FOREST STRUCTURE AND COMPOSITION IN THE LOWER MONTANE RAIN FOREST OF THE LUQUILLO MOUNTAINS, PUERTO RICO

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SUMMARY

Six groups of three plots stratified by aspect and topography and varying in elevation were used to sample forest structure and tree species composition within the lower montane rain forest (tabonuco forest) of the Luquillo Experimental Forest (LEF) in Puerto Rico. Stem density, tree height, and total above ground biomass varied by site. Significant differences in canopy height were evident between leeward and windward sites, and declined from ridge to slope to ravine for all sites combined. Total aboveground biomass was significantly greater on ridges than in ravines. Prestoea montana *(R. Grah.) Nichols and* Dacryodes excelsa *Vahl accounted for 31% of the 1394 stems and 69 species that were tallied. Correspondence analysis showed that species' abundances for 37 species with ≥6 occurrences (94 percent of all stems) varied by aspect and topographic features, and that windward plots contained some species associated with wetter sites at higher elevation. Hurricanes impact the LEF with sufficient frequency to maintain its forests in a continuous stage of recovery. Forest composition at any site is a function of environmental gradients, major climatic events, and tree species attributes.*

The Luquillo Experimental Forest (LEF) ranges in elevation from 120 to 1174m and occupies 11300ha of the Luquillo Mountains in northeastern Puerto Rico. The lower montane rain forest (Beard, 1949), hereafter called tabonuco forest, grows between 120 and 600m in elevation and occupies nearly three-quarters of the LEF (Wadsworth, 1951). The tabonuco forest is a mosaic of species and forest structure that varies in time and space. Its composition locally reflects the response of tree species that differ in shade tolerance, size, and longevity to landscape variables such as elevation, topography, aspect, and exposure. At the time of the arrival of Europeans, the largest tree in tabonuco forest, *Dacryodes excelsa* (tabonuco tree), was common, reaching sizes >30m tall and 2m in diameter (Wadsworth, 1950). Ascending the LEF, montane rain forest grows between 600 and 900m, and dwarf forest on the Luquillo Mountain summits.

Much is known about the typical sizes and general distributions of the 168 tree species found in tabonuco forest (Little and Wadsworth, 1964; Little, 1970; Little *et al*., 1974). However, relatively few studies have concentrated on tree species distributions along gradients (White, 1963; Crow and Grigal, 1979; Weaver, 1991; Basnet, 1992; Gould *et al*., 2006; Barone *et al*., 2008). The purpose of this report is to synthesize new and existing information on forest structure and the occurrence of tree species in stands differing in elevation, topography, and aspect (i.e., Mameyes *vs* Quebrada Sonadora watersheds) within the tabonuco forest.

Setting

Rainfall averages about 3550mm in tabonuco forest; moreover, it increases with elevation and is greater on windward than leeward exposures (Ewel and Whitmore, 1973; García-Martinó *et al*., 1996). In addition, hurricanes are frequent large scale disturbances that recurrently impact the mountains and influence tree species survival and regeneration (Walker *et al*., 1991, 1996).

Tabonuco forest was heavily disturbed by past human activities (timber cutting, agriculture, grazing, tree planting, and silviculture) at lower elevations near the LEF border (Marrero, 1948; Aide *et al*., 1996; Thomlinson *et al*., 1996). Lower parts of both the Mameyes and Quebrada Sonadora watersheds were logged for valued timbers like *Dacryodes excelsa*, *Buchenavia tetraphylla*, *Guarea guidonia*, *Manilkara bidentata*, and *Sloanea berteroana* among others; at somewhat higher elevations, *Magnolia splendens* and *Ocotea moschata* were harvested (Wadsworth, 1950; Weaver, 1987). Timber stand improvement involved tree cutting and charcoal production of a mix of species of limited utility, including *Cyrilla racemiflora* (Wadsworth, 1970; Snyder *et al*., 1987). Thinning was designed to stimulate growth on saplings of timber species by removing less useful species. Subsequent forest changes were minimal however, because the species cut were transitory in secondary stands and

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made up only a minor component of mature forests; moreover, follow-up field operations were never implemented (Wadsworth, 1970). Other forestry activities (establishment of plantations and some very light thinning of secondary forest) were carried out mainly along the lower northern and western slopes of the LEF (Marrero, 1948; Wadsworth, 1970). Plantations, if successful, led to new forest cover; if unsuccessful, to secondary forest with scattered tree plantings.

Methods

Eighteen sample plots selected in closed forest were partitioned into six groups of three each by topography (ridge, slope, ravine), with one-half of the groups within the Mameyes watershed and the remainder in the Quebrada Sonadora watershed. All groups of plots were between 380 and 560m in elevation. Sampled plots in the Mameyes watershed faced northeast (windward) and those in the Quebrada Sonadora watershed northwest (leeward) and were separated by a ridge between El Yunque peak and Mt. Britton. None of the plots showed evidence of past harvest. Variations in forest cover and species composition in nearby areas, however, reflected past land use nearly 70 years earlier (Thompson *et al*., 2002).

All measurements were made on 50×10m plots, a size large enough to encompass common tabonuco forest species yet small enough to be situated entirely on the topographic feature. Ridge plots were on convex topography, ravine plots on concave or level topography, and slope plots on terrain without pronounced convex or concave features. Local aspects (i.e., orientation or compass bearings) and slopes varied according to individual plots. All trees ≥4cm dbh (diameter at breast height or 1.4m above the ground) were measured and heights were estimated with a rangefinder. Tree crowns (dominant, co-dominant, intermediate, or suppressed) were also classified (Baker, 1950). Plant nomenclature follows recent taxonomic studies (Liogier, 1985-97).

Total aboveground biomass (hereafter biomass) was determined by previously derived equations: ferns (Weaver, 2000a), palms (Frangi and Lugo, 1985), and broadleaf species (Weaver and Gillespie, 1992). ANOVAs were carried out to determine statistical differences among means for stem density, canopy height (dominant and co-dominant trees only), and biomass by aspect and topography at α=0.05. In addition, the number of species was tallied by aspect and topography but statistical tests were omitted because of the small sample sizes. Linear regressions were run for tree height, tree density, and biomass by elevation. Several species-area curves were developed, including one each by topographic position regardless of aspect, one each for windward and leeward plots regardless of topography, and one for the forest type. Relationships among species and habitat variables were explored using correspondence analysis (McCune and Mefford, 1999). Input data included the number of trees by species. Plot information included elevation (m), watershed or aspect (windward or leeward), and topographic position (ridge, slope, or ravine). All species with ≥6 occurrences (54% of the species and 94% of the stems) were used to produce the ordination.

TABLE I
MEAN VALUES OF FOREST STRUCTURE PARAMETERS BY ASPECT AND TOPOGRAPHY FOR 18 PLOTS IN THE LOWER MONTANE RAIN FOREST (TABONUCO FOREST) IN THE LUQUILLO MOUNTAINS

Forest parameter Topography	Aspect[1]		Combined	
	Leeward	Windward	Mean	Range
Stem density (stem/ha)				
Ridge	1840.0 ±110.1	1513.3 ±253.3	1676.7 ±174.0	1020-2040
Slope	1693.3 ±148.9	1553.3 ±415.9	1623.3 ±200.0	1060-2380
Ravine	1386.7 ±160.1	1353.3 ±354.1	1370.0 ±174.0	680-1880
Combined mean	1640.0 ±97.2	1473.3 ±176.5	1556.7 ±99.8	680-2380
Stem height (m) [2]				
Ridge	24.2 ±0.9[a]	18.1 ±2.9[b]	21.1 ±1.9[c]	14.2-25.9
Slope	21.3 ±0.8	17.6 ±2.0	19.3 ±1.2[c,d]	15.5-22.5
Ravine	18.7 ±1.6	17.1 ±1.9	17.9 ±1.2[d]	14.2-22.0
Combined mean	21.3 ±1.0[a]	17.6 ±1.2[b]	19.4 ±0.9	14.2-25.9
Biomass ($t\cdot ha^{-1}$) [3]				
Ridge	328.1 ±46.7	393.2 ±64.4	360.7 ±0.7[e]	281.1-511.5
Slope	210.4 ±28.1	248.4 ±55.9	229.4 ±29.2[f]	182.0-359.6
Ravine	98.4 ±1.7	183.3 ±11.5	142.4 ±20.3[g]	95.2-206.1
Combined mean	212.3 ±36.7	276.0 ±39.2	244.1 ±27.7	95.2-511.5
Species richness (number)				
Ridge	18.0 ±2.6	17.0 ±3.2	17.5 ±1.9	12-23
Slope	21.0 ±2.1	13.0 ±0.6	17.0 ±2.0	12-25
Ravine	13.3 ±2.0	14.0 ±3.0	13.7 ±1.6	10-20
Combined mean	17.4 ±1.6	14.7 ±1.4	16.0 ±1.1	10-25

[1] Each aspect has nine plots, three each by topographic position.
[2] Stem height: superscripts a and b indicate significant differences in height on ridges and for combined means by aspect. Superscripts c and d indicate significant differences in heights for combined means by topography.
[3] Biomass: superscripts e, f, and g indicate significant differences in biomass for combined means by topography.

The Río Mameyes plots were measured in 1988 and the Quebrada Sonadora plots in 1999 after Hurricanes Hugo (1989) and Georges (1998). Hurricane Hugo passed 15km northeast of the mountains with maximum sustained winds of $165km\cdot h^{-1}$ (Brennan, 1991; Scatena and Larsen, 1991). Hurricane Georges passed about 15km south of the mountains with maximum winds of $185km\cdot h^{-1}$ and gusts of $240km\cdot h^{-1}$ (U.S. Geological Survey, 1999). Some sample plots in Quebrada Sonadora suffered minor crown damage during the storms; however, no treefalls were encountered. The pre- and post-hurricane measurement dates within different watersheds should not be a major concern except for the presence of *Cecropia schreberiana*, *Psychotria berteroana*, and *Schefflera morototoni* (see Discussion). Earlier hurricanes (Bates, 1929; Salivia, 1972) included San Felipe, the island's legendary storm (1928), San Nicolas (1931), and San Cipriano (1932).

Results

Virtually all tree species can grow on most sites (i.e., aspect, topography, and elevation) within the tabonuco forest. Typically, however, mature forest species survive better on particular sites whereas shorter-lived secondary species dependent on disturbance are more cosmopolitan.

Forest structure

Stem density on the 18 plots varied by 3.5 times, canopy stem height by 1.8, biomass by 5.4, and species numbers by 2.5 times (Table I). Stem density averaged 1557 stems/ha and ranged from 680 to 2380 stems/ha on individual plots. Combined stem density tended to be greater on the leeward as compared to the windward, and greater on ridges and slopes as compared to ravines. Differences, however, were not significant.

Combined canopy stem height for all plots averaged 19.4m and ranged from 14.2 to 25.9m on individual plots (Table I). Combined canopy stem height was significantly greater to the leeward than to the windward; moreover, canopy stem height on ridge plots to the leeward was greater than ridge plots to the windward. Also, combined canopy stem heights on ridge plots exceed those on ravine plots. Canopy stem height varied with elevation, as follows: Y (all plots combined)= -0.024X + 30.45, r^2= 0.28, n= 18; and Y (windward plots alone)= -0.058X + 42.2, r^2= 0.54, n= 9. In both cases, Y= height (m) and X= elevation (m). Canopy stem height also tended to decline on leeward plots but the relationship was not significant.

Biomass averaged 244t·ha^{-1} on all plots and varied from 95.2 to 511.5t·ha^{-1} on individual plots (Table I). Combined biomass was greater to the windward than the leeward, but variation among plots was considerable and the differences were not significant.

Species relationships

Slightly more than 40% of the known tabonuco forest species were sampled on only 0.9ha of closed forest (Figure 1). The species curve for the forest became asymptotic near 0.45ha. In addition, species' numbers to the windward initially rose more rapidly than to the leeward but showed similar totals at 0.45ha. Ridge and slope plots contained greater numbers of species than equal numbers of ravine plots (Figure 1).

Prestoea montana, the most common species, accounted for about 20% of all stems, and the 10 most common species for nearly two-thirds of the total. Thirty-two species had ≤5 stems apiece. The number of species averaged 16 per plot (Table I) and varied from 10 to 25 on individual plots. The combined mean number of species was greater on the leeward than on the windward even though the total number of species tallied to the windward was slightly greater (Table I, Figure 1). Also, the combined mean number of species decreased from ridge to slope to ravine topography.

The ordination shows (Figure 2) distributions of species by elevation (Axis 1) and by aspect (watershed) and topography (Axis 2). Among the more common species,

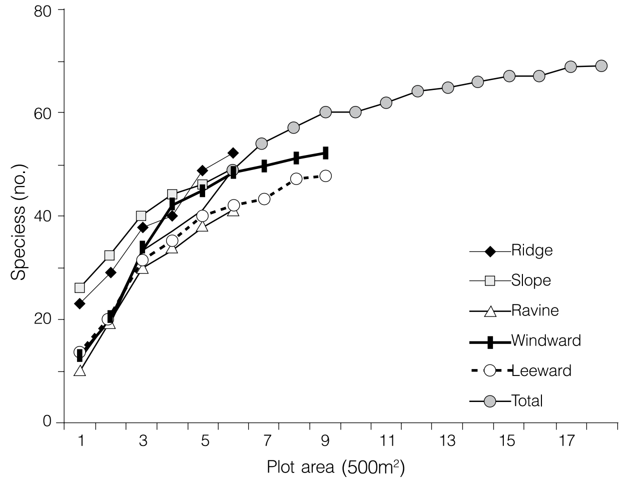

Figure 1. Species-area curves for tabonuco forest by topographic position (ridge, slope or ravine), regardless of aspect; by aspect (Río Mameyes watershed – windward and Quebrada Sonadora watershed – leeward), regardless of topography; and for the entire tabonuco forest, regardless of aspect or topography.

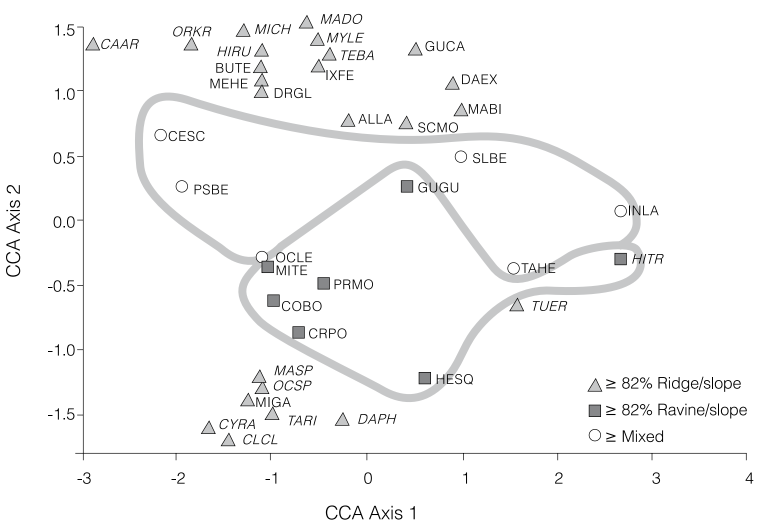

Figure 2. Correspondence analysis for species with ≥6 stems in tabonuco forest. Axis 1 represents elevation (high at left and low at right); axis 2 represents watershed or aspect (i.e., Quebrada Sonadora (top) and Río Mameyes) (bottom); triangles, squares, and dots indicate species occurrence by topographic features (see legend). The 15 acronyms in italics indicate species recorded exclusively in one watershed and those in standard print indicate species recorded in both watersheds.

Species acronyms (stem numbers) are ALLA: *Alchornea latifolia* Sw. (8), BUTE: *Buchenavia tetraphylla* (Aublet) R. Howard (6), *CAAR*: *Casearia arborea* (L.C. Rich) Urban (6), CESC: *Cecropia schreberiana* Miq. (48), *CLCL – Clusia clusoides* (Griseb.) D'Arcy (7), COBO: *Cordia borinquensis* Urban (23), CRPO: *Croton poecilanthus* Urban (51), *CYRA*: *Cyrilla racemiflora* L. (36), DAEX: *Dacryodes excelsa* Vahl (150), *DAPH*: *Daphnopsis philippiana* Krug & Urban (49), DRGL: *Drypetes glauca* Vahl (55), GUGU: *Guarea guidonia* (L.) Slumer (12), GUCA: *Guatteria caribaea* Urban (8), HESQ: *Henriettea squamulosa* (Cogn.) Judd (34), *HIRU*: *Hirtella rugosa* Pers. (13), *HITR*: *H. triandra* Sw (6), INLA: *Inga laurina* (Sw.) Wild (9), IXFE: *Ixora ferrea* (Jacq.) Benth. (8), *MASP*: *Magnolia splendens* Urban (7), MABI: *Manilkara bidentata* (A. DC.) Chev. (80), *MADO*: *Matayba domingensis* (DC.) Radlk. (14), MEHE: *Meliosma herbertii* Rolfe (13), MITE: *Miconia tetrandra* D. Don. (8), MIGA: *Micropholis garciniifolia* Pierre (83), *MICH*: *M. guyanensis* (A. DC.) Pierre (19), *MYLE*: *Myrcia leptoclada* DC. (20), OCLE: *Ocotea leucoxylon* (Sw.) Lanessan (13), *OCSP*: *O. spathulata* Mez (19), *ORKR*: *Ormosia krugii* Urban (9), PRMO: *Prestoea montana* (R. Grah.) Nichols (285), PSBE: *Psychotria berteroana* DC. (21), SCMO: *Schefflera morototoni* (Aubl.) Maguire (23), SLBE: *Sloanea berteroana* Choisy (60), TAHE: *Tabebuia heterophylla* (DC.) Britton (7), *TARI*: *T. rigida* Urban (32), *TEBA*: *Tetragastris balsamifera* (Sw.) Kuntze (52), *TUER*: *Tetrazygia urbanii* Cogn (17).

Croton poecilanthus, *Henriettea squamulosa*, and *Prestoea montana* were more common in ravines and on slopes, and *Cecropia schreberiana* and *Sloanea berteroana* were mixed in occurrence by topography. In contrast, *Cyrilla racemiflora*, *Dacryodes excelsa*, *Tetragastris balsamifera*, *Micropholis guyanensis*, *Schefflera morototoni*, *Micropholis garciniifolia*, and *Manilkara bidentata* favored ridges and slopes. With regard to aspect, *C. poecilanthus*, *C. racemiflora*, *H. squamulosa*, *M. garciniifolia*, and *P. montana*, were more common to the windward whereas *C. schreberiana*, *D. excelsa*, *M. bidentata*, *Micropholis guyanensis*, *S. morototoni*, *S. berteroana*, and *T. balsamiera* were more common to the leeward. In addition, three species, *Clusia clusioides*, *Ocotea spathulata* and *Tabebuia rigida*, species largely confined to montane rain and dwarf forests, were encountered on ridge topography to the windward.

Discussion

Sampling dates

Hurricanes cause widespread defoliation but major structural damage is patchy (Bates, 1929; Walker, 1991; Bellingham *et al*., 1992). The fact that the Quebrada Sonadora plots averaged nearly 4m taller than those in the Mameyes watershed suggests that storm impacts were minor (Table I). The presence of pole-size *Cecropia schreberiana* along with smaller *Psychotria berteroana* and *Schefflera morototoni*, however, indicates that defoliation and crown opening were sufficient to stimulate their regeneration. The above three species rapidly colonize gaps in tabonuco forest (Crow, 1980; Weaver, 2002) and may have added about 140 stems/ha to the combined mean stem density of the Quebrada Sonadora plots. Other tree species grow more slowly (Weaver, 1983) and their ingrowth on the plots should not be detected for >10 years.

The ordination shows that *Psychotria* and *Schefflera*, both with narrow crowns, survive best on ridges and slopes (Figure 2); *Cecropia*, with a spreading crown, regenerates throughout the forest but survives best in ravines. The ravines, dominated by the narrow-canopied *Prestoea montana*, are characterized by periodic flooding and poor soil aeration (Frangi and Lugo, 1985). More than 70% of the above three species were tallied in Quebrada Sonadora reflecting the recent passage of Hurricane Hugo (Figure 2).

Forest structure

The large variation within the parameters measured was partially attributable to the comprehensive sampling design and the relatively small plot sizes. The means for combined stem density by aspect and by topography in tabonuco forest largely parallels previously reported patterns for LEF's montane rain forest (Weaver, 2000b). Moreover, the means for the combined canopy stem height were greater to the leeward than the windward in both forest types. In montane rain forest, however, height increased from ridge through slope to ravine, the reverse of that in tabonuco forest (Table I). Certain factors may account for this pattern. First, *Dacryodes excelsa* and *Manilkara bidentata*, the tallest species within the Luquillo Mountains, are common and best developed at lower elevations on protected ridges and slopes (Wadsworth, 1951). Second, at higher elevations within the mountains, trees in ravines and lower slopes are better protected from prevailing winds than those on ridges. Combined biomass in both forest types is also greater on ridges and slopes than in ravines because of differences in species composition and structure (Table II). Both *Prestoea montana* and *Cecropia schefflera*, most common in ravines, have a low specific gravity and contribute proportionately less to biomass.

Species composition

The comparatively large number of species sampled is also attributable to sampling design. Early botanists working in Caribbean forests noted that environmental gradients influenced tree species composition and forest structure, and attributed these changes to variation in rainfall, fog, wind, humidity, and light (Shreve, 1914; Beard, 1949).

Topographic variation in tree species' occurrence is evident (Figures 1 and 2; Table I). At Bisley, a watershed located between 260 and 450m to the windward, *Dacryodes excela* was associated with ridges, *Manilkara bidentata* with slopes, and *Prestoea montana* and *Guarea guidonia* with ravines (Basnet, 1992). The dominance of *Dacryodes* on ridges was attributed to better soil drainage, better anchorage, and root grafting, making the trees more resistant to wind throw (Lugo and Wadsworth, 1990; Basnet *et al*., 1993). Low crown-to-bole ratios were reported for *Dacryodes* trees in Dominica, an island prone to frequent storms (Bell, 1976). Hurricane survival combined with longevity may reduce the crown size of *Dacryodes* trees, making them more resistant to subsequent storms. *Dacryodes* on ridges and *Prestoea* in ravines were also reported on a plot near 350m elevation in the Quebrada Sonadora watershed (Johnston, 1990).

An earlier study dealt with three additional tracts within tabonuco forest -Sabana 4, Sabana 8 to the windward, and Río Grande to the leeward (Crow and Grigal, 1979). Sabana 4, between 210 and 600m, is undisturbed; in contrast, at Río Grande, between 420 and 600m, has secondary forest at low elevations and is largely undisturbed above. Several species-site relationships were apparent. At Sabana 4 and Río Grande, *D. excelsa* had its best development on ridges, *Cyrilla racemiflora* and *Micropholis garciniifolia* on slopes and ridges, and *P. montana*, *Cecropia schreberiana*, and *Sloanea berteroana* on bottomlands and riverbanks. *Prestoea* was well distributed in both areas. Sabana 8, between 180 and 360m, was mainly secondary forest (Crow and Grigal, 1979). *Ormosia krugii*, *Tabebuia heterophylla*, and *Schefflera morototoni* were found on a variety of topographic positions, but most commonly on ridges. *Inga laurina*, previously planted as coffee shade, grew in a variety of positions. *Buchenavia tetraphylla* and *Manilkara bidentata* were found together on upper slopes. Finally, secondary species like *Alchornea latifolia* and *Tabebuia heterophylla* dominated some stands.

The patterns for tree species richness in the tabonuco forest (Table I) were also similar to those observed in the montane rain forest (Weaver, 2000b). Greater rainfall and cloud cover make mid-elevation tabonuco sites to the windward more similar to montane rain and dwarf forest habitats where solar insolation is reduced and soil water is increased. *Clusia clusoides*, *Ocotea spathulata*, and *Tabebuia rigida*, all more common in dwarf forest and higher elevations in montane rain forest, survive in the tabonuco forest, mainly on windward upper slopes and ridges with exposed conditions similar to the summits (Wadsworth, 1951; Weaver, 1983, 2002). Other species such as *Croton poecilanthus*, *C. racemiflora*, *Henriettea squamulosa*, and *M. garciniifolia* are proportionally more common in montane rain forest than in tabonuco forest and favor windward sites in the latter (Wadsworth, 1951). Long ago, Beard (1949) noted that tabonuco forest within the Lesser Antilles extended to higher elevations on leeward exposures than to the windward. Moreover, classification of tabonuco forest using Holdridge's (1967) ecological life zone system designated the Mameyes watershed as Subtropical rain forest and the Quebrada Sonadora as Subtropical wet forest (Ewel and Whitmore, 1973). Among the characteristics used to distinguish between them were greater total rainfall and a higher frequency of *P. montana* in the rain forest life zone.

The climatic factor

Hurricanes in and around the Luquillo Mountains are frequent enough so that their effects are always evident. Hurricanes pass directly over the mountains on the average of once every 62 years and within 60km once every 22 years (Salivia, 1972; Scatena, 1989). All hurricanes caused some defoliation, breakage, uprooting, and removal of epiphytes. On impacted sites, maximum canopy height was reduced after Hurricane Hugo in all LEF forest types, especially in tabonuco forest (Brokaw and Grear, 1991). Hugo affected >85% of the trees in the Bisley watershed with large trees >70cm in dbh being susceptible to defoliation and uprooting (Basnet *et al*., 1992). *D. excelsa*, and to a lesser extent *Sloanea berteroana* and *Guarea guidonia*, suffered less impact than other species. Topography also played a role. Trees in valleys suffered greater damage than those on slopes or ridges, possibly due to more humid soil conditions or poor drainage (Basnet *et al*., 1992). Uprooted trees created openings, which despite their small areas, varied in light, litterfall, and nutrient availability, factors that influence plant regeneration and diversity (Devoe, 1989; Walker, 2000).

Long-term changes in forest structure (stem numbers and sizes), species composition (primary vs. secondary), and species richness were evident after Hurricane San Cipriano (Crow, 1980; Weaver, 1983, 1989). During recovery, *C. schreberiana* and *S. morototoni* declined considerably in numbers as mature forest species gradually dominated the stands.

Tree life cycles

Tree adaptations, as evidenced during their life cycles, influence the occurrence and persistence of trees within forests (Gómez-Pompa and Vázquez-Yanes, 1974; Francis and Lowe, 2000). Species such as *Alchornea latifolia*, *C. schreberiana*, *S. morototoni*, and *Psychotria berteroana*, which regenerate in openings after disturbance, are relatively short-lived (Little and Wadsworth, 1964; Brokaw, 1998; Weaver, 2002). *Cecropia* showed a sudden increase and rapid decline in stem numbers after San Cipriano of 1932 and Hugo of 1989 (Crow, 1980; Weaver, 2002). Occasionally, however, *Cecropia* may attain a diameter of 60cm in 50 years (Silander, 1979; Doyle, 1981). *Pre-*

TABLE II
OCCURRENCE, TENTATIVE SERAL STAGE CLASSIFICATION, AND SITE PREFERENCES FOR TREE SPECIES RECORDED IN THE LOWER MONTANE RAIN FOREST (TABONUCO FOREST) OF THE LUQUILLO MOUNTAINS

Species[1]	Inventories[2]		Seral stage[3]		General description of ocurrence in the Luquillo Mountains[4]
	Tab (%)	Mont (%)	Tab	Mont	
Alchornea latifolia	1.56	0.16	8	0	Secondary, variable soils and slope positions, low to mid elevation
Alchorneopsis floribunda[1]	1.34	0.02	4	0	Secondary, mainly on slopes at low elevation
Andira inermis[1]	0.38	0	--	--	Slopes on a variety of sites at low elevation
Buchenavia tetraphyla	0.19	0.11	16	0	Ridges and upper slopes at low to mid elevation
Byrsonima spicata[1]	0	0.81	17	0	Wet sites or disturbed areas at low to mid elevation
Cecropia schreberiana	10.73	0.73	1	1	Secondary, variety of disturbed sites and ravines, rapidly colonizes gaps, from low elevation to summits on protected sites
Cordia sulcata[1]	0	0	6	0	Variety of soils and topography, at low to mid elevations
Croton poecilanthus	3.22	3.98	11	16	Common in ravines, low to high elevation
Cyrilla racemiflora	1.27	2.86	3	3	Ridges and slopes, regenerating in gaps, mid elevation to summits
Dacryodes excelsa	9.81	0.50	19	0	Ridges and upper slopes at low to mid elevations
Guarea guidonia	0.96	0	25	0	Lower slopes, moist bottomlands and river banks at low elevation; formerly used as coffee shade
Henriettea squamulosa	3.06	13.38	12	15	Variety of topographic sites, mainly mid elevation to summits
Homalium racemosum[1]	0.25	0.13	9	0	Uncommon on a variety of sites, riverbanks, low to mid elevations
Inga laurina	2.29	0.34	22	0	Variety of sites at low to mid elevation; formerly used as coffee shade
Inga vera[1]	1.75	0.12	13	0	Common along river banks and sheltered ravines at low to mid elevation; formerly used as coffee shade
Magnolia splendens	1.05	0.87	0	4	Mainly upper slopes and ridges at mid elevations and in ravines at summits, regenerating in openings
Manilkara bidentata	1.34	0.02	15	0	Variety of soils, upper slopes, at low to mid elevation
Matayba domingensis	1.15	1.32	20	7	Ridges and upper slopes, from low to high elevation
Miconia tetratandra	0	1.71	2	0	Variable topography, colonizing gaps, low to high elevations
Micropholis garciniifolia	5.76	10.00	21	12	Ridges and slopes, low elevations to summits
Micropholis guyanensis	0.80	4.28	0	10	Mainly on ridges and upper slopes, more common to leeward, at mid to high elevation
Myrcia fallax[1]	0	1.16	0	13	Common on ridges, low to high elevation
Ocotea spathulata	0	4.79	0	18	Mainly on ridge and slope topography to windward, mid elevation to summits where abundant
Ormosia krugii	0.29	0.01	23	0	Slopes and ridges, low to mid elevation
Prestoea montana	32.26	16.69	18	9	Unstable soils on steep, windward facing slopes, ravines at low elevation to protected sites at summits
Pterocarpus officinalis[1]	0	0	--	--	Stream banks and bottomlands at low elevations
Sapium laurocerasus[1]	1.18	0.37	7	5	Common in ravines and lower slopes, low to mid elevation
Schefflera morototoni	2.16	0.17	14	2	Secondary, variety of soils and topography, colonizing gaps, low to mid elevation
Sloanea berteroana	4.20	0.34	27	0	Steep slopes, lower slopes, bottomlands, low to mid elevation
Tabebuia heterophylla	0.57	0.09	10	0	Secondary, variety of soils and degraded sites, low to mid elevation
Tabebuia rigida	0	8.38	0	8	Mainly ridge and slope topography, more common to windward, mid elevation to summits where abundant
Tetragastris balsamifera	0.92	0.01	29	0	Ridges and upper slopes, low to mid elevation
Other species	11.41	26.65			
Total	100.00	100.00			

[1] Species + author names for ≤5 stems and not cited in Figure 2: *A. floribunda* (Benth.) Muell.; *A. inermis* (W. Wright) DC.; *B. spicata* (Cav.) HBK; *C. sulcata* DC.; *H. racemosum* Jacq.; *I. vera* Willd.; *M. fallax* (Poir) DC.; *P. officinalis* Jacq.; and *S. laurocerasus* Desf.
[2] Tab: percentage of trees by species on 4 ha of tabonuco forest sampled in mid-1940s (Wadsworth, 1951). Sample based on 3,140 trees at different sites. Mont: percentage of trees by species on 3.75 ha of undisturbed Montane rain forest sampled during the early 1980s (Weaver, 1991). Sample based on 8090 trees at several sites. Zero indicates that the species was not found or that it was uncommon, and therefore not ranked (see footnote below).
[3] Tab: tabonuco forest (Smith, 1970). Mont: montane rain forest (Weaver, 1992). Tree species in the tabonuco forest were ranked from 1 (most secondary) to 29 (most primary) and those in montane rain forest from 1 (most secondary) to 20 (most primary). Species ranked by the authors but not found in this study were excluded from the table. Zero indicates a species that was ranked by one author but not the other. A dash indicates a species that was not ranked but for which information exists on its occurrence (Francis and Lowe, 2000).
[4] Sources: Wadsworth, 1951; Little and Wadsworth, 1964; Little *et al*., 1974; Crow and Grigal, 1979; Weaver, 1991, 1992, 2001, this study; Basnet, 1992. Approximate elevation ranges in the LEF: low, 200-400m; mid, 400-700m; high, 700-900m; summits ≥900m.

stoea montana can reach 20m in height and perhaps 180 years in age (Van Valen, 1975). In contrast, at least four mature forest species dominate the landscape for extended periods. *D. excelsa* and *C. racemiflora* probably grow to about 1m in 600 to 650 years and *Magnolia splendens* may reach 65cm in 500 years (Weaver, 1986, 1987, 2002). *Manilkara bidentata*, the remaining large species, also attains >1m in dbh (Little and Wadsworth, 1964). Seedlings may persist with little growth in the understory for years. Trees measuring 0.6m in dbh were estimated to be nearly 250 years old (You, 1991). It is likely that the largest specimens about 1in dbh are ≥600 years old.

Twenty-nine common tabonuco forest canopy species within the Quebrada Sonadora watershed were ranked from most pioneer-like (*C. schreberiana*) to most primary (*Tetragastris balsamifera*) based on four criteria: seed size, wood density, and the survival of seedlings and saplings in the understory (Smith, 1970). A similar ranking of 20 canopy species was carried out in the montane rain forest (Weaver, 1992). Specific rankings are shown for canopy trees that were sampled in this study (Table II). Also indicated is the relative abundance of tree species tallied in a 4ha inventory in tabonuco forest along with descriptive information on species occurrence with regard to aspect, topography, and elevation in the Luquillo Mountains.

Although *P. montana* was first classed as a successional species based on its capacity to regenerate on steep slopes where landslides were common (Beard, 1949), autecological research in the Quebrada Sonadora watershed showed that *Prestoea* 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). *Prestoea*, however, is ubiquitous in the Luquillo Mountains between 400m and the summits, reproducing in forest gaps and openings as well (Crow, 1980; Weaver, 1983). Other tree species of mature tabonuco forest that regenerated well in post-Hurricane Hugo conditions were *Manilkara bidentata* (You and Petty, 1991) and *Sloanea berteroana* (Weaver, 2002).

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ESTRUCTURA Y COMPOSICIÓN DEL BOSQUE MONTANO BAJO DE LA SELVA LLUVIOSA EN LAS MONTAÑAS DE LUQUILLO, PUERTO RICO

Peter L. Weaver

RESUMEN

Seis grupos de tres parcelas estratificadas por aspecto y topografía, y de diferente elevación, fueron usados para muestrear la estructura y la composición de especies arbóreas del bosque montano bajo en la selva lluviosa (bosque de tabonuco) de la Estación Experimental de Luquillo (EET) en Puerto Rico. La densidad de tallos, altura de árbol, y biomasa aérea total varió por sitio. Hubo diferencias significativas entre sotavento y barlovento en altura de dosel, que declinó de las alturas a ladera y al barranco para todos los sitios combinados. La biomasa aérea total fue significativamente mayor en las alturas que en los barrancos. Prestoea montana *(R. Grah.) Nichols y* Dacryodes excelsa *Vahl representaron 31% de los 1394 tallos y 69 especies consideradas. El análisis de correspondencias mostró que la abundancia de 37 especies con ≥6 ocurrencias (94% de los tallos) varió de acuerdo a características de aspecto y topografía, y que las parcelas de barlovento contenían algunas especies asociadas a sitios más húmedos a mayor altura. Los huracanes impactan la EET con suficiente frecuencia para mantener su bosque en un continuo estado de recuperación. La composición del bosque en cualquier sitio es una función de gradientes ambientales, eventos climáticos mayores y atributos de las especies arbóreas.*

ESTRUTURA E COMPOSIÇÃO DO BOSQUE MONTANO BAIXO DA SELVA CHUVOSA NAS MONTANHAS DE LUQUILLO, PORTO RICO

Peter L. Weaver

RESUMO

Seis grupos de três lotes estratificados por aspecto e topografia, e de diferente elevação, foram usados para mostrar a estrutura e a composição de espécies arbóreas do bosque Montano Baixo na selva chuvosa (bosque do tabonuco) da Estação Experimental de Luquillo (EET) em Porto Rico. A densidade de caules, altura da árvore, e biomassa aérea total variaram conforme o local. Houve diferenças significativas entre sotavento e barlavento em altura do dossel, que declinou das alturas a ladeira e ao barranco para todos os locais combinados. A biomassa aérea total foi significativamente maior nas alturas que nos barrancos. Prestoea montana *(R. Grah.) Nichols e* Dacryodes excelsa *Vahl representaram 31% dos 1394 caules e 69 espécies consideradas. A análise de correspondências mostrou que a abundância de 37 espécies com ≥6 ocorrências (94% dos caules) variou de acordo a características de aspecto e topografia, e que os lotes de barlavento continham algumas espécies associadas a locais mais úmidos quanto maior altura. Os furacões impactam a EET com suficiente frequência para manter seu bosque em um contínuo estado de recuperação. A composição do bosque em cualquer parte é uma junção de gradientes ambientais, eventos climáticos maiores e atributos das espécies arbóreas.*