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Impacts of Hurricane Hugo on the Dwarf Cloud Forest of Puerto Rico's Luquillo Mountains

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ABSTRACT.—Stratified sampling by topography in the dwarf cloud forest of the Luquillo Experimental Forest indicated that many common tree species showed topographic preferences, favoring either ravines or slopes and ridges. Delayed post-hurricane mortality (≥1.3 and ≤6.3 yrs) on permanent plots established after the passage of Hurricane Hugo in September 1989 reduced the number of stems on Pico del Este by 21%, most notably impacting the smallest dbh and height classes on ridges. Mortality varied by species, with the palm *Prestoea montana* (R. Grah.) Nichols showing the best survival and the tree *Clusia clusoides* (Griseb.) D'Arcy the poorest. Regressions of epiphytic biomass expressed as a function of bole dbh or crown area did not correlate as well in post-hurricane conditions as they did in pre-hurricane conditions. Although total litterfall was virtually the same, the leafy fraction declined and the woody fraction increased. Tree mortality decreased aboveground biomass after the storm. Total aboveground net primary productivity sampled from 1.3 to 2.3 yrs after Hugo was 20% greater than before the storm when a 5-yr estimate of average coarse debris (from 1.3 to 6.3 years post-hurricane) was added.

RESUMEN.—Un muestreo estratificado por topografía en el bosque enano nublado del Bosque Experimental de Luquillo, indicó que muchas especies de árboles comunes demostraron preferencias topográficas, favoreciendo hondonadas o pendientes y cerros. La mortalidad retrasada pos-huracán (≥1.3 y ≤6.3 años) en parcelas permanentes establecidas después del huracán Hugo en septiembre 1989, redujo el número de tallos en Pico del Este en un 21%, un efecto que fue más evidente en las clases más pequeñas de d.a.p. y altura en los cerros. La mortalidad varió por especies, con la palma *Prestoea montana* (R. Grah.) Nichols mostrando la mejor sobrevivencia y el árbol *Clusia clusoides* (Griseb.) D'Arcy la peor. Las regresiones de la biomasa epifítica, derivadas como una función del d.a.p. del tronco o del área de la copa, correlacionaron menos después del huracán que antes. Aunque la caida de hojarasca quedó casi igual, la proporción frondosa se redujo y la proporción maderera aumentó. La mortalidad de árboles disminuyó la biomasa sobre el terreno después de la tormenta. La productividad total sobre el terreno, muestreada entre 1.3 a 2.3 años después de Hugo, fue 20% mayor que antes de la tormenta cuando se añadió un estimado promedio bruto de detrito leñoso de un período de 5 años (eg., entre 1.3 y 6.3 años después de la tormenta).

INTRODUCTION

Tropical montane cloud forests are found in the Americas, Africa, and Asia, and scattered throughout the summits of the East and West Indies. These forests are usually remote, invariably humid, enveloped in clouds much of the time, and frequently cool and windswept (Kerfoot 1968; Stadtmüller, 1986). A recent bibliography listed 426 references on tropical cloud forests, about 10% of which concerned Puerto Rico's Luquillo Experimental Forest (LEF) (Hamilton et al., 1993; Watt et al., 1993) which contains the best studied montane cloud forests in the world.

Although the initial investigations of the LEF's flora and ecology began in the early 20th century, it is only within the past 30 years that ecological studies have been undertaken in the dwarf [elfin] cloud forest, hereafter called dwarf forest. These studies include more than 3 years of climatic observations on El Yunque (Briscoe, 1966), 17 studies of the flora and dwarf forest environment on Pico del Oeste between 1968 and 1977 (see Howard, 1968; Foerster, 1971; Fulford et al., 1970, 1971; Russel and

Miller, 1977), and studies of cloud moisture interception, transpiration rates, biomass increment, and succession near Pico del Este (Weaver, 1972a, 1990; Weaver et al., 1973, 1986; Byer and Weaver, 1977).

The main objectives of this study are to: (1) describe the variation in tree species composition by topography in the dwarf cloud forest; (2) compare forest structure, epiphyte loads, and forest dynamics after Hurricane Hugo of 1989 with pre-hurricane data from the same locality; and (3) relate dwarf forest monitoring to similar research in the LEF's other forest types.

The Dwarf Forest Setting

The Luquillo Mountains of northeastern Puerto Rico rise to 1075 m within 8 km of the ocean. The forest types (Beard, 1944, 1949) are classified as lower montane below 600 m, montane between 600 and 900 m, and dwarf forest on the summits, with palm brake scattered on steep slopes and in ravines. Locally, these forest types are called tabonuco, colorado, dwarf, and palm, respectively. More recently, the forest types were classified according to the Holdridge (1967) life zone system in which subtropical wet, subtropical rain, subtropical lower montane wet, and subtropical lower montane rain forests occupy most of the LEF (Ewel and Whitmore, 1973). The summits above 900 m, or dwarf forest, are classified as an atmospheric association within the subtropical lower montane rain forest.

The summit vegetation is short, dense, frequently contorted, covered with epiphytes including bromeliads, mosses, and liverworts, and contains relatively few tree species when compared to lower elevation forests. Rainfall on the summits is mainly orographic at night and convective during the day (Baynton, 1969) with easterly waves, cold fronts, tropical depressions, and tropical storms, and hurricanes as major rain-producing mechanisms. Annual rainfall on the summits averages 4500 mm (Briscoe, 1966; Baynton, 1968; Weaver, 1972a). The peaks, enveloped in clouds much of the time, only receive about 60% of the solar insolation recorded in coastal areas (Briscoe, 1966; Baynton, 1969). Cloud droplets, filtered by trees and epiphytes, add about 10% more moisture to the soil surface than annual rainfall alone (Baynton, 1968; Weaver, 1972a).

The mean annual temperature on the summits is 18°C, ranging from about 16°C in January to 20°C in October (Briscoe, 1966; Baynton, 1968). Mean relative humidity is high, averaging 98% for the year with minima occurring during the early afternoon. Transpiration rates of canopy leaves are low (Gates, 1969; Weaver et al., 1972a; Weaver, 1975) and evaporation is low as radiation, temperature, and vapor pressure deficits are all reduced (Hamilton et al., 1993).

Wind velocity on nearby El Yunque peak ranges from an average of 9.2 km/hr during November to 25.0 km/hr during July (Briscoe, 1966). Gusts as high as 110 km/hr have been measured on the summits during periods of normal winds elsewhere on the island (Wadsworth, 1948). Hurricanes have traversed over or very near the summit vegetation at least five times between 1766 and 1989, the last major storm being Hurricane Hugo in September of 1989 (Weaver, 1994a). These five hurricanes along with other storms with more distant trajectories have influenced forest structure and composition throughout the LEF.

Methods

In December of 1990 and 1995, all stems ≥4 cm in dbh (or 1.4 m above the ground) were sampled on 6 plots within the dwarf forest. The plots, 10 × 25 m, were stratified into 2 groups of 3 (i.e. on ridge, slope, and ravine topography) at slightly over 1000 m. All stems were identified to species, tagged, and their heights and dbhs were measured to the nearest 0.1 m and 0.1 cm, respectively.

Plot data on species composition from three other sampling sites in the LEF (Pico del Oeste, El Yunque, and El Toro) were combined with those from Pico del Este to produce a composite sample of 0.525 ha of dwarf forest above 900 m. Differences in species occurrence by topography were tested for all species with >25 individuals using chi-square (Freese 1980). Post hurricane differences in mortality for tree species with more than 4 individuals were tested using the G-statistic for independence (Sokal and Rohlf, 1981).

In January and February of 1990, five months after the passage of Hurricane Hugo, 31 dwarf forest trees of 4 species, varying from 7.1 to 29.9 cm in dbh, were selected to follow epiphyte recovery. These trees, located on exposed ridges or upper slopes near Pico del Este, were completely stripped of epiphytes by the storm. In February and March of 1991, all epiphytes, mainly bryophytes and small bromeliads, were removed from 17 of the pre-selected trees. Sampling was repeated on the remaining 14 trees in January and February of 1997. Tree heights, dbhs, crown diameters (the mean of the longest crown dimension and the perpendicular that bisects it), and crown areas were recorded before epiphyte removal on each sampling date.

Crown areas were estimated by using an extension pole to mark eight crown projections (each at 45°) on the ground with stakes, and then visually sketching on graph paper the crown edges between the stakes. Crown diameter-to-bole dbh ratios (CD/BD ratios) were then derived for each tree. Linear regressions were run for: crown diameter vs. bole dbh, total epiphytic biomass vs. bole dbh, and total epiphytic biomass vs. crown area.

Litterfall was collected biweekly from 20 litterfall traps of 0.25 m^2 from January 1, 1991 through December 31, 1991. These were located in the same site where pre-hurricane collections had been made (Weaver et al., 1986). All samples were oven dried and weighed, and data was grouped into 13 consecutive periods of 28 days. Loose litter was collected from 10 subplots of 0.25 m^2 during February, May, August, and October.

The total aboveground biomass for dicot species was estimated from the equation,

$$\ln Y = -3.478 + 1.008 \ln X, r^2 = 0.95$$

where Y is the biomass in kilograms and X equals D^2H where D is the bole dbh in centimeters and H is the tree height in meters (Weaver and Murphy, 1990).

The total aboveground biomass of the palm *Prestoea montana* (R. Grah.) Nichols was determined from the relationship,

$$Y = 7.7 X + 4.5, r^2 = 0.90$$

where Y is the total aboveground biomass in kilograms and X is the height of the palm in meters (Frangi and Lugo, 1985).

Due to the lack of information on the tree ferns *Cyathea arborea* (L.) J. E. Smith and *C. bryophila* (R. Tryon) Proctor, biomass sampling was conducted in March 1997. Entire ferns ranging from 1.0 to 11.2 m in height were cut, transported to the laboratory, oven dried, and weighed. Linear regressions of dry weight biomass vs. tree fern dbh were then developed. Plant nomenclature follows that of Liogier (1985-97) for dicots and Proctor (1989) for ferns.

RESULTS

Forest structure.—The mean dbh and height of all stems that survived from 1990 to 1995, were 10.1 cm and 4.9 m, respectively. The mean stem density in 1990, 2953 stems/ha, declined by an average of 21% for the 6 plots during the 5-yr period (Table 1). The greatest losses were recorded on the ridge plots. Ingrowth averaged 73 stems/ha, yielding an average density of 2320

TABLE 1. Changes in stem density from 1990 to 1995 in Pico del Este's dwarf forest after Hurricane Hugo[1].

	Topography			
	Ridge	Slope	Valley	Means
Parameter	stems/ha			
Stem density (1990)	3560	2700	2600	2953
Mortality (1990-95)	1100	600	420	707
Ingrowth (1990-95)	60	100	60	73
Stem density (1995)	2520	2200	2260	2320
Percent change	-29.2	-18.5	-13.8	-21.4

[1]Data for each topographic entry were derived from two stratified groups (ridge, slope and ravine) of 250 m^2 plots about 300 m apart.

stems/ha in 1995. Total mortality varied by size classes, with the greatest proportional losses in the smallest dbh and height classes on ridge topography (Table 2).

Tree fern sampling provided the following relationship,

$$Y = 4.46 X - 7.72, r^2 = 0.81, n = 13$$

where Y is the total aboveground biomass in kilograms and X is the total tree fern height in meters.

Total epiphyte biomass showed several positive correlations with bole dbh and crown area (Table 3). In all cases, Y is the total epiphytic biomass in grams and X is the tree dbh (cm) or the crown area (m^2).

The 1991 and 1996 epiphyte loads on small and large branches of the crown ranged from 21.6 to 86.5% of the total epiphyte load (crown + bole), averaging 70% for both years. In general, larger trees had proportionately greater crown loads, while smaller trees usually had either greater bole loads or a more even distribution of epiphyte loads. The mean CD/BD ratio was 16.7 ± 0.74 (n = 30). The linear regression of crown diameter vs. bole diameter was not significant.

Species composition.—Sixteen tree species were recorded on the six plots on Pico del Este: 13 dicots, two ferns and one palm (Table 4). Of the 443 individuals sampled in 1990, dicots comprised 65%, ferns 33%, and the palm 2%. Two species, *Cyathea bryophila* and *Ocotea spathulata* Mez accounted for 55% of the stems tallied. *Prestoea montana* was confined to ravines, where 65% of the ferns were also sampled. Only 3% of the tree ferns were tallied on ridges. Dicots, in contrast, comprised nearly 98% of the stems on ridges.

Of the trees that perished between 1991 and 1996 (Table 4), the greatest losses were recorded for *Ocotea spathulata* and *Cyathea bryophila*, the most common species. Significant differences in mortality were observed for the 12 species tested (Table 4). *Prestoea montana* was the most resistant and *Clusia clusoides* (Griseb.) D'Arcy the most prone to post-hurricane mortality.

The tree species composite of four dwarf forest areas showed 2331 stems of 30 species with a mean density of 4440 stems/ha (Table 5). Slope and ridge plots, with 5274 and 5006 trees/ha, respectively, were denser than ravine plots with 3030 stems/ha. Of the 30 species tallied, five accounted for more than 73% of the total stems; the 16 least common species, with fewer than 10 individuals, accounted for 2.6% of the stems (Table 5). Moreover, many of the species showed topographic preferences.

Forest dynamics.—The mean annual dbh increment for the 201 surviving dicot stems during the 5-yr period was 0.024 cm/yr. The mean annual dbh increments for the four most common species accounting for

TABLE 2. Structure of Pico del Este's dwarf forest in 1990 and 1995.

	Stems in 1990 and percent decline in 1995 by topography							
	Ridge		Slope		Valley		Totals	
Parameters	No.	%	No.	%	No.	%	No.	%
Dbh classes (cm)								
4.1-9.9	124	36.3	96	20.8	63	17.5	283	-26.7
10.0-14.9	41	22.0	20	20.0	33	24.2	94	-22.2
15.0-19.9	9	—	9	44.4	23	4.4	41	-12.2
>20.0	4	25.0	10	10.0	10	10.0	24	-12.5
Totals	178	30.9	135	22.2	130	16.2	443	-23.9
Height classes (m)								
<2.9	22	63.6	48	20.8	19	26.3	89	-32.6
3.0-4.9	75	28.0	26	30.8	58	8.6	159	-21.4
5.0-6.9	66	28.8	39	20.5	33	21.2	138	-24.6
7.0-8.9	15	6.7	12	25.0	13	23.1	40	-17.5
9.0-10.9	—	—	10	10.0	7	14.3	17	-11.8
Totals	178	30.9	135	22.2	130	16.2	443	-23.9

TABLE 3. Equations for prediction of total epiphyte biomass load in dwarf forest.

Factor Year	Equation[1]	r^2	n	Range of Values
Crown area (m^2)				
1969	$Y = 407.0 X$	0.96	21	1.0-28.0
1991	$Y = -103.1 + 146.4 X$	0.77	17	1.0-15.1
1997	$Y = -71.9 + 186.0 X$	0.73	14	0.8-17.0
Bole dbh (cm)				
1969	$\log Y = 0.088 X + 1.96$	0.85	21	1.6-30.0
1991	$\log Y = 0.036 X + 1.96$	0.28	17	7.1-29.9
1997	$\log Y = 0.073 X + 1.57$	0.78	14	7.1-27.1

[1]Y = biomass load (g); x = crown area (m^2) or bole dbh (cm).

84% of the stems were: *Eugenia borinquensis* Britton, 0.035 cm/yr (n = 34); *Ocotea spathulata*, 0.025 cm/yr (n = 55); *Tabebuia rigida* Urban, 0.030 cm/yr (n = 39); and *Micropholis garciniifolia* Pierre, 0.020 cm/yr (n = 40). The remaining 33 dicot stems representing eight species averaged 0.010 cm/yr.

The total aboveground net primary productivity (NPP), including coarse debris, for the dwarf forest was estimated at 4.63 t ha^{-1} yr^{-1} (Table 6). The mean annual litterfall was 2.9 t ha^{-1} yr^{-1}, 51% leaf litter, 35% woody, and 14% fruit and miscellaneous (Fig.s 1-5). Total bi-weekly litterfall during the year ranged between 0.4 t/ha during the 5th collection period (April 23-May 20) to 0.12 t/ha during the 13th period (December 2-30). Leaf litter showed the same low and high collection periods, with gradual decline from the 1st (January 1-28) through the 5th periods, and a general increase (with fluctuations) from the 6th (May 21-June 17) through 13th periods. Woody litterfall varied between about 0.01 to 0.04 t/ha, with a series of peaks and low points. Fruit litterfall peaked in the 4th period (March 26-April 22) at >0.006 t/ha, and miscellaneous litterfall in the 9th period (August 13-September 9) at >0.15 t/ha.

TABLE 4. Percentage of dead stems by species with four or more individuals in Pico del Este's dwarf forest.

Tree Species	Dead		Unaffected	Total
	Percent[1]	No.	No.	No.
Prestoea montana	9.1[a]	1	10	11
Tabebuia rigida	9.3[a]	4	39	43
Micropholis garciniifolia	11.1[a]	5	40	45
Cyathea bryophila	13.5[a]	19	122	141
Calyptranthes krugii	15.0[a]	3	17	20
Eugenia borinquensis	20.9[ab]	9	34	43
Magnolia splendens	37.5[ab]	3	5	8
Ocotea spathulata	46.7[b]	49	56	105
Henriettea squamulosa	50.0[b]	4	4	8
Cyathea arborea	50.0[b]	2	2	4
Hedyosmum arborescens	75.0[b]	3	1	4
Clusia clusiodes	80.0[b]	4	1	5
Subtotals				
12 species	24.3	106	331	437
4 species[2]	—	—	6	6
Totals				
16 species	23.9	106	337	443

[1]Comparisons were made using the G-statistic for independence (Sokal and Rohlf, 1981). Percentages with the same superscripts are not significantly different.

[2]Species with ≤3 individuals: *Cyrilla racemiflora* (2), *Myrcia deflexa* (1), *Psychoteria berteriana* (2), *Torralbasia cuniafolia* (1).

TABLE 5. Species composition by topography in the dwarf forest of the Luquillo Experimental Forest[1].

	Totals		Percent of total			
	stem No.	stem %	Ravine	Slope	Ridge	Chi-square[2]
Ferns						
Cyathea bryophila (R. Tryon) Proctor	397	17.0	43.4	50.1	6.5	186.0
Cyathea arborea (L.) J. E. Smith	42	1.8	19.1	59.5	21.4	7.4
Palm						
Prestoea montana (R. Grah.) Nichols	33	1.4	100.0	—[3]	—	115.6
Dicotyledons						
Tabebuia rigida Urban	531	22.8	13.9	41.6	44.5	25.6
Ocotea spathulata Mez	374	16.0	8.0	37.7	54.3	64.0
Eugenia borinquensis Britton	283	12.1	15.9	40.6	43.5	8.6
Henriettea squamulosa (Cogn.) Judd.	221	9.5	47.9	19.5	32.6	85.3
Micropholis garciniifolia Pierre	153	6.6	3.3	49.6	47.1	33.2
Calyptranthes krugii Kiaersk.	103	4.4	9.7	45.6	44.7	10.1
Clusia clusoides (Griseb.) D'Arcy	64	2.8	9.4	54.7	35.9	8.8
Haenianthus salicifolius Griseb. var. *obovatus* (Krug & Urban) Knobl.	25	1.1	16.0	34.0	50.0	5.4
19 remaining species[2]	105	4.5	37.1	14.3	48.6	29.8
Totals	2331	100.0	22.8	39.6	37.6	579.8[4]

[1]Data derived from 0.525 ha of plots stratified in groups of 3 by topography (ravine, slope and ridge) as follows: 6 plots 25 × 10 m on Pico del Este (1000 m in elevaton); 3 plots 25 × 10 m on Pico del Oeste (1050 m in elevation); 3 plots 50 × 10 m on El Yunque (900 m in elevation); and 3 plots 50 × 10 m on El Toro (970) m in elevation.

[2]Tree species with <25 stems: *Citharxylum caudatum* L. (2); *Cordia borinquensis* Urban (5); *Croton poecilanthus* Urban (7); *Cyrilla racemiflora* L. (18); *Daphnopisis philippiana* Krug & Urban (15); *Ditta myricoides* Griseb. (2); *Hedyosmum arborescens* Sw (6); *Ilex sideroxyloides* (Sw.) Griseb. (8); *Magnolia splendens* Urban (12); *Mecranium latifolium* (Cogn.) Skean (1); *Miconia pachyphylla* Cogn. (7); *Miconia tetrandra* (Sw.) D. Don ex G. Don (1); *Myrcia deflexa* (Poir.) DC. (1); *Myrcia fallax* (A. Rich.) DC. (1); *Ocotea leucoxylon* (Sw.) Mez (5); *Psychoteria berteriana* DC. (3); *Ternstroemia luquillensis* Krug & Urban (4); *Torralbasia cuneifolia* (C. Wright) Krug & Urban (4); *Xylosma schwaneckeanum* (Krug & Urban) Urban (3).

[3]Dashes indicate that no trees were recorded.

[4]Chi-square listed by row. Total chi-square highly significant. Comparative value at alpha = 0.01 and 22 df is 40.29.

Total aboveground biomass declined at an average rate of 1.73 $t/ha^{-1}\ yr^{-1}$ during the 5-yr period, with variation among different taxonomic groups: the palms increased, the ferns remained about the same, and the dicots decreased (Table 6). The litter turnover rate, estimated for the non-steady state conditions in post-hurricane conditions, was 0.84 times per year.

DISCUSSION

Forest structure.—The small trees in the dwarf forest (Tables 1 and 2; Weaver, 1972a, 1990) are characteristic of Puerto Rico's montane areas where the greatest proportion of the island's original forests have survived human activities (Wadsworth, 1950). Tree density increases with ascent in the LEF while the average heights and diameters of trees, the number of species, and basal area, all decline (Wadsworth, 1951; White, 1963; Weaver and Murphy, 1990). The small stature and species impoverishment of the summits have been attributed to various factors, among them fog, cool temperatures, reduced solar insolation, low nutrient availability, saturated soils, impeded root respiration, and slow mineralization of organic matter (Weaver, 1995). At all elevations in the dwarf forest, however, trees on lower slopes and ravines are larger than those on ridges and summits (Table 2).

The greater mortality in the smallest tree size classes, particularly on ridges (Table 2), may be due to their exposed location and restricted root systems. From 80 to 90 percent of dwarf forest woody roots are concentrated in the top 2 to 10 cm of soil (Lyford, 1969). Moreover, roots growing between the litter and the "mucky" surface

TABLE 6. Comparison of productivity in Pico del Este's dwarf forest before and after hurricane Hugo.

Dynamic factors	Sampling dates	
	1981-82[1]	1991[2]
Litterfall (t ha^{-1} yr^{-1})	3.10	2.90
Leaf	2.45	1.50
Wood	0.28	1.02
Fruit	—[3]	0.07
Miscellaneous	0.37	0.34
Looselitter (t ha^{-1})	4.34	3.46
Litterfall/looselitter	0.70	0.84
Herbivory rate (t ha^{-1} yr^{-1})	0.13	—
Aboveground biomass change (t ha^{-1} yr^{-1})		
Increase	0.45	—
Decrease	—	1.73[4]
Total aboveground NPP (t ha^{-1} yr^{-1})	3.70	4.63

[1]Source: Weaver and Murphy, 1990.
[2]Data collected in post-hurricane non-steady state conditions.
[3]Dashes indicate that data were not recorded.
[4]The decrease of 1.73 t ha^{-1} yr^{-1} is comprised of three components: a decrease in dicots and ferns of -1.95 and -0.10, respectively; and an increase in palms of 0.32, for a net change of -1.73 t ha^{-1} yr^{-1}.

are free of adhering soil and as "clean as though washed with water" (Lyford, 1969). With little protection being provided by dwarf forest canopy, violent, prolonged winds could rip tree roots in the soil. Studies at lower elevation in the tabonuco forest showed that live fine roots to a depth of 10 cm declined to zero in a 3-mo period after Hurricane Hugo (Parrotta and Lodge, 1991). Similar effects were observed in dwarf forest (J. Parrotta, unpubl. data), a condition which could negatively influence the capacity of trees to absorb nutrients released from litterfall (Parrotta and Lodge 1991; Lodge et al., 1991), and affect their survival.

Dwarf forest CD/BD ratios are low compared to other tropical forests. Past measurements in Puerto Rico showed a decline from about 35:1 for small *Bucida buceras* L. trees in low elevation xeric environments to about 22:1 for *Micropholis chrysophylloides* Pierre and *Terebraria resinosa* (Vahl) Sprague in montane rainforest (Weaver and Pool, 1979). Measurements in lower montane rainforest in Dominica averaged 18:1 for large *Dacryodes excelsa* Vahl and other commercial timber species (Bell, 1976). The generally low dwarf forest ratios appear partly due to direct pruning by Hurricane Hugo in 1989, but may also reflect an adaptive response to growth in dense stands on wind-exposed summits. The lack of correlation between crown and bole diameters may reflect the same factors.

The pre-hurricane regressions of epiphyte biomass vs. either bole dbh or crown area yielded better correlations than the post-hurricane regressions (Table 3). These differences may be due to uneven recovery and differential growth rates after the storm. Lighter bryophytes had noticeably colonized most tree surfaces, whereas the heavier bromeliads were less abundant and small. Moreover, crown area appears to be a better predictor of epiphyte biomass than bole diameter because epiphyte biomass tends to be concentrated in tree crowns (particularly for larger stems).

Using the equations to determine epiphyte biomass based on crown area (Table 3), and assuming a tree with a crown area of 10 m^2, the rate of epiphyte recovery during the 16 months between Hurricane Hugo and the January 1991 measurement averaged about one-third of the biomass recorded in 1969. From 1991 to 1997, about 10% was added to the total, bringing biomass recovery to less than half of that recorded in 1969. These recovery rates are very different: about 23% per year for the first 1.3 yr, and <2%/yr for the next 6 yr. The apparent anomaly in the recovery rate appears related to climatic events during

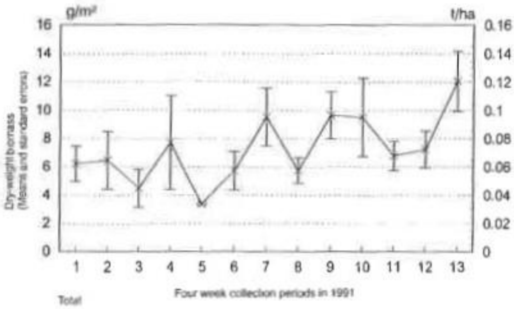

FIG. 1. Post-hurricane total litterfall in the dwarf forest of the Luquillo Experimental Forest.

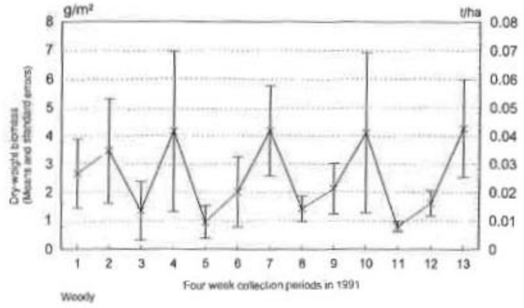

FIG. 3. Post-hurricane woody litterfall in the dwarf forest of the Luquillo Experimental Forest.

the mid-1990s. Puerto Rico suffered a prolonged drought during the summer of 1994 which may have affected epiphyte colonization. Moreover, in September of 1995, just 16 months before the 2nd measurement, Hurricane Marilyn, with a trajectory between Puerto Rico and the Virgin Islands, caused minor damage to the summit vegetation.

Species composition.—*Prestoea montana*, the most common tree in the LEF (Wadsworth, 1951; Weaver, 1983), is abundant in ravines (Table 5). The palm grows from 150 m in elevation to the summits, where it is less common than many of the dicot species. *Cyathea bryophila*, a common dwarf forest understory tree fern (Little et al., 1974), is mainly found on ravine and slope topography near summits, particularly in the extremely humid conditions of Pico del Este and Pico del Oeste. *Cyathea arborea* ranges throughout the LEF, frequently growing in openings (Little and Wadsworth, 1964). Of the dicots, *Henriettea squamulosa* (Cogn.) Judd. was more common in ravine topography (Table 5). In contrast, the remaining dicot species listed individually grow more frequently on slope and ridge topography. Of these, *Tabebuia rigida*, *Ocotea spathulata* and *Micropholis garciniifolia* showed the same topographic preferences in a survey of the colorado forest (Weaver, 1991). *Micropholis garciniifolia*, one major dicot species that grows at all elevations in the LEF, also shows preference for upper slopes in the tabonuco forest (Crow and Grigal, 1979).

Differential post-hurricane mortality rates by tree species (Table 4) have been reported for other forest types in the Caribbean Basin. For example, after the 1956 Hurricane Santa Clara in Puerto Rico and the 1989 Hurricane Hugo in St. John, the percent damage by several species common to both areas followed the same rank order (Wadsworth and Englerth, 1959; Weaver, 1994b). In both cases species of the genus *Clusia*, possibly because of incomplete defo-

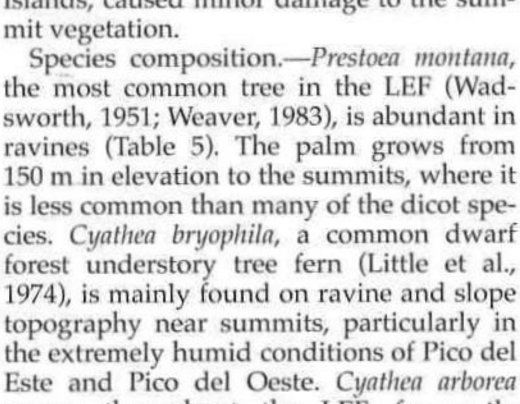

FIG. 2. Post-hurricane leafy litterfall in the dwarf forest of the Luquillo Experimental Forest.

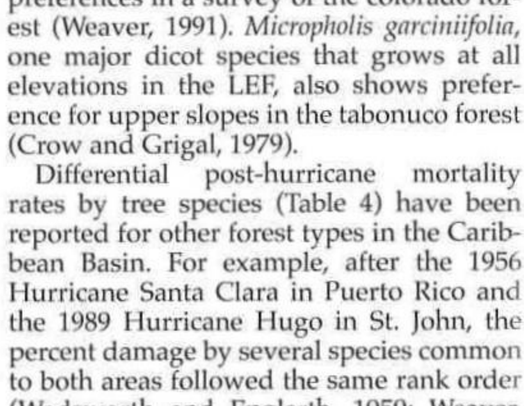

FIG. 4. Post-hurricane fruit litterfall in the dwarf forest of the Luquillo Experimental Forest.

liation (Francis and Gillespie, 1993), or their superficial rooting habit, had the greatest proportion of dead stems (Table 4).

Forest dynamics.—Hurricane Hugo had both immediate and delayed (≥1.3 and ≤6.3 yrs post-Hugo) impacts on Pico del Este's dwarf forest. The immediate effects were defoliation, loss of epiphytes, breakage of limbs, snapping of roots, windthrow, and standing mortality. Litterfall in tabonuco forest resulting directly from Hugo's passage was estimated at 680 times the daily mean before the storm (Lodge et al., 1991). Another storm, Hurricane Eloise of 1975, passing north of Puerto Rico, reduced the dwarf forest leaf area index by 8% (Benedict, 1976).

Delayed post-hurricane mortality has been observed elsewhere: after 3 months on Mauritius (Sauer, 1962); combined with drought effects during the following summer in New Zealand (Shaw, 1983); after 17 months on the Yucatan peninsula (Whigham et al., 1991); and after 10 and 19 months on St. John, U. S. Virgin Islands (Weaver, 1994b). Delayed mortality is a common phenomenon not peculiar to the dwarf forest. It may result from damage to the cambium and bark tissues caused by twisting and flexing of stems (Sauer, 1962), root damage for the same reasons, or both.

The post-hurricane dbh growth rates reported in this study are similar to those measured on Pico del Este between 1976 and 1981 (Weaver, 1983). Although all surviving trees had been exposed to Hugo and suffered varying degrees of damage, the post-hurricane forest with fewer stems provided more growing space for survivors than before the storm (Table 1).

Productivity.—Post-hurricane total litterfall was only slightly less than the pre-hurricane estimate because the leafy component declined after the storm and the woody component increased (Table 6). The decline in leafy litterfall was caused by complete defoliation during Hugo, followed by partial refoliation of the impacted trees during 1990. The increase in woody debris was due to the fall of small branch and bark fragments from trees damaged by the storm.

The 20 percent decrease in loose litter may be attributed to the slight decline in total litterfall immediately after the storm, as well as a slight increase in organic matter decomposition. Leaves of dwarf forest trees and epiphytes filter cloud moisture, adding water to the soil (Baynton, 1968; Weaver, 1972a). The hurricane's stripping of epiphytes and leaves reduced foliar biomass, which would reduce cloud moisture interception and allow more light to reach the soil surface. The reduction of moisture and increased light should make the summit forests effectively drier and stimulate organic matter breakdown.

Total NPP in the pre-hurricane study included an estimate for biomass change (biomass accumulation) averaged over a 5-yr period (Table 6). Using the same approach, the average biomass change over the 5-yr period after the storm was negative and is tallied as coarse debris added to the soil, yielding an apparent post-hurricane increase in NPP. The dwarf forest was not in steady state during the period of measurement, and with recurrent climatic events, may seldom approach steady state. An alternative calculation of NPP could exclude post-hurricane coarse debris.

Hurricane San Cipriano of 1932 left an imprint evident for nearly 50 years on the LEF's lower elevation forests, as witnessed by gradual changes in structure and species composition (Crow, 1980; Weaver, 1989). Given the dwarf forest's low net primary productivity (Weaver et al., 1986) and slow biomass accumulation after disturbance (Byer and Weaver, 1977; Weaver, 1990), one might suggest that the recovery process from major disturbances could span decades, and in some instances centuries,

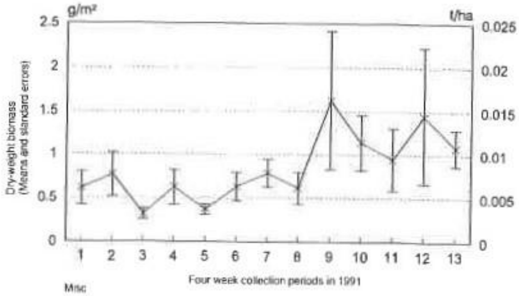

FIG. 5. Post-hurricane miscellaneous litterfall in the dwarf forest of the Luquillo Experimental Forest.

being interrupted one or more times by other major climatic events. Part of this slowness is attributable to the general lack of secondary tree species in the dwarf forest and part to environmental constraints.

Although limited in extent, Puerto Rico's dwarf cloud forest is an important vegetation type. High humidity and low transpiration rates, combined with direct interception of cloud moisture, ensures comparatively high runoff from the summit areas (Weaver, 1972b; Lugo, 1986). Moreover, many relatively uncommon species of plants and animals are either endemic or largely confined to these high elevation refugia (Weaver, 1972b).

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