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Dwarf Forest Recovery after Disturbances in the Luquillo Mountains of Puerto Rico

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Abstract.—Dwarf forest in Puerto Rico's Luquillo Mountains varies according to substrate and topography with very short, dense forest growing on exposed, rocky sites. High elevation level sites suffered considerable damage during past hurricanes whereas the trees on certain lower slopes were protected by ridges or spurs. Post-disturbance recovery of dwarf forest on two types of sample plots near East Peak was slow. Nearly 37 years after a 1968 airplane crash, *Cyathea bryophila* (R. Tryon) Proctor and *Eugenia borinquensis* Britton accounted for 71% of the 25.3 t ha^{-1} total aboveground dry weight biomass (hereafter biomass) on 780 m^2 of the crash site. This is only 30% of the 80 t ha^{-1} average biomass of the surrounding dwarf forest prior to Hurricane Hugo of 1989. Also, six 250 m^2 permanent plots (stratified by topography with sites on ridges, slopes, and ravines) showed delayed post-hurricane mortality, declining in mean stem numbers from 2,956 stems ha^{-1} in 1990 to 2,268 stems ha^{-1} in 2005. Average plot biomass decreased from 72.8 t ha^{-1} in 1990 to 61.6 t ha^{-1} in 2000, increasing slightly to 62.9 t ha^{-1} in 2005. Recovery on all sites was characterized by an immediate invasion of grass cover along with an influx of ferns, followed by dicotyledonous seedlings and saplings, and finally small trees. More than one-half of the arborescent species growing in dwarf forest are endemic to Puerto Rico where they play a prominent role in post disturbance recovery; moreover, 85% of the trees do not exceed 15 m in height anywhere in the Luquillo Mountains.

Introduction

Cloud forests in the Caribbean grow on mountain summits that penetrate the base of trade wind cumulus clouds (Baynton 1968). Above 900 m in elevation in Puerto Rico's Luquillo Mountains, the arborescent vegetation is diminished in stature; moreover, close to the summits and nearby exposed ridges, it grows as a dwarf or elfin forest (Wadsworth 1951).

In 1968, a C-119 military plane crashed near East Peak, the easternmost summit in the Luquillo Mountains, clearing a swath estimated at 1000 m^2 (Byer and Weaver 1977). The day before the crash, a narrow foot trail was opened from the East Peak Road to a ridge within 50 m of where the plane fell. The crash and subsequent burning destroyed or damaged trees and disturbed the soil (Byer and Weaver 1977). Since that day in December of 1968, the plane wreck has become the major Luquillo Mountain site for the study of dwarf forest recovery after disturbance (Fig. 1). In addition, Hurricane Hugo of 1989 (also Georges of 1998) damaged much of the dwarf forest. In 1990, permanent plots were established near East Peak to observe post-Hugo recovery. The purpose of this paper is to report on the most recent monitoring of tree species composition and growth on previously disturbed dwarf forest sites.

Methods

The airplane wreck site and the permanent monitoring plots are in close proximity near East Peak. In 2005, the 780 m^2 wreck site used for previous sampling was partitioned into two areas based on canopy cover. Area one was dominated principally by mixed grasses and ferns <0.5 m tall, and area two by ferns and woody dicotyledons (woody dicots) ≥0.5 m tall. In the first area, five 1 m^2 (a 5.3% sample) samples of aboveground vegetation were harvested, partitioned into three classes (grasses, ferns, and the woody vine, *Marcgravia sintenisii* Urban), dried, and weighed. In the second area, stem diameters at ground level and total heights were recorded for all woody

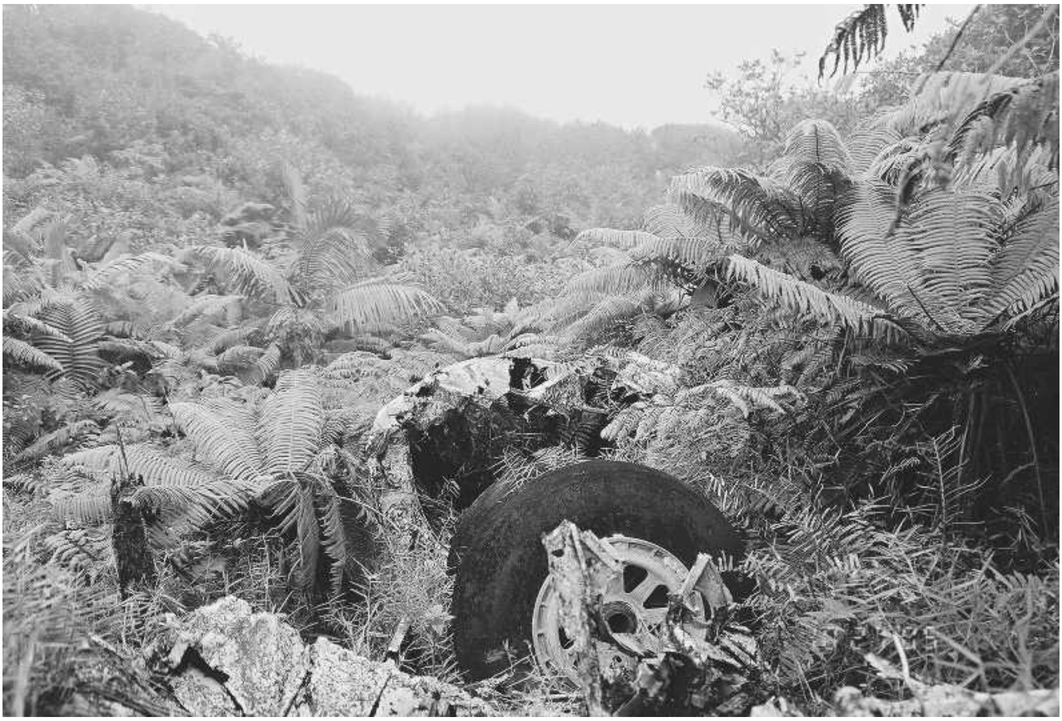

FIG. 1. Recovery of dwarf forest at the plane wreck site after 37 years. *Cyathea bryophylla* and *Eugenia borinquensis* are the dominant plants.

dicot stems between 0.5 and 2.0 m tall. Also, dbh (diameter at 1.4 m above the ground) and total height were recorded for woody dicot stems ≥2.0 m in height. Ferns and palm heights ≥0.5 m tall were also tallied. All heights were measured with a tape or an extension pole to the nearest 0.1 m, and all diameters were determined with a tape to the nearest 0.1 cm.

Biomass for area one was determined by extrapolating the means for grasses, ferns, and *Marcgravia sintinisii* to the entire area covered by low vegetation. Biomass in area two was estimated using the following equations: (A) for woody dicots without dbh, $\ln Y = -3.60 + 1.05 \ln X$ ($r^2 = 0.85$, $n = 20$) (Weaver 1990) where ln Y is equal to biomass in kilograms and ln X is equal to the ground level diameter squared times height (D^2H, cm^2, m); (B) for woody dicots with dbh, $Y = 0.2847\ D^{1.4417}$ ($r^2 = 0.72$, $n = 69$) when ≤4.0 cm in dbh, or (C) $Y = 1.3145 + 0.0323\ (D^2H)$ ($r^2 = 0.79$, $n = 47$) when ≥4.1 cm, where Y is the biomass in kilograms, D^2 is the bole dbh squared in centimeters, and H is the total height in meters (Weaver and Gillespie 1992); (D) for the palm *Prestoea montana*, $Y = 7.7X + 4.5$ ($r^2 = 0.90$) where Y is the biomass in kilograms and X is the height in meters (Frangi and Lugo 1985); and (E) for ferns, $Y = -1.09 + 3.00\ X$ ($r^2 = 0.91$, $n = 10$) where Y is the total biomass in kilograms and X is the total stem height in meters. The latter equation was derived from samples of *Cyathea bryophila*, which accounted for 92% of the ferns recorded on the wreck site.

The six dwarf forest permanent plots, each 10 x 25 m, were established in 1990 to follow forest development after Hurricane Hugo. All stems ≥4.1 cm in dbh (or 1.4 m above the ground) were sampled in 1990, 1995, 2000, and 2005. The plots were stratified by topography (i.e., two each on ridge, slope, and ravine topography). In 1995 and later, ingrowth ≥4.1 cm in dbh and mortality were tallied. Dicot and palm biomass was estimated using equations C and D above. Fern biomass was estimated with the relationship $Y = 3.82X - 3.62$ ($r^2 = 0.83$, n = 17) where Y is the total biomass in kilograms and X is the height of the fern in meters (Weaver 2000). Nomenclature followed that of local references (Liogier 1985-97; Liogier and Martorell 2002).

Mean dbh growth by species was determined for trees that survived 15 years on the permanent plots. Moreover, mean dbh growth was estimated for the largest trees (i.e., ≥4.1 cm in dbh) at the plane wreck by arbitrarily assuming that they had regenerated 25 years earlier. Between 1968 and 2005, the dwarf forest was visited on numerous occasions, notably the area between East and West Peaks and along the road to El Yunque Peak. Casual observations were always made regarding forest structure and growth, and after 1989, on hurricane impacts and recovery.

Results and Discussion

Airplane wreck

In 2005, 61% of the wreck site was in woody dicot cover, 27% in ferns, and 12% in mixed grass and scattered ferns. By comparison, the 1998 plot measurements showed 44% in woody dicots, 12% in ferns, 30% in mixed grasses and ferns, and 4% in airplane debris (Weaver 2000). Early estimates of cover and biomass are unavailable, but published photographs after 4.2 years (Byer and Weaver 1977) and 8.3 years (Weaver 2000) show the wreck site in a low cover of grasses and scattered ferns, with more ferns on the latter date.

Stems ≥0.5 m in height numbered 1,415 (18,141 ha^{-1}) in 2005, decreasing from 1,458 (18,692 ha^{-1}) in 1999 (Table 1). Stems ≥2.0 m

TABLE 1. Number of arborecent stems ≥0.5 m in height for the entire 0.078 ha wreck site after 37 years.

	Number of stems by height class (m)[1]						Biomass	
Species	0.5-1.9	2.0-3.9	4.0-5.9	≥6.0	Totals	Stems (%)	(kg)	(%)
Ferns								
Cyathea arborea	25	—	—	—	25	1.8	19.9	1.1
Cyathea bryophila	296	10	—	—	306	21.6	593.5	31.9
Subtotals	321	10	—	—	331	23.4	613.4	33.0
Palm								
Prestoea montana	3	2	—	—	5	0.4	97.7	5.2
Dicotyledons								
Alchornia latifolia	—	5	—	—	5	0.4	6.8	0.4
Calyptranthes krugii	2	10	—	—	12	0.8	5.2	0.3
Clidemia cymosa	1	2	—	—	3	0.2	1.0	0.1
Clusia clusoides	1	6	3	4	14	1.0	150.8	8.1
Eugenia borinquensis	206	452	55	1	714	50.5	714.9	38.4
Henriettea squamulosa	85	68	—	—	153	10.8	73.4	4.0
Ilex sintenisii	40	—	—	—	40	2.8	4.1	0.2
Miconia faveolata	4	9	—	—	13	0.9	19.7	1.1
Miconia pachyphylla	2	11	—	—	13	0.9	10.1	0.5
Miconia sintenisii	2	4	—	—	6	0.4	0.7	—
Micropholis garciniifolia	1	10	5	1	17	1.2	30.6	1.6
Ocotea spathulata	22	12	2	—	36	2.5	13.8	0.7
Psychotria berteroana	6	18	1	—	25	1.8	14.5	0.8
Tabebuia rigida	5	15	8	—	28	2.0	102.9	5.5
Subtotals	377	622	74	6	1079	76.2	1148.7	61.8
Totals	701	634	74	6	1415	100.0	1859.8	100.0
Totals (1999)[2]	1807	591	31	—	1458	100.0	1362.0	100.0
Totals (1986)[3]	1041	126	5	—	1172	100.0	359.2	100.0

[1]Dashes indicate no occurrences.

[2]Total values from 1999 (Weaver 2000) are provided for comparative purposes. The smallest category reported in that year (i.e., 0.15-1.0 m in height) contained 1660 plants of which 989 ranged from 0.5 to 1.0 m in height.

[3]Total values from 1986 (Weaver 1990).

(i.e., with a measurable dbh) totaled 714 (9,154 ha^{-1}) in 2005 and 622 (7,974 ha^{-1}) in 1998. In 2005, the wreck site had 65 woody dicots with a dbh ≥4.1 cm (the minimum dbh measured on permanent plots in the Luquillo Mountains), as follows: eight *Clusia clusioides* averaging 8.76 ± 0.86 cm (range 5.4-12.5 cm); 10 *Tabebuia rigida*, 6.82 ± 0.56 cm (range 5.1-11.4 cm); two *Henriettea squmulosa*, 5.20 ± 0.90 cm (range 4.3-6.1); five *Micropholis garciniaefolia*, 5.28 ± 0.34 cm (range 4.6-6.5 cm); and 40 *Eugenia borinquensis* averaging 5.15 ± 0.14 cm (range 4.1-8.0 cm). Two *Prestoea montana* and 10 *Cyathea bryophila* also attained 1.8 m in height and were tallied. The 77 stems yield a density of 987 stems ha^{-1}. The aforementioned 65 woody dicots would have had an average growth between 0.11 and 0.34 cm yr^{-1} had they all regenerated simultaneously 37 years ago. Evidence of numerous woody seedlings and saplings, however, was not apparent until the mid-1980s (Weaver 1990) in which case their regeneration would probably date to the early 1980s. Assuming that the oldest trees were 1.4 m tall 25 years ago, their average dbh growth today would be between 0.16 and 0.50 cm yr^{-1}.

In 2005, *Eugenia borinquensis* accounted for one-half of the stems and nearly 40% of the total biomass and *Cyathea bryophila* for nearly one-quarter of the stems and one-third of the biomass (Table 1). *Clusia clusioides*, *Tabebuia rigida*, and *Prestoea montana*, with only 3.4% of the stems, totaled nearly 20% of the biomass. In 1998, these species showed similar relationships. *Eugenia borinquensis* was common with 29% of the stems and 22% of the biomass, and *Cyathea bryophila*, with only 11% of the stems had 47% of the biomass (Weaver 2000). *Henriettea squamulosa*, with 36% of the stems, mainly in the smallest height class, accounted for only 3% of the biomass. *Clusia clusioides*, *Tabebuia rigida*, and *Prestoea montana* again had a disproportionately large amount of biomass for their combined stem density. Rapid dbh increment in the case of *Clusia* and *Tabebuia*, and stem form in the case of *Prestoea*, account for their proportionately greater biomass.

The average biomass recovery on the plane wreck was 25.3 t ha^{-1} after 37 years, and ranged from 13.6 to 43.6 t ha^{-1} on the 13 subplots (Table 2). If the average pre-hurricane biomass is assumed to be about 80 t ha^{-1} in this part of the dwarf forest (Table 3), recovery averages about 32% on the entire plot, and ranges between 17 and 54% on the subplots. The patchy recovery is partially due to differential disturbance when the plane crashed (Byer and Weaver

TABLE 2. Total aboveground biomass by subplots at the plane wreck site after 37 years.

Subplot	Biomass (kg)					Biomass (t ha^{-1})
	Dicots	Palm	Mixed	Fern	Total	
1	192.33	—	—	69.33	261.66	43.61
2	133.15	—	—	23.36	156.51	26.08
3	65.68	—	4.06	26.47	96.21	16.04
4	30.67	—	14.81	36.43	81.91	13.65
5	65.86	—	43.23	10.10	119.19	19.86
6	141.36	—	17.68	6.39	165.43	27.57
7	100.68	—	—	23.80	124.48	20.75
8	65.92	10.66	19.94	52.72	149.24	24.87
9	131.04	—	13.73	85.21	229.96	38.33
10	114.77	—	—	59.45	174.22	29.04
11	65.50	—	—	69.79	135.29	22.55
12	33.07	14.51	—	85.10	132.68	22.11
13	8.64	72.55	—	65.15	146.34	24.39
Totals	1148.67	97.72	113.45	613.30	1973.12	328.85
Means	88.36	7.52	8.73	47.18	161.78	25.30 ± 2.48

[1]Each subplot measures 5 by 12 m (total area = 780 m^2).
[2]Mixed = ferns + grasses + the vine (*Marcgravia sintenisii* Urban).

TABLE 3. Summary of stand composition changes on six permanent plots near East Peak from 1990 to 2005.[1]

	Stems (no. ha^{-1})				Aboveground total biomass (t ha^{-1})			
Tree species	1990	1995	2000	2005	1990	1995	2000	2005
Ferns								
Cyathea arborea	26.7	26.7	26.7	26.7	0.12	0.14	0.15	0.14
Cyathea bryophila	940.5	853.6	820.4	793.7	9.23	8.77	9.11	8.26
Subtotals	967.2	880.5	847.1	820.4	9.35	8.91	9.26	8.40
Palm								
Prestoea montana	73.4	73.4	86.6	133.4	4.09	5.02	5.25	6.81
Dicotyledons								
Calyptranthes krugii	133.4	120.1	133.4	133.4	0.57	0.43	0.50	0.51
Clusia clusoides	33.4	6.7	20.0	20.0	1.27	0.18	0.27	0.37
Cyrilla racemiflora	13.3	13.3	13.3	13.3	0.08	0.07	0.08	0.08
Eugenia borinquensis	286.8	246.8	246.8	253.5	7.25	5.09	5.33	5.56
Hedyosmum arborescens	26.7	6.7	—	—	0.26	0.10	—	—
Henriettea squamulosa	53.4	26.7	26.7	26.7	0.23	0.07	0.11	0.14
Magnolia splendens	53.4	33.4	40.0	40.0	15.27	16.00	16.36	16.36
Miconia pachyphylla	—	—	—	6.7	—	—	—	0.02
Micropholis garciniifolia	300.2	266.8	273.5	280.1	15.68	15.49	13.47	13.75
Myrcia deflexa	6.7	—	—	—	0.04	—	—	—
Ocotea spathulata	700.4	380.2	286.8	260.1	8.33	4.48	2.93	2.60
Psychotria berteroana	13.3	46.7	73.4	53.4	0.08	0.17	0.29	0.30
Tabebuia rigida	288.1	266.6	233.4	220.1	10.23	8.22	7.66	7.95
Torralbasia cuniafolia	6.7	6.7	6.7	6.7	0.04	0.04	0.04	0.05
Subtotal	1915.8	1420.9	1354.0	1314.0	59.33	50.34	47.04	47.69
Total	2956.2	2374.8	2287.8	2267.8	72.77	64.27	61.55	62.89

[1]Values rounded. Dashes indicate no data.

1977), and partially to the advance of woody seedlings and saplings from the surrounding forest toward the center of the wreck site (Weaver 1990).

Biomass increased continuously during the 37 years, averaging 0.68 t ha^{-1} yr^{-1} (Table 4). The 1977 estimate of biomass for the entire wreck site is unavailable; however, grasses and scattered ferns first dominated the site, followed by a massive influx of ferns, and then by woody dicots, which gradually shade and replace other plants. Fluctuations in the recovery rate probably reflect the dynamics among plant types. In addition, although the wreck site is largely protected by surrounding elfin woodland, it has probably suffered minor damage associated with hurricanes and delayed mortality afterwards (Weaver 1999, 2000).

Permanent plots

The post-Hurricane Hugo period showed immediate mortality resulting

TABLE 4. Biomass accumulation from 1968 through 2005 on the plane wreck site.

	Total biomass (t ha^{-1})			Biomass accumulation (t ha^{-1} yr^{-1})		
Plant class	1986	1998	2005	1968-86	1986-98	1998-05
Mixed[1]	2.00	1.78	1.47[2]	0.11	−0.02	−0.04
Ferns	2.43	10.75	7.86	0.14	0.69	−0.41
Palms	0.98	1.24	1.25	0.05	0.02	0
Dicots	2.35	8.33	14.72	0.13	0.50	0.91
Total	7.76	22.1	25.30	0.43	1.19	0.46

[1]Mixed = grasses and ferns ≤0.5 cm tall.
[2]Includes grasses + ferns + vine (*Marcgravia sintenisii* Urban).

from storm impacts, and a delayed mortality after the storm. Since measurements did not commence for a little more than 1 yr after the storm, the amount of storm damage was uncertain but appeared to average about 10%. Between 1990 and 1995, the average stem density declined by nearly 20%, and by 2005, slightly more than 23% (Table 3). Woody dicots suffered the greatest 15-year losses, decreasing by more than 31% while ferns declined by slightly more than 15%. In 2000, after Hurricane Georges, >40% of all sampled arborescent stems were either leaning or prostrate, notably the ferns. Fallen stems may remain alive for several years, and in the case of woody dicots, often form an impenetrable tangle of branches, some of which later grow into new trees.

Biomass varied considerably by species, plot, and date. In 1990, five species, *Cyathea bryophila*, *Eugenia borinquensis*, *Magnolia splendens*, *Ocotea spathulata*, and *Tabebuia rigida*, accounted for nearly 70% of the biomass (Table 3). By 2005, virtually all species had declined in biomass, notably *Ocotea spathulata*. Only *Prestoea montana* had increased in biomass.

Biomass for all 6 plots averaged 72.8 t ha^{-1} in 1990 and 62.9 t ha^{-1} in 2005 with plot values ranging from 111.5 t ha^{-1} on one ravine site in 1990 to 21.8 t ha^{-1} on one slope site in 2005 (Table 5). The average biomass for the ravine plots was greater than the average for either slopes or ridges.

The 5-yr mean annual total biomass change (1990 to 1995) for all plots combined averaged −1.70 t ha^{-1} yr^{-1}, and the 15-year change (1990 to 2005) averaged −0.66 t ha^{-1} yr^{-1} (Tables 3 and 5). In general, the 15-year biomass losses were proportionately greatest on ridges and least in ravines (Table 5). The 5-year period (2000-2005), however, showed a slight mean annual gain of 0.3 t ha^{-1} yr^{-1}. Palm biomass increased on the ravine plots, accounting for 85% of the positive increment for all plots combined (Tables 3 and 5). Palms, with their comparatively large diameters, contribute significantly to biomass in a dwarf forest full of small dimension woody dicots; *Cyathea bryophila*, also comparatively large in diameter, is abundant, and may grow for considerable distances leaning or prostrate.

Mean dbh increment rates for stems that survived the entire period varied from 0 for *Calyptranthes krugii* and *Cyrilla racemiflora* to 0.08 cm yr^{-1} for *Eugenia borinquensis* (Table 6). The mean increment for the 163 surviving stems of 10 species combined was 0.03 cm yr^{-1}. This is the same mean value that was determined from 1976 to 1981 for 62 stems of six dwarf forest species in the same vicinity (Weaver 1983). Dbh growth

TABLE 5. Total aboveground biomass for six dwarf forest permanent plots Near East Peak.

	Total aboveground biomass (t ha^{-1})		Biomass change 1990-2005 (t ha^{-1})	
Topography (sites)[1]	1990	2005	Ingrowth[3]	Mortality[4]
Ridge (wreck)	46.97	34.05	3.18	17.59
(road)	71.01	52.17	0.49	27.88
Slope (wreck)	43.58	21.79	2.37	26.60
(road)	84.66	87.26	2.43	5.39
Ravine (wreck)	111.46	103.00	8.23	30.53
(road)	78.68	78.92	8.07	20.55
Mean[5]	72.8 ± 10.3	62.9 ± 13.0	4.1 ± 1.3	21.4 ± 3.8
Dicots	59.3 ± 7.6	47.7 ± 10.3	1.4 ± 0.4	17.6 ± 3.2
Ferns	9.3 ± 5.0	8.4 ± 4.3	0.7 ± 0.3	3.2 ± 1.6
Palms	4.1 ± 2.7	6.8 ± 4.8	2.1 ± 1.4	0.6 ± 0.6

[1]Sites: wreck = near airplane wreck; road = near East Peak road.
[2]Standing biomass values adjusted for ingrowth and mortality.
[3]Total surviving biomass in 2005 due to ingrowth.
[4]Total biomass lost by mortality between 1990 and 2005 including both the original stems and ingrowth that died before 2005.
[5]Mean and standard error for all six plots. Total mean values were 64.2 ± 13.6 in 1995 and 61.5 ± 12.5 in 2000.

TABLE 6. Dbh growth rates of tree species on East peak for all stems that survived from 1990 to 2005.

Tree species	Dbh growth rates[1] Mean ± SE, N (cm yr^{-1})
Calyptranthes krugii	0.00 ± 0.01, 15
Clusia clusoides	0.07 ± 0.00, 1
Cyrilla racemiflora	0.00 ± 0.00, 2
Eugenia borinquensis	0.08 ± 0.01, 32
Henriettea squamulosa	0.07 ± 0.03, 2
Magnolia splendens	0.07 ± 0.00, 5
Micropholis garciniifolia	0.03 ± 0.00, 38
Ocotea spathulata	0.01 ± 0.00, 36
Tabebuia rigida	0.02 ± 0.01, 31
Torralbasia cuniafolia	0.00 ± 0.00, 1
Total	0.03 ± 0.00, 163

[1]All values for the period 1990-2005, rounded. Se = standard error and N = number of stems.

in mature dwarf forest is slow; moreover, residual stems do not appear to respond positively to a decrease in stem density caused by the hurricanes, at least during a 15-year period. The reduction in stem density, however, was mainly in the smallest dbh classes and not in the larger canopy trees (Weaver 1999).

Other observations

One explanation suggested to account for dwarf forest is that the arborescent species growing there do not attain large size. Of the 54 species most frequently associated with the dwarf forest, only eight (about 15%) regularly approach 15 m or more in height at lower elevations (Appendix Table A). They are *Cyrilla racemiflora*, *Henriettea squamulosa*, *Magnolia splendens*, *Micropholis garcinaefolia*, *Ocotea spathulata*, *Prestoea montana*, and *Ternstroemia luquillensis* as components in mature forest, and *Cecropia schreberiana* on disturbed sites. *Cecropia* is an opportunist, *Ternstroemia* is rare, *Cyrilla* and *Magnolia* are uncommon, *Henriettea* and *Prestoea* are common, and *Micropholis* and *Ocotea* are abundant. The remaining abundant species, *Cyathea bryophila*, *Eugenia borinquensis*, and *Tabebuia rigida*, rarely reach 10 m in height anywhere in the Luquillo Mountains (Appendix Table A). Another 19 species more common at lower elevations have been recorded during surveys (Appendix Table A, bottom group). These species do not attain large size in the dwarf forest. Most arborescent species in the dwarf forest are small; however, the forest does contain a few species that reach greater heights at lower elevations in the Luquillo Mountains. Most notable among these is *Magnolia splendens*.

The 18 tree species with ≥10 individuals in the dwarf survey accounted for nearly 99 % of the stems tallied; moreover, the nine species with ≥50 individuals accounted for nearly 92% (Appendix Table A). In addition, 30 of the tree species listed for dwarf forest are endemic to Puerto Rico, 21 of those to the island and nine solely to the Luquillo Mountains (Appendix Table A, top group). Cloud forests are known as places of high endemism but not necessarily as areas with rich biotas (Lewis 1971, Myers 1969). During the 1920s, taxonomists exploring the Luquillo Mountains reported a great number of endemic species, many of which were later discovered elsewhere or were found synonymous by monographers (Howard 1968). Despite recent research, high endemism still characterizes dwarf forest trees, notably so during recovery at the plane wreck site (Weaver 2000).

Substrate and topography are among the most important factors allowing the survival of dwarf forest trees during hurricanes. Some very exposed areas are covered with short, dense dwarf forest. Among the most notable patches are around El Yunque Rock and Los Picachos, and the east-facing exposure below Mt. Britton. The roots of dwarf forest trees at these sites are securely anchored in rocks.

Other extremely exposed areas, for example, much of the strip >975 m between East and West Peaks, appears to have suffered considerable damage during the most recent hurricanes, including the ridge to the airplane wreck. During the late 1960s, a couple of large patches of grass were observed along the trail to the wreck; these patches are still evident today, although ferns and woody dicots have invaded. A few surviving trees with damaged crowns 2 to 3 m above the current regeneration are evidence of the past canopy height along the trail (Fig. 2). The explanation for this

FIG. 2. Highly disturbed dwarf forest on the trail to the airplane wreck. Remnant trees indicate the height of canopy dominants before the recent hurricanes.

heavy damage is not entirely clear but may be related to the prolonged exposure of upland level areas to high winds during hurricanes. In mountainous Dominica, forest growing on high elevation level lands suffered more from Hurricane David than forest on other topographies (Lugo et al. 1983). Similar observations were made after Hurricane Hugo in the much drier forests of Cinnamon Bay watershed, St. John, U.S. Virgin Islands (Weaver 1998).

There are some protected areas in dwarf forest, albeit extremely small, with taller trees. These areas are usually on lower slopes to the leeward of ridges or spurs. One small patch at 980 m in elevation, east of the ridge road to El Yunque, has four *Eugenia borinquensis* nearly 10 m in height and from 17.0 to 24.2 cm in dbh. Most *Eugenia borinquensis* growing above 975 m on East Peak or West peak are short and scrubby in appearance. A *Magnolia splendens* with a dbh of 78 cm also grows on the site, surviving with a damaged crown. This tree may be approaching 500 years old (Weaver 1987).

A complete recovery of the relatively small wreck site would involve attaining typical mature forest conditions in biomass, forest structure (i.e., a mixture of stem sizes), and species composition, as well as typical stand dynamics. Biomass recovery was projected to take about 200 years (Weaver 2000). The small stature of dwarf forest means that trees have to grow less to attain typical structural dimensions than in lower forests (Table 7). In addition, relatively few tree species are common in the dwarf forest and they are already present on the wreck site (Tables 1, 4, Appendix A). Earlier observations showed that disturbed dwarf forest sites might recover without passing through intermediate stages since secondary tree species adapted to summit conditions appeared to be lacking (Byer and Weaver 1977). Under such conditions, recovery on the wreck site could largely coincide with the accumulation of the original

TABLE 7. Comparison of typical structural and stand dynamics data in four forests of the Luquillo Mountains.[1]

Parameter	Forest type			
	Lower montane	Montane	Palm	Dwarf
Elevation range of forest (m)[2]	150-600	600-900	150-900	>900
Structure: pre-Hurricane Hugo				
Canopy height (m)[3]	20-30	8-20	17	3-5
Dbh range (cm)[3]	4-50	4-30	4-30	4-15
Aboveground woody biomass (t ha^{-1})[3,4]	190-226	130	174	80
Hurricane Hugo losses (damage)				
Aboveground woody biomass (t ha^{-1})[4]	113	NA	16	~20
Proportion of pre-storm biomass (%)[4]	50	NA	10	~25
Dynamics: pre-Hurricane Hugo				
Dbh growth (cm yr^{-1})[3,5]	0.09-0.14	0.10	0.23	0.03
Volume accumulation (m^3 ha^{-1} yr^{-1})[5]	0.85-2.63	0.48-1.44	0.07	NA
Biomass accumulation (t ha^{-1} yr^{-1})[3]	2.50	0.57	3.30	0.45
Net primary productivity (t ha^{-1} yr^{-1})[3]	10.5	7.6	19.5	3.7
Post-Hurricane Hugo recovery				
Biomass accumulation (t ha^{-1} yr^{-1})[6]	12.8	NA	9.2	−1.3

[1]Data are for different sites and periods. Forest structure, composition, and growth vary in space and time, and hurricane damage varies over short distances. NA indicates that information was not available.
[2]Source: Wadsworth 1951.
[3]Source: All forests (Weaver and Murphy 1990); also, Lower montane (Scatena et al. 1996) and Palm (Frangi and Lugo 1985).
[4]Sources: Lower montane (Scatena et al. 1996); Palm (Frangi and Lugo 1998); Dwarf (Weaver, this paper). The estimated sum for damage includes both immediate and delayed mortality.
[5]Source: Weaver 1983. Estimates were made from 1946 to 1976 except for dwarf forest which was from 1976 to 1981.
[6]Sources: Lower montane (Scatena et al. 1996); Palm (Frangi and Lugo 1998); Dwarf (Weaver, this paper). Estimates were for 1989 to 1995 except for dwarf forest which was from 1990 to 2005.

biomass. Longer recovery times could be associated with particular site conditions. One example would be cases where disturbed sites had contained large specimens of *Cyrilla racemiflora* or *Magnolia splendens* which could take three or four centuries to grow back to their pre-storm dimensions. Another example would be where disturbance leads to the formation of alpine meadows which may persist for an undetermined period.

Comparisons of forest recovery among forest types in the Luquillo Mountains are complicated by several factors including site variables and the duration of observations (i.e., a few years vs. >50 years in some cases). Site variables include the nature and size of the disturbance (i.e., airplane wreck, hurricane damage, or past agricultural activities such as farming and grazing) and the environmental setting (i.e., elevation, aspect, topography, and exposure). In general, the rates of growth and recovery decrease with an increase in elevation (Table 7). Palms, however, appear less prone to wind damage than dicotyledonous trees, and commonly abound in depressions or valleys where tree growth is often more rapid than in other topographic positions (Frangi and Lugo 1998; Weaver 1989).

SUMMARY

The recovery of dwarf forest after disturbance is slow. On the wreck site, species dominated in stages. For the first 10 years, a low, dense growth of grasses and ferns accounted for most of the stems and biomass (Weaver 2000). During the next 10 years, *Cyathea bryophila* dominated along with grass as seedlings of 15 woody dicots entered, notably *Eugenia borinquensis* and *Henriettea squamulosa.* During the following

15 years, woody dicots became more prominent as grass cover and many ferns declined as the canopy closed. Grasses and ferns, however, will persist in small canopy openings and will colonize again in response to disturbance. On the permanent plots, Hurricane Hugo killed several trees before monitoring began. Grasses soon entered openings in abundance along with scattered ferns. From 1990 to 2005, delayed mortality exceeded ingrowth and stem numbers and biomass declined. After 15 years of monitoring, only *Prestoea montana* showed major gains in biomass.

The dwarf forest varies in structure and composition and is well-adapted to the summits of the Luquillo Mountains. Most arborescent species are small with only 15 % growing to 15 m in height anywhere in the Luquillo Mountains; moreover, more than one-half are endemic to the island, and play a prominent role during the recovery process. Some of the shortest, densest, and most persistent high elevation patches of dwarf forest occur where trees are anchored in exposed, rocky substrates. In contrast, the tallest trees persist on middle to lower slopes protected by nearby ridges or spurs. Much of the dwarf forest on relatively level ridges with deeper soils is currently in stages of recovery from past hurricane disturbance. These areas are characterized by a mixture of vegetation including: small patches dominated by grasses and ferns; fallen trees, some with trunk sprouts; remnant stems, many exposed and severely damaged and others largely intact; and scattered, dense regeneration.

The slow growth of mature dwarf forest, notably on ridges and upper slopes, assures that recovery will take a couple of centuries and would likely be interrupted by the passage of another major hurricane. In some clearings like the plane wreck, however, individual specimens of *Clusia clusioides* and *Tabebuia rigida* may initially increase rapidly in dbh before surrounding competition slows growth rates.

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APPENDIX TABLE A. Dwarf forest arborescent species (54) and lower montane species (19) of the Luquillo Mountains tallied during numerous surveys of dwarf forest vegetation. Abundances are given numerically or subjectively, according to the source.[1]

	Dimensions[2]									
Species	Height (m)	Dbh (cm)	Occur[3]	Status[4]	Dwarf survey[5]	Mt. Britton[6]	Picachos[6]	West Peak[6]	West Peak[7]	East Peak[8]
Dwarf Forest arborescent species										
Ferns										
Cyathea arborea (L.) J. E. Smith	10	12	C		43	1	43			C
Cyathea bryophila (R. Tryon) Proctor	5	15	C	PR	421					A
Conifer										
Podocarpus coriaceus L. C. Rich.	9	25	R							
Palm										
Prestoea montana (R. Graham) Nichols	15	20	A		135	5	15			C
Dicotyledons										
Ardisia luquillensis (Britton) Alain	5	10	R	LM	10		1	1	O	
Brunfelsia lactea Krug & Urban	6	10	R	PR						
Calyptranthes krugii Kiaersk.	5	8	C	PR	61					
Calyptranthes portoricensis Britton	4	8	R	PR						
Calyptropsidium sintensii Kiaersk.	8	15	R	PR						
Cecropia schreberiana Miq.	22	60	O		5				R	
Cestrum marophyllum Vent.	6	8	C							
Citharexylum cauatum L.	9	20	U		3					R
Cleyera albo-punctata (Griesb.) Krug & Urban	12	30	R						O	
Clibadeum erosum (Sw.) DC.	6	8	O							O
Clidemia cymosa (Wendl.) Alain	4	8	C	PR						U
Clusia clusioides (Griesb.) D'Arcy	12	30	C		76	6		7	O	C
Clusia minor L.	6	12	C							
Coccoloba swartzii Meisner	12	20	U							
Cybianthus sintenisii (Urban) Agostini	4	10	R	LM	1					R
Cyrilla racemiflora L.	15	90	C		30					U
Daphnopsis philippiana Krug & Urban	6	10	C	PR	43				R	U
Eugenia borinquensis Britton	8	20	A	PR	432	92	26			A
Haenianthus salicifolius Grised.	13	20	C		48		1		R	
Hedyosmum arborescens Sw.	6	10	C		7				O	U
Henriettea squamulosa (Cogn.) Judd.	15	30	A	PR	357	90	2	2	C	A

APPENDIX TABLE A. Continued.

Species	Dimensions[2] Height (m)	Dbh (cm)	Occur[3]	Status[4]	Dwarf survey[5]	Mt. Britton[6]	Picachos[6]	West Peak[6]	West Peak[7]	East Peak[8]
Ilex macfadyenii (Walp.) Rehder	12	25	R							
Ilex sintenisii (Urban) Britton	5	8	R	PR	4				O	R
Magnolia splendens Urban	23	120	C	LM	22				R	U
Marliera sintenisii Kiaersk.	6	15	R	LM						
Mecranium latifolium (Cogn.) Skean	8	12	C		1				O	R
Miconia faveolata Cogn.	4	8	C	LM					C	C
Miconia pachyphylla Cogn.	6	12	U	PR	8				C	U
Miconia pycnoneura Urban	4	0.08	U	PR					I	
Miconia sintenisii Cogn.	8	10	U	PR	5				R	U
Micropholis garciniifolia Pierre	15	50	A	PR	362	38	31	12	O	A
Myrcia fallax (A. Rich.) DC.	9	15	U	PR	3					R
Ocotea spathulata Mez	14	50	A		565	79		28	D	A
Ouratea striata (v. Tiegh) Urban	4	15	R							
Palicourea croceoides W. Hamilton	4	5	C		33					
Piper blatarum Spreng.	4	8	U	PR						
Psidium sintenisii (Kiaersk.) Alain	8	15	R	PR						
Psychotria berteroana DC.	6	10	C		12				C	C
Rhamnus sphaerosperma Sw.	6	8	R							
Schefflera gleasonii (Britton & Wilson) Alain[9]	5	8	R	PR						
Solanum nudum HBK ex Dunal	6	10	O							
Symplocus micrantha Krug & Urban	9	15	R	PR					R	
Tabebuia rigida Urban	9	20	A	LM	844	287	35	31	D	A
Ternstroemia heptasepala Krug & Urban	8	12	R	LM						
Ternstroemia luquillensis Krug & Urban	20	25	R	LM	2					R
Ternstroemia subsessilis (Britton) Kobuski	6	8	R	PR						
Torralbasia cuneifolia (C. Wright) Krug & Urban	10	20	U		14				O	R
Turpina occidentalis (Sw.) G. Don.	9	15	U							
Wallenia lamarckiana (A. DC.) Mez	3	8	R	PR						
Xylosma schwaneckeanum (Krug & Urban) Urban	8	8	R	PR	3					R
Subtotals					**3550**	**598**	**154**	**81**		

Appendix Table A. Continued.

Species	Dimensions[2] Height (m)	Dimensions[2] Dbh (cm)	Occur[3]	Status[4]	Dwarf survey[5]	Mt. Britton[6]	Picachos[6]	West Peak[6]	West Peak[7]	East Peak[8]
Lower elevation arborescent species tallied in Dwarf Forest surveys										
Alchornea latifolia Sw.	13	38	C							R
Byrsonima wadsworthii Little	12	20	R	PR	2					
Chionanthus domingensis Lam.	18	25	U		2	4	1			
Cordia borinquensis Urban	9	12	C	PR	25	1			R	U
Croton poecilanthus Urban	9	25	A	LM	11					U
Ditta myricoides Griseb.	11	15	U		5					R
Eugenia stahlii (Kiaersk.) Krug & Urban	18	25	U	PR			1			
Ilex nitida (Vahl.) Maxim	13	35	U		3					
Ilex sideroyyloides (Sw.) Griseb.	12	18	R							R
Miconia laevigata (L.) DC.	8	15	C		2					
Miconia tetrandra (Sw.) D. Don	18	30	C		1					R
Micropholis guyanensis (A. DC.) Pierre	18	60	A		1					
Myrcia deflexa (Poiret) DC.	8	15	C		1					R
Ocotea leucoxylon (Sw.) Lanessan	15	25	A		10					R
Ocotea portoricensis Mez	15	25	U	PR	2					
Psychotria maleolens Urban	3	8	C	PR						R
Rondeletia portoricensis Krug & Urban ex Urban	8	15	C	PR					O	
Sapium laurecerasus Desf.	18	60	C	PR	2					
Trichilia pallida Sw.	9	15	C						I	R
Subtotals					**67**	**6**	**2**	**0**		
Totals					**3617**	**603**	**156**	**81**		

[1]Species in the top group are generally recognized as species that occur in the dwarf forest (i.e., above 900 m in elevation). Those in the lower group are common at lower elevation, but were tallied during surveys of the dwarf forest. Blanks indicate that the species were not recorded during the cited surveys.

[2]Dimensions: common sizes that may be attained by the species anywhere in the Luquillo Mountains.

[3]Occurrence: classes apply to trees growing anywhere above 150 m in the Luquillo Mountains. A = abundant, C = common, U = incommon, R = rare (Little and Wadsworth 1964; Little et al. 1974).

[4]Status: PR = endemic to Puerto Rico; LM = endemic to Luquillo Mountains.

[5]Arborescent species with dbh ≥4.1 cm recorded during surveys of dwarf forest plots on El Yunque, East Peak, and West Peak (Weaver, unpublished data).

[6]Independent surveys for all arborescent species with dbh ≥10 cm (reported in Weaver et al. 1986).

[7]Arborescent species reported for West Peak (Howard 1968): A = abundant, C = common, D = dominant, I = infrequent, O = occasional, R = rare.

[8]Arborescent species reported for East Peak: A = abundant, C = common, O = openings (roadsides), U = uncommon, R = rare (Weaver 1972, 1983, 1990, 2000, this paper; Weaver et al. 1986).

[9]Very rare; recorded near East Peak in November 1968.