilis* (yunque colorado). All four species are endemic to Puerto Rico and exist only in the Luquillo Mountains (Santiago Valentín and Rivera 1993). In 2009, the U.S. Fish and Wildlife Service initiated a 5-year review of the state of these species to consider programs that propagate and re-introduce some of these species into their native ranges. Another endangered tree species, *Callicarpa ampla* (capá rosa), which previously had distribution in the U.S. Virgin Islands, is now restricted to the Luquillo Mountains. Other rare and threatened species of concern include the tree *Pleodendron macranthum* (chupacallos) and *Lepanthes eltoroensis*, the Luquillo Mountain babies' boots orchid (fig. 73).



Figure 73.—*Lepanthes eltoroensis*, the Luquillo Mountain babies' boots orchid. Photo by Raymond Tremblay.