

Tree species distribution and forest structure along environmental gradients in the dwarf forest of the Luquillo Mountains of Puerto Rico

Peter L. WEAVER¹

¹ U.S. Department of agriculture
Forest service
International institute
of tropical forestry
Jardín botánico sur
1201 Calle Ceiba
San Juan 00926-1119
Puerto Rico



Photograph 1.

East Peak Road: the East Peak road links both East and West peaks, sites where several ecological studies were carried out after the mid-1960s. Summits are typically occupied by dwarf forest. Patches of sierra palm are common in protected ravines.

Photograph I. Vicéns.

RÉSUMÉ

DISTRIBUTION DES ESSENCES ET STRUCTURE FORESTIÈRE SELON LES GRADIENTS ENVIRONNEMENTAUX DE LA FORÊT NAINES DES MONTS LUQUILLO À PUERTO RICO

Onze groupes de trois placettes stratifiées selon leur exposition (face au vent/sous le vent), la topographie (arête, pente ou ravin) et l'altitude, entre 880 et 1000 mètres environ, ont servi à un échantillonnage de la structure forestière et de la composition floristique de la forêt naine des monts Luquillo à Puerto Rico. La densité des tiges face au vent est sensiblement plus importante sur les pentes, et pour l'ensemble des topographies, que sous le vent. Le couvert sous le vent est sensiblement plus élevé sur les pentes, et pour l'ensemble des topographies, que face au vent. En outre, dans tous les sites, la densité totale médiane décroît à mesure que l'on descend de l'arête vers les pentes et jusqu'aux ravins, alors que cette tendance s'inverse pour la hauteur moyenne de l'ensemble du couvert. Pour les deux types d'exposition, la biomasse est plus importante sur les arêtes et les pentes que dans les ravins. La biomasse est plus importante sous le vent que face au vent pour l'ensemble des topographies; cependant, aucune relation biomasse n'est significative. *Tabebuia rigida* Urban est l'essence la plus abondante, avec plus de 23 % des 3 619 tiges recensées, et *Eugenia borinquensis* Britton la plus largement présente, sur 90 % des placettes. La moitié des 42 essences recensées totalisent moins de 2 % de l'ensemble des tiges. La forêt naine, adaptée à la survie sous des conditions rudes, évolue sous l'influence de facteurs édaphiques, climatiques et physiologiques. Ces forêts naines apportent de nombreux bénéfices : elles représentent un habitat critique pour de nombreuses espèces de faune et flore endémiques, renferment de précieuses ressources en eau et offrent des paysages panoramiques et bon nombre d'opportunités récréatives.

Mots-clés : forêt naine, flore et faune endémiques, structure forestière, gradients environnementaux, Puerto Rico.

ABSTRACT

TREE SPECIES DISTRIBUTION AND FOREST STRUCTURE ALONG ENVIRONMENTAL GRADIENTS IN THE DWARF FOREST OF THE LUQUILLO MOUNTAINS OF PUERTO RICO

Eleven groups of three plots stratified by aspect (windward vs. leeward) and topography (ridge, slope, and ravine) and varying in elevation from 880 to about 1,000 metres were used to sample forest structure and species composition within the dwarf forest of the Luquillo Mountains of Puerto Rico. Stem density to windward was significantly greater on slopes, and for all topographies combined, than to leeward. The leeward canopy height was significantly greater on slopes, and for all topographies combined, than to windward. In addition, combined mean density declined from ridge through slope to ravine for all sites whereas the opposite was true of the combined mean canopy height. Biomass was greater on ridges and slopes than in ravines for both aspects combined. Also, biomass to leeward was greater than to windward for all topographies combined; however, none of the biomass relationships was significant. *Tabebuia rigida* Urban was the most abundant species, accounting for > 23 % of the 3,619 stems counted, whereas *Eugenia borinquensis* Britton was the most widespread, occurring on 90 % of the plots. One-half of the 42 recorded species accounted for < 2 % all stems. Climatic, edaphic, and physiological factors account for dwarf forest, which is adapted for survival under rigorous conditions. Dwarf forest provides numerous benefits, including critical habitat for many endemic flora and fauna, valuable water supplies, panoramic vistas, and recreational opportunities.

Keywords: dwarf forest, endemic flora and fauna, forest structure, environmental gradients, Puerto Rico.

RESUMEN

DISTRIBUCIÓN DE ESPECIES Y ESTRUCTURA FORESTAL A LO LARGO DE GRADIENTES AMBIENTALES EN EL BOSQUE ENANO DE LA SIERRA DE LUQUILLO EN PUERTO RICO

Se utilizaron once grupos de tres parcelas estratificadas según su exposición (barlovento o sotavento), topografía (cresta, pendiente y barranco) y escalonamiento altitudinal (entre 880 y 1000 m aproximadamente) para muestrear la estructura forestal y la composición florística en el bosque enano de la sierra de Luquillo en Puerto Rico. La densidad de tallos a barlovento fue significativamente mayor en las pendientes, y en todas las topografías, que a sotavento. La altura del dosel a sotavento fue significativamente mayor en las pendientes, y en todas las topografías, que a barlovento. Además, en todos los sitios, la densidad promedio total va disminuyendo de la cresta a la pendiente y de la pendiente al barranco, mientras que la altura promedio del conjunto del dosel muestra la tendencia opuesta. En ambos tipos de exposición, la biomasa es más importante en crestas y pendientes que en los barrancos. La biomasa es más importante a sotavento que a barlovento en todas las topografías; sin embargo, ninguna de las relaciones de biomasa es significativa. *Tabebuia rigida* Urban es la especie más abundante, con más del 23 % de los 3619 tallos contabilizados, y *Eugenia borinquensis* Britton la más generalizada, en el 90 % de las parcelas. La mitad de las 42 especies registradas representan menos del 2 % del total de tallos. El bosque enano, adaptado para sobrevivir en condiciones rigurosas, evoluciona bajo la influencia de factores edáficos, climáticos y fisiológicos. Estos bosques enanos aportan numerosos beneficios: representan un hábitat crítico para numerosas especies de fauna y flora endémicas, encierran preciosos recursos hídricos y ofrecen paisajes panorámicos y muchas posibilidades de ocio.

Palabras clave: bosque enano, flora y fauna endémicas, estructura forestal, gradientes ambientales, Puerto Rico.

Introduction

Tropical cloud forests are isolated ecosystems where clouds impinge mountainous vegetation. They occupy about 500,000 km² worldwide and are characterized by dense tree cover and an abundance of mosses, ferns, and leafy liverworts (STADTMULLER, 1986). Their extension has been correlated with the presence of Cyatheaceae. Cloud forests in the greater Caribbean Basin, ranging from southern Mexico to western Panama, and from Cuba to Trinidad, occupy between 7,000 and 15,000 km² (LABASTILLE, POOL, 1978). Trees growing on exposed ridges and peaks within cloud forests have been called elfin woodland or dwarf forest (HOWARD, 1968; STADTMULLER, 1986).

Dwarf forest within the Luquillo Experimental Forest (LEF) has a single story of trees that commonly range from 1 to 6 meters (m) in height (WADSWORTH, 1951). Trees are branchy and their trunks are seldom straight. The upper canopy is relatively uniform and leaves are generally small, thick, and concentrated at the ends of branches. Roots are superficial, aerial roots are common, and grasses, sedges, and ferns occupy openings. Virtually all flowering plants within the type may grow at some time as epiphytes (HOWARD, 1968). It is likely that high winds associated with storms have probably “planted” epiphytic tree seedlings on the forest floor after crown breakage (LAWTON, PUTZ, 1988). Although no tree species is confined to dwarf forest, relatively few are adapted to survive on the exposed summits (NEVLING, 1971) leading some to consider the type as an impoverished variation of montane rain forest (WADSWORTH, 1951). The presence of certain genera (e.g., *Podocarpus*, *Ocotea*, *Magnolia*, and *Ilex*), the dominance of relatively few species, and the abundance of mosses are all characteristics shared with temperate rain forest habitats (DANSERAU, 1966).

The first excursions to the LEF summits were by horseback during the early 1920s. Dwarf forest became more accessible after completion of PR route 191 through the middle of the forest in the mid-1930s. Summit areas were reached with tributary roads to Mt. Britton and El Yunque Peak in 1938, and to Pico del Este and Pico del Oeste in 1962 (photo 1). Subsequent field work provided more data on the size and distribution of tree species (LITTLE, WADSWORTH, 1964; LITTLE, WOODBURY, 1976; LITTLE *et al.*, 1974). Beginning in the mid-1960s, detailed studies of the summit vegetation were carried out on Pico del Oeste, including microclimate, species composition, and soils (BAYNTON, 1968; HOWARD, 1968; LYFORD, 1969). On nearby Pico del Este, plots were established to monitor forest cloud moisture interception, forest structure and dynamics, and recovery after disturbance (WEAVER, 1972, 1991, 2000a, 2000b).



Photograph 2.

Plot survey: the international institute of tropical forestry (IITF) maintains six permanent plots in dwarf forest near Pico del Este, the easternmost summit in the Luquillo Experiment Forest. The dwarf forest plots were established in 1990; however, several permanent plots in lower forest types date to the mid-1940s. Photograph I. Vicéns.

The phenomenon of caribbean dwarf forests

Changes in elevation within the mountainous caribbean islands determine a progression of forest types ranging from tall, lower montane rain forest < 600 m, through montane rain forest between 600 and 900 m, to dwarf forest at the summits (BEARD, 1949; WADSWORTH, 1951; WEAVER, MURPHY, 1990). The 600 m cloud base marks the point where clouds envelop mountain summits and approximates the boundary between the two rain forest types (BAYNTON, 1968; WADSWORTH, 1951). The higher boundary between the montane rain and dwarf forests varies somewhat by exposure, being higher on taller, more massive mountains than on smaller mountains or outlying ridges (GRUBB, 1977). This phenomenon, called the “massenerhebung” effect, was first recorded in the European Alps.

The name dwarf forest in the LEF has traditionally referred to areas > 900 m where trees are generally short in stature; most dwarf forest observations, however, have been made near the 1,000 m summits where trees often become stunted, gnarled, and sometimes form a tangle of impenetrable stems (HOWARD, 1968; WADSWORTH, 1951). Dwarf forest is also called elfin woodland, which implies a “fairylend of flora”, an impression supported by the abundance of aerial roots and epiphytes (bromeliads, liverworts, mosses) growing in suspended soil-like material (GILL, 1969; HOWARD 1968; LYFORD, 1969). On Pico del Oeste, trees and shrubs near the summit are 2 to 4 m tall whereas those in protected leeward ravines a short distance away approach 10 m in height (HOWARD, 1968). At lower elevations, dwarf forest grades into the upper reaches of montane rain forest where taller species gradually increase in number.

Early researchers in the LEF recognized that dwarf forest was exposed to low temperatures, persistent winds, water-soaked soils, and high humidity caused by frequent fog and heavy precipitation (GLEASON, COOK, 1926). Low air temperature and reduced insolation, both influenced by persistent cloud cover, are primary factors in the growth and distribution of tropical montane forests (GRUBB, 1977). On LEF summits, solar radiation is only 60 % of that received in nearby lowlands (BAYNTON, 1968). The cool temperatures and saturated environment retard nutrient cycling, slowing the decay and mineralization of humus (GRUBB, 1977).

Summit soils in the LEF, saturated most of the year, impede root respiration and restrict 90 % of the root growth to a depth of 10 cm (GILL, 1969). The pachyphyllous leaves (i.e., thick with a high specific leaf area) that characterize tropical montane forests are expensive to replace (GRUBB, 1977). Also, wood density tends to be greater for trees on exposed sites suggesting that they expend critical resources to survive (LAWTON, 1984). Dwarf forest productivity is low in comparison to LEF forests at lower elevations (WEAVER, MURPHY, 1990). Dwarf forest trees grow slowly supporting the contention that surviving stress is more important than productivity (GRUBB, 1977).

Although wind is not considered a limiting factor in summit areas, it influences cloud moisture deposition (BAYNTON, 1968; WEAVER, 1972). In the Canary Islands, the presence of fog reduced tree transpiration considerably (RITTER *et al.*, 2009). In the cloud forests of Fiji, where trees are short for their corresponding stem diameters, the height of canopy trees closely correlated with estimated transpiration rates (ASH, 1987). Transpiration rates, although low (GATES, 1969), are not considered to be a limiting factor in

tree growth (GRUBB, 1977). At least 22 species in the LEF's dwarf forest have aerial roots, which should help stabilize plants in an environment where the combined weight of epiphytes, water, and eroding soils could topple them (GILL, 1969). Aerial roots should also shorten the distance nutrients move in trees and promote their survival.

Complete post-hurricane recovery of dwarf forest structure on heavily impacted sites could be delayed for a couple of centuries (WEAVER, 1999). Hurricanes in the LEF, however, occur on the average of every 70 years (SCATENA, LARSEN, 1991). Thus, some of the shortest and densest dwarf forest could result from recurrent disturbance and partial forest recovery.

Objectives

The main purpose of this work was to explore the effects of environmental gradients (i.e., elevation, aspect, and topography) on dwarf forest structure and tree species composition. This information should help to define the abundance, distribution, and status of tree species within the LEF, especially rare endemics. Information on species' occurrence may serve future researchers in determining the effects of climate change on plant survival and migration in forest landscapes. Also, dwarf forest climate, tree growth, and wildlife values are reviewed to highlight the distinct nature of dwarf forest and its importance to island residents.

Methods

Thirty-three plots, stratified by aspect (windward and leeward) and topography (ridge, slope, and ravine), were used to sample forest structure and tree species composition (photo 2). Plots were situated on outlying ridges above 880 m to the windward and leeward of Pico del Este, and 900 to 1,000 m to the windward and leeward of the ridge between El Yunque and El Toro Peaks, and near the summit of Pico del Oeste.

Measurements were made on 25 by 10 m plots with closed canopies situated along different transects. Plot size was large enough to encompass the most common species locally yet small enough to be situated on a single topographic feature. Ridge plots were on convex topography, ravine plots on concave or nearly level topography, and slope plots were on slopes without pronounced convex or concave features. An altimeter was used to determine elevation. Percent slope and orientation (compass bearings) of plots varied. Measurements were carried out at different times after 1990 when some



Photograph 3.

Plane crash: The Luquillo Experimental Forest has experienced at least five airplane wrecks since the 1940s, one of which was the 1968 crash of a Fairchild C-119 (Flying boxcar) in dwarf forest near Pico del Este. After 30 years the crash site is covered by broadleaf species and ferns. Complete recovery may take 200 years.

Photograph P. L. Weaver.

plots had experienced minor canopy damage due to hurricane Hugo in 1989. All trees ≥ 4.1 cm diameter at breast height (dbh) were measured at 1.4 m above the ground and heights were measured with extension poles. Only canopy trees were used to characterize plot height. All species were identified using local taxonomic texts (LIOGIER, 1985-97). Few species, small stems, and high density facilitated the use of small plots.

Total aboveground biomass (hereafter, biomass) was determined using published equations for ferns, the sierra palm, and broadleaf species (WEAVER, 2000b). ANOVAs at $P = 0.05$ were used to explore differences in stem density, canopy tree height, and biomass by aspect and topography. Also, the G-test and chi-square at $P = 0.01$ were used to explore relationships by aspect and topography for species with ≥ 10 individuals (SOKAL, ROHLF, 1981). Linear regressions were run for tree height, tree density, and biomass vs. elevation, none of which was significant. Species-area curves were developed: one for each topographic position, regardless of aspect; one for leeward and windward plots, regardless of topography; and one curve for the entire forest.

Results

Forest Structure

Combined stem density for all plots averaged 3,328 per hectare (ha) and ranged from 1,320 to 6,040 stems/ha on individual plots (table I). Mean stem density was significantly greater on windward slopes than on leeward slopes; likewise, mean stem density for all topographies combined was significantly greater to the windward than to the leeward. Mean stem density was also significantly greater on ridges and slopes than in ravines.

Mean canopy height averaged 8.8 m for all plots and ranged between 4.0 and 13.5 m (table I). Canopy height was significantly greater on slopes to the leeward than to the windward; likewise, mean canopy height for all topographies combined was significantly greater to the leeward than to the windward. Canopy heights increased from ridges through slopes to ravines in all instances, with the windward plots and combined means showing significant differences.

Table I.
Mean values of forest structural parameters by aspect and topography for 33 plots in the Dwarf forest of the Luqillo Mountains.

Forest parameter Topography	Aspect ¹		Combined	
	Leeward	Windward	mean	range
Stem density (no. ha ⁻¹) ²				
Ridge	3,236±494 ^c	4,413±508 ^c	3,878±386 ^c	2,080-5,920
Slope	2,796±618 ^{A, c, d}	4,717±431 ^{B, c}	3,843±460 ^c	1,920-6,040
Ravine	1,960±227 ^d	2,517±218 ^d	2,264±173 ^d	1,320-3,240
Combined mean	2,664±291 ^A	3,882±322 ^B	3,328±242	1,320-6,040
Canopy stem height (m) ³				
Ridge	8.7±1.1	6.4±0.6 ^c	7.4±0.7 ^c	4.0-12.0
Slope	10.0±0.9 ^A	6.9±0.5 ^{B, c, d}	8.3±0.7 ^{c, d}	5.5-12.7
Ravine	11.6±0.8	10.0±0.6 ^d	10.7±0.5 ^d	7.2-13.5
Combined mean	10.1±0.6 ^A	7.8±0.5 ^B	8.8±0.4	4.0-13.5
Biomass (t ha ⁻¹)				
Ridge	201.1±42.1	164.4±30.5	181.1±24.7	84.9-356.4
Slope	205.4±28.6	156.0±16.5	178.5±16.8	84.8-290.2
Ravine	144.9±26.1	150.4±24.2	147.9±16.9	76.1-255.9
Combined mean	183.8±19.1	156.9±13.3	171.9±12.2	76.1-356.4
Species richness (no.)				
Ridge	8.6±1.6	8.7±0.6	8.6±0.7	5-14
Slope	8.4±1.3	8.7±0.8	8.5±0.7	6-12
Ravine	8.6±0.9	9.5±0.9	9.1±0.6	7-13
Combined mean	8.5±0.7	8.9±0.4	8.8±0.4	5-14

¹ Leeward plots = 15 (5 each on ridge, slope, and ravine) and windward plots = 18 (6 each by topography).

² Stem density: superscripts A and B indicate significant differences in density by aspect; superscripts c and d indicate significant differences by topography. All values rounded to the nearest whole number.

³ Canopy stem height includes only trees in canopy; subordinate trees are not included in analyses. Superscripts A and B indicate significant differences in height by aspect; superscripts c and d indicate significant differences by topography.

Biomass averaged 172 tons per hectare (t/ha) and ranged from 76 to 356 t/ha (table I). Biomass tended to be greater to the leeward than to the windward, and on ridges and slopes

than in ravines, but none of these trends was significant. Moreover, none of the regressions between stem density, tree height, or biomass vs. elevation were found to be significant.

Table II.
Species composition in dwarf forest for 3,619 stems of 42 tree species on 33 plots each 250 m² in the Luquillo Mountains of Puerto Rico.

Species	Elevation (m) ¹		Totals		Aspect ²		Topography ³		
	Mean	(range)	Plots	Stems	L	W	R	S	V
<i>Ardisia luquillensis</i> (Britton) Alain ⁴	981	(920-990)	4	10	0	10	3	6	1
<i>Calyptranthes krugii</i> Kiaersk ⁵	954	(880-1 000)	19	61	8	53	30	21	10
<i>Clusia clusioides</i> (Griseb.) D'Arcy	954	(880-1 000)	11	76	56	20	24	34	18
<i>Cordia borinquensis</i> Urban ⁵	947	(920-960)	3	25	25	0	0	4	21
<i>Croton poecilanthus</i> Urban ⁴	951	(920-960)	3	11	11	0	0	2	9
<i>Cyathea arborea</i> (L.) J.E. Smith	937	(880-970)	8	43	28	15	10	25	8
<i>Cyathea bryophila</i> (R. Tryon) Proctor ⁵	947	(880-1 000)	21	421	61	360	41	176	204
<i>Cyrilla racemiflora</i> L.	940	(900-970)	6	30	28	2	22	7	1
<i>Daphnopsis philippiana</i> Krug & Urban ⁵	918	(880-970)	10	43	21	22	14	22	7
<i>Eugenia borinquensis</i> Britton ⁴	937	(880-1 000)	30	432	109	323	173	183	76
<i>Haenianthus salicifolius</i> Griseb.	951	(900-1 000)	10	48	39	9	23	12	13
<i>Henriettea squamulosa</i> (Cogn.) Judd. ⁵	926	(880-1 000)	25	357	184	173	129	96	132
<i>Magnolia splendens</i> Urban ⁴	928	(880-990)	11	22	13	9	9	6	7
<i>Micropholis garciniifolia</i> Pierre ⁴	943	(880-1 000)	26	362	221	141	166	169	27
<i>Ocotea leucoxydon</i> (Sw.) Lanessan	923	(880-970)	7	10	7	3	4	3	3
<i>Ocotea spathulata</i> Mez	961	(880-1 000)	22	566	175	391	292	215	59
<i>Palicourea croceoides</i> W. Hamilton	938	(925-940)	3	33	33	0	21	11	1
<i>Prestoea montana</i> (R. Grah.) Nicholls	934	(880-970)	12	135	92	43	0	5	130
<i>Psychotria berteriana</i> DC.	929	(880-970)	8	12	8	4	0	2	10
<i>Tabebuia rigida</i> Urban ⁴	950	(880-1 000)	27	844	192	652	378	372	94
<i>Torrabasia cunefolia</i> (C. Wright) Krug & Urban	925	(900-1 000)	4	14	14	0	12	2	0
Subtotals for species listed above			3-30	3 555	1 325	2 230	1 351	1 373	831
Subtotals for species not listed above ⁶			1-4	64	45	19	25	10	29
Totals			1-30	3 619	1 370	2 249	1 376	1 383	860
Percent of total stems (rounded)				100	38	62	38	38	24

¹ Mean elevation for the species weighted by the number of occurrences on each sampled plot. Mean elevation for all plots = 946 m (range 880 to 1,000 m).

² Aspect: L = leeward; and W = windward. G statistic for aspect is 769, which is highly significant (i.e., chi-square at P = 1% and 21 df = 39).

³ Topography: R = ridge, S = slope, and V = ravine. Total chi-square for species distribution by topography is 914, which is highly significant (i.e., chi-square at P = 1% and 26 df = 46). Cells with < 5 replications were combined with adjacent cells.

⁴ Tree species endemic to the Luquillo Mountains.

⁵ Tree species endemic to Puerto Rico.

⁶ Tree species (21) with ≤ 8 stems in dwarf forest and weighted mean elevation: *Brysonima wadsworthii* Little⁵ (2 stems, 925 m); *Cecropia schreberiana* Mig. (5 stems, 933 m); *Chionanthes domingensis* Lam. (2 stems, 920 m); *Citharexylum caudatum* L. (3 stems, 955 m); *Cybianthus sintenisii* (Urban) Agostini⁴ (2 stems, 950 m); *Ditta myricoides* Griseb. (5 stems, 922 m); *Hedyosmum arborescens* Sw. (7 stems, 961 m); *Ilex nitida* (Vahl) Maxim. (3 stems, 906 m); *Ilex sintenisii* (Urban) Britton⁴ (4 stems, 1,000 m); *Mecranium latifolium* (Cogn.) Skeeon (1 stem, 960 m); *Miconia laevigata* (L.) DC. (2 stems, 920 m); *Miconia pachyphylla* Cogn.⁵ (8 stems, 972 m); *Miconia sintenisii* Cogn.⁵ (6 stems, 1,000 m); *Miconia tetrandra* (Swartz) D. Don (1 stem, 890 m); *Micropholis guyanensis* (A. DC.) Pierre (1 stem, 900 m); *Myrcia deflexa* (Poirot) DC. (1 stem, 880 m); *Myrcia fallax* (A. Rich.) DC. (3 stems, 923 m); *Ocotea portoricensis* Mez⁵ (2 stems, 900 m); *Sapium laurocerasus* Desf.⁵ (2 stems, 925 m); *Ternstroemia luquillensis* Krug & Urban⁴ (2 stems, 1,000 m); *Xylosma schwaneckeanum* (Krug & Urban) Urban⁴ (3 stems, 967 m).

Tree Species Occurrences

The entire dwarf forest sample contained 3,619 trees and 42 species. Twenty of the species are endemic to Puerto Rico, 10 of which are restricted solely to the LEF (table II). Four of these species with a total of nine stems — *Cybianthus sintensisii*, *Ternstroemia luquillensis*, *Ilex sintensisii*, and *Xylosma schwaneckeanum* — are rare and have been designated as species of concern to forest managers.

Numbers of species ranged from 5 to 14 on individual plots, averaging 9 per plot with slight differences by aspect and topography (table I). The 10 most common species accounted for > 90 % of the stems whereas the least common 21 species accounted for < 2 % of the stems (table II). *Tabebuia rigida*, with > 23 % of the stems, was the most abundant species. *Eugenia borinquensis*, growing on 30 plots, was the best distributed species; moreover, 11 other species were well-distributed, occurring on 10 or more plots.

The species area curve for all tree species tallied on all plots began to level near 0.30 ha (figure 1). When species' numbers were plotted by aspect, leeward plots initially rose more rapidly than windward plots yet both were similar at 0.30 ha. When species numbers were plotted by topography, ravine plots contained slightly more species (figure 1). The mean number of tree species per plot, however, varied little by aspect or topography (table I).

Of the tree species with ≥ 10 occurrences, most had ample elevational ranges with eight being tallied throughout the dwarf forest (table II). *Palicourea croceoides* was the exception. *Ilex sintensisii*, *Miconia sintensisii*, and *Ternstroemia luquillensis* had the highest mean elevations, and *Miconia tetrandra* and *Myrcia deflexa* the lowest. *Calyptanthus krugii*, *Cyathea bryophila*, *Eugenia borinquensis*, *Ocotea spathulata*, and *Tabebuia rigida*, accounting for 65 % of the total stems, were more frequently encountered to the windward. *Ardisia luquillensis* was recorded only to the windward, and *Cordia borinquensis*, *Croton poecilanthus*, *Palicourea croceoides*, and *Torrallbasia cunefolia* only to the leeward. All remaining species were proportionately more common to the leeward than to the windward. No species with ≥ 10 stems was confined to a single topographic position (table II). Of the species with > 100 stems, *Ocotea spathulata* was tallied > 50 % of the time on ridges and *Prestoea montana* > 95 % of the time in ravines. *Eugenia borinquensis*, *Micropholis garciniifolia* and



Photograph 4.

Amazona vittata: The puerto rican parrot was most likely one of the first bird species to be seen and heard by spanish explorers. By 1972, the parrot, considered one of the 10 most endangered species in the world, was reduced to only 13 birds, all confined to the upper forests of the Luquillo Experimental Forest. Photograph G. P. Bauer.

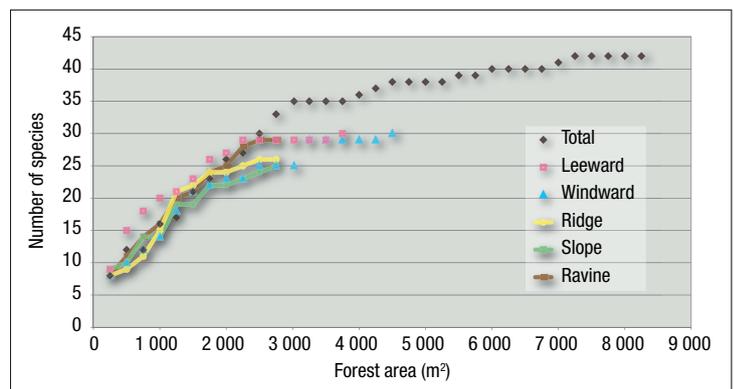


Figure 1.

Six species-area curves for the dwarf forest of the Luquillo Mountains, based on topographic position (ridge, slope, or ravine), aspect (windward or leeward), and the entire forest.

Tabebuia rigida were recorded on ridges and slopes > 80 % of the time, and *Cyathea bryophila* on slopes and ravines > 90 % of the time. In contrast, the distribution of *Henriettea squamulosa* was more uniform with regard to topography. *Haenianthus salifolius*, *Magnolia splendens*, and *Ocotea leucoxylon*, less common species, also had more uniform topographic distributions.

Discussion

Wind and cloud cover deposit more total moisture (rain-fall and fog deposition) on exposed windward sites than to the leeward. Moreover, at any particular elevation, topography influences soil formation, organic matter concentrations, soil moisture content and water movement, and erosion. Ridges and upper slopes, in general, are more exposed and have better drained soils than lower slopes and ravines. These factors, along with elevation, influence forest structure and species occurrence as shown by previous studies within the LEF's lower montane rain and montane rain forests (WEAVER, 1991, 2000a, 2010). Early Caribbean botanists noted that changes in forest composition and structure correlated with aspect, topography, and exposure. For example, slope forests in the mountains of Jamaica had vegetative characteristics intermediate between those of ridges and ravines (SHREVE, 1914). Also, in the mountainous Lesser Antilles, lower montane rain forest was observed to grow at higher elevations on leeward slopes than on windward slopes (BEARD, 1949).

Forest Structure

Greater stem density on ridges and slopes and taller trees in ravines appears related to prevailing climatic conditions and differences in species composition. Likewise, greater stem density on windward sites and taller trees to the leeward may be partially due to the differential survival of small species such as *Cyathea bryophila*, *Eugenia borinquensis*, and *Tabebuia rigida* that rarely exceed 8 m anywhere in the LEF (LITTLE, WADSWORTH, 1964; LITTLE *et al.*, 1974). *Ocotea spathulata*, the remaining abundant windward species, occasionally attains greater height at lower elevations (table II). Five species more common to the leeward, *Cyrilla racemiflora*, *Henriettea squamulosa*, *Magnolia splendens*, *Micropholis garciniifolia*, and *Prestoea montana*, may exceed 10 m in height on lower, protected, dwarf forest sites. Within the LEF's lower montane rain forest, taller trees with larger diameters were more prone to uprooting during hurricanes than smaller ones (WALKER, 1991). Similarly, in a Colombian cloud forest at Serranía de Macuira, windward

Table III.

Occurrence, tentative seral stage classification, and site preferences for the most common tree species found during the survey of dwarf forest in the Luquillo Experimental Forest (LEF) of Puerto Rico.

Species	Stems (%) ²	Seral stage ³	General description ⁴
<i>Ardisia luquillensis</i>	0.3	U	Rare, small tree, high elevation windward slopes and ridges
<i>Calyptanthes krugii</i>	1.7	U	Occasional, small tree, high elevation windward ridges and slopes
<i>Clusia clusoides</i>	2.1	S	Occasional, regenerates in openings, leeward sites
<i>Cordia borinquensis</i>	0.7	M	Rare, lower elevation leeward ravines and slopes
<i>Croton poecilanthus</i>	0.3	M	Rare, lower elevation leeward ravines and slopes
<i>Cyathea arborea</i>	1.2	S	Occasional, in openings and along roadsides
<i>Cyathea bryophila</i>	11.6	S	Abundant, openings in windward ravines and slopes
<i>Cyrilla racemiflora</i>	0.8	M-S	Rare, large tree, openings on low elevation leeward ridges and slopes
<i>Daphnopsis philippiana</i>	1.2	U	Occasional, small tree, lower elevations
<i>Eugenia borinquensis</i>	11.9	M-S	Abundant, high elevation windward slopes and ridges, and openings
<i>Haenianthus salicifolius</i>	1.3	U	Occasional, leeward sites, variable topography
<i>Henriettea squamulosa</i>	9.9	M	Abundant, well distributed by elevation, aspect, and topography
<i>Magnolia splendens</i>	0.6	M	Rare, large tree, mainly lower elevation sites, variable topography
<i>Micropholis garciniifolia</i>	10.0	M	Abundant, leeward slopes and ridges
<i>Ocotea leucoxydon</i>	0.3	U	Rare, small tree, low elevation leeward sites, variable topography
<i>Ocotea spathulata</i>	15.7	M	Abundant, high elevation windward ridges and slopes
<i>Palicourea crocoides</i>	0.9	S	Rare, small tree, leeward ridges and slopes
<i>Prestoea montana</i>	3.7	M	Common, ravines at all elevations
<i>Psychotria berteriana</i>	0.3	S	Rare, small tree, leeward ravines
<i>Tabebuia rigida</i>	23.3	M	Abundant, high elevation windward ridges and slopes
<i>Torralsbasia cunefolia</i>	0.4	U	Rare, small tree, leeward ridges
21 other species	1.8	—	Variable by species
Total	100.0		

¹ Tree species with ≥ 10 occurrences.

² Percent of 3,619 tallied stems.

³ Broad seral stages: M = mature forest species; S = secondary, regenerates after disturbance; U = uncertain.

⁴ Abundant is $\geq 9.9\%$; common is $\geq 3.0\%$ to 9.8% ; occasional is $\geq 1.0\%$ to 2.9% ; rare is $\leq 0.9\%$. Distributions refer to occurrences within dwarf forest only. The sites mentioned are those where the species is most frequently encountered.

LEF dwarf forest influences

Climate

High rainfall and humidity accompanied by frequent cloud cover and persistent wind characterize the LEF summits. Precipitation, averaging 4,500 mm per year, was recorded on 350 days during one year and reached 485 mm on one day in May of 1969 (BAYNTON, 1968; WEAVER, 1972). Moreover, cloud moisture intercepted by summit vegetation as clouds pass through increases total moisture delivered to the soil surface by 10 % annually. If cloud moisture interception counterbalances minor losses by evaporation and transpiration, virtually all rainfall within the 400 ha of dwarf forest should result in runoff, making it the island's highest unit area contributor of water supplies to the surrounding lowlands.

Hurricanes vary in occurrence, trajectory, and intensity, and cause both immediate and long-lasting effects, including defoliation, snapping, and uprooting of trees, and removal of epiphytes (WALKER, 1991). Permanent plots in dwarf forest showed that *Clusia clusoides*, *Cyathea bryophila*, and *Ocotea spathulata* suffered the greatest losses due to Hurricane Hugo and *Prestoea montana* the least. Post-hurricane biomass change on the same plots was initially negative, averaging -1.1 t/ha per year during 10 years. This decline, or delayed mortality, appears related to fine root mortality suffered during the storm (PARROTTA, LODGE, 1991). After hurricanes, cloud cover appears to elevate leaving the LEF summits clear for extended periods (SCATENA, LARSEN, 1991). Loss of leaves and epiphytes combined with higher clouds could temporarily reduce cloud moisture deposition.

Tree and Forest Growth

Diameter at breast height increment on permanent plots in undisturbed dwarf forest averaged 0.03 cm per year for all stems over a 5-yr period; moreover, biomass recovery on a plane wreck site was very slow, averaging only 0.68 t/ha per year over 37 years (WEAVER, 2008). Initially, grasses and ferns, including *Cyathea bryophila*, dominated the site. After 20 years, broadleaf species regenerated, 90 percent of which were endemics (WEAVER, 2000b). Small patches of grasses and ferns, however, were still evident after 40 years. Similarly, scattered openings caused by Hurricane Hugo were quickly occupied by grasses and ferns forming patches of "alpine meadows" that could persist for decades.

Two of the island's largest tree species, *Cyrilla racemiflora* and *Magnolia splendens*, regenerate in forest openings, may attain ages of >600 years, and are rare near the summits (WEAVER, 1986, 2008; table III). Large specimens, probably the oldest trees on the island, are a tribute to the island's past, most likely having germinated before the island's discovery by the Spanish.

slopes were observed to have greater stem density than leeward slopes (DUPUY *et al.*, 1993). Wind throw in this same forest caused greater losses of large trees on leeward sites whereas the typically smaller stems to the windward suffered less damage.

The lack of significance for regressions of stem density, canopy tree height, or biomass vs. elevation may be partially due to the relatively small range of elevations for most sample plots and to the variation in measured parameters over short distances at any particular elevation (e.g., along the local gradient from ridges to nearby ravines). In addition, stem density may increase at any site where lateral branches or adventitious shoots subsequently develop on fallen trunks (HOWARD, 1969). Wind-thrown specimens of *Cyrilla racemiflora* occasionally develop shoots that root in the soil, grow into the canopy, and persist into a new generation (WEAVER, 1986). Similar observations were made in cloud forests on Margarita Island, Venezuela (SUDGEN, 1986). Plot biomass is strongly affected by the sporadic occurrence of large specimens of *Cyrilla racemiflora*, *Magnolia splendens*, *Micropholis garciniifolia*, and *Tabebuia rigida* that may attain sizes much larger than the average dwarf forest tree. Large trees tend to inflate biomass estimates on the small plots used in this study.

Species Composition

About 40 tree species are typically associated with dwarf forest (WEAVER, 2008). *Tabebuia rigida*, *Ocotea spathulata*, *Eugenia borinquensis*, *Cyathea bryophila*, and *Calypttranthes krugii* (in descending order of abundance) are the tree species most frequently associated near the summits (tables II, III). Small tree species such as *Ardisia luquillensis*, *Ilex sintenisii*, *Miconia sintenisii*, and *Ternstroemia luquillensis*, also largely confined to summit areas, are rare.

Previous surveys near Pico del Este showed that *Cyathea bryophila* and *Prestoea montana* were significantly more abundant in ravines and *Ocotea spathulata* on ridges (WEAVER, 1999). *Henriettea squamulosa*, in contrast, had a more uniform distribution pattern (tables II, III). The latter was also the most abundant species at an airplane wreck site in dwarf forest after 30 years (photo 3) where it accounted for nearly one-half of the seedlings (WEAVER, 2000b).

Clusia clusoides, *Henriettea squamulosa*, *Micropholis garciniifolia*, and *Prestoea montana* are very common in montane rain forest (tables II and III; WEAVER, 1991). The last three are also present in the lower montane rain forest (WADSWORTH, 1951). In addition, *Cyrilla racemiflora*, most frequently encountered on ridges, *Magnolia splendens* found on different topographic positions, and both *Cordia borinquensis* and *Croton poecilanthus*, most often found in ravines (tables II, III), are better represented in montane rain forest than dwarf forest. *Cecropia schreberiana*, *Palicourea croceoides*, and *Psychotria berteriana* are secondary species that grow in dwarf forest openings (table II). The first is uncommon in dwarf forest, especially at high elevations (BROKAW, 1998), and the last two are small, short-lived trees.

**Photograph 5.**

Dwarf forest: Short, gnarled, epiphyte laden trees composed of a few species, many endemic to dwarf forest, grow above 900 m elevation in the Luquillo Experimental Forest. Forest trails provide scenic vistas and recreational opportunities for visitors.
Photograph P. L. Weaver.

Wildlife

Several native wildlife species use dwarf forest as critical habitat. Of the LEF's 14 species of reptiles, four are known to occur in the dwarf forest: *Anolis cristatellus* (Puerto Rican crested anole), *A. evermannii* (Everman's anole), the endemic *A. occultus* (Pygmy anole), and *Sphaerodactylus klauberi* (Klauber's least gecko) (JONGLAR, 2005; RIVERO, 1978). The LEF also has 11 species of endemic tree frogs of the genus

Eleutherodactylus, 9 of which have been found within or close to dwarf forest: *Eleutherodactylus coqui* (common coqui), *E. eneidae* (mottled coqui), *E. gryllus* (green coqui), *E. hedricki* (tree hole coqui), *E. locustus* (warty coqui), *E. portoricensis* (upland coqui), *E. richmondi* (bronze coqui), *E. unicolor* (elfin coqui), and *E. wightmanii* (melodious coqui). *E. unicolor* is endemic to the highest peaks in the LEF above 675 m in elevation. Recent exhaustive searches for *E. eneidae* have been unsuccessful and some fear that the species may be extinct. Also, recent data suggest that *E. locustus*, *E. portoricensis*, and *E. richmondi* are less abundant than formerly. Whether these population declines are related to normal fluctuations or migrations is uncertain. Recent hurricane damage may have caused temporary changes in the LEF's understory resulting in local losses of populations or migrations to other sites within the LEF. Another possible cause could be the chytridiomycosis fungus that has affected frog species elsewhere (DASZAK *et al.*, 2003).

Among the better known bird species reported in dwarf forest are: *Buteo jamaicensis* (Red-tailed hawk), *Columba squamosa* (Red-necked pigeon), *Amazona vittata* (Puerto Rican parrot), *Anthracothorax viridis* (Green mango), *Chlorostilbon maugaens* (Puerto Rican emerald hummingbird), *Cypseloides niger* (Black swift), *Dendroica angelae* (Elfin woods warbler), *Loxigilla portoricensis* (Puerto Rican bullfinch), *Megascops nudipes* (Puerto Rican screech owl), *Melanerpes portoricensis* (Puerto Rican woodpecker), *Nesoingus speculiferus* (Puerto Rican tanager), *Saurothera vielloti* (Puerto Rican lizard cuckoo), *Spindalis zena* (Stripe-headed tanager), and *Todus mexicanus* (Puerto Rican tody). All but the first two are island endemics.

At least 11 species of bats have been reported in some part of the LEF. Of those, *Artibeus jamaicensis* (Fruit bat), *Brachnyphylla cavernarum* (Cave bat), *Eptesicus fuscus* (Big brown bat), *Erophylla sezekorni* (Brown flower bat), *Mormoops blainvillii* (Blainvillee's leaf-chinned bat), *Pteronotus quadridens* (Sooty moustached bat), and *Monophyllus redmanii* (Greater Antillean long-tongued bat) have been captured near 800 m in elevation, only a short distance from dwarf forest (GANNON *et al.*, 2005). The last bat, native exclusively to the Greater Antilles, has been placed on the U.S. Forest Service's list of sensitive species for which population viability is a concern.

Dwarf forest management

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, POOL, 1978; STADTMULLER, 1986). Although limited in extent, the LEF's dwarf forest provides numerous benefits. As noted long ago, the dense, undisturbed forest helps to protect the highest slopes and summits from erosion (MURPHY, 1916). It also serves as habitat for 20 endemic tree species (LITTLE, WOODBURY, 1976) and numerous wildlife species. Two of bird species are well-known island endemics — the rare and endangered *Amazona vittata* (Puerto Rican Parrot) (photo 4) and *Dendroica angelae* (Elfin Woods Warbler) (SNYDER *et al.*, 1987).

The dwarf forest accounts for about one-sixth of the LEF's 2,270 ha of pristine forest. The summit areas, with < 10 % disturbed by communication facilities and roads, have survived with less impact from alien plants and human influence than the lowlands (OLANDER *et al.*, 1998). Numerous trails and vistas offer opportunities for hiking and photography (photo 5). Heavy rainfall and cloud moisture interception combined with low productivity and low consumptive use of water by the vegetation assure continuous stream flow to the surrounding lowlands. Also, dwarf forest represents a terminus, albeit limited in extent, along the LEF's elevational gradient for the possible migration of flora and fauna during global warming.

Conclusions

Dwarf forest is a distinct vegetation type adapted to survive in the rigorous environment of mountain summits. The type provides abundant, pristine water supplies for island residents and serves as critical habitat for flora and fauna, many endemic to Puerto Rico or the Luquillo Experimental Forest (LEF). Further human intervention should be restricted to best protect its resources and benefits.

Dwarf forest varies in structure. Stem densities on ridges and slopes average more than in ravines, and windward densities more than leeward densities. Canopy trees in ravines are taller than on ridges, and canopy trees to the leeward are taller than to the windward. Biomass varies considerably; however, biomass on ridges and slopes tends to be greater than in ravines, and leeward biomass averages more than windward biomass.

Many dwarf forest tree species grow successfully between 900 m and the LEF summits. Although the number of species tallied per plot varies little by topography, ravines contain slightly more total species than other topographic positions. Some species appear to survive better on windward or leeward aspects. Likewise, some species survive better on certain topographic positions, often favoring either ridges and upper slopes, or ravines and lower slopes. Only a couple of species appear to be well distributed topographically.

Acknowledgments

Juan Ramírez, Alberto Rodríguez, and Iván Vicéns helped with the field work. Danilo China, William A. Gould, and Frank H. Wadsworth reviewed earlier versions of the ms. Journal reviewers also made helpful comments on content and organization. This work was carried out in cooperation with the University of Puerto Rico at Río Piedras.

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