Long-term changes in structure and composition following hurricanes in a primary lower montane rain forest in Puerto Rico

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Dacryodes excelsa Vahl (Burseraceae) in lower montane rain forest: The tree, called tabonuco in Puerto Rico and gommier in the Lesser Antilles, was used by indigenous peoples for making and caulking boats, for torches, as incense in religious ceremonies, and for medicinal purposes. During the early 20th century, the timber was used for making furniture and general construction. The scene shows the impacts of Hurricane Hugo on TR-1 in 1989. Photograph P. L. Weaver.

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RÉSUMÉ

CHANGEMENTS A LONG TERME DE STRUCTURE ET DE COMPOSITION D'UNE FORET PRIMAIRE HUMIDE DE BASSE MONTAGNE SUITE AU PASSAGE D'OURAGANS A PUERTO RICO

Dacryodes excelsa, espèce arborée connue sous les noms de tabonuco à Puerto Rico et de gommier aux Petites Antilles, domine les sommets de la forêt tropicale humide de basse montagne (selon Beard) de l'archipel des Caraïbes ; où périodiquement les ouragans passent à travers les îles modifiant la structure des massifs forestiers, leur composition en essences et leur dynamique. Au nord-est de Puerto Rico, l'étude chronologique post-ouragans menée entre 1946 et 2010 a permis de suivre les modifications de la végétation sur une parcelle de 0,40 hectare à 380 metres d'altitude dans la forêt expérimentale de Luquillo. Celle-ci a montré : (1) la défoliation, la casse et les chablis provoqués par le vent induisant une mortalité immédiate entraînent une déstructuration de forêt en perte du nombre de tiges, de hauteur des arbres et de biomasse ; (2) la mortalité différée de d'autres arbres blessés s'accompagne d'un rapide et abondant recrutement de *Cecropia schreberiana* et d'espèces cicatricielles, augmentant le nombre de tiges dans la forêt ; (3) une accélération de la croissance en diamètre et l'accumulation de la biomasse pendant une vingtaine d'années après l'ouragan, suivie du déclin de leur ratio ; (4) un très fort taux de survie après l'ouragan et une augmentation de la vitesse de croissance en diamètre de *Dacryodes excelsa* ; (5) toujours suite à l'ouragan, une augmentation de la richesse en espèces pendant une période de 20 ans au cours de laquelle les espèces primaires et secondaires grandissent ensemble, suivie dune chute d'abondance liée la concurrence ; (6) enfin, des conditions d'évolution asymptotiques aussi bien pour les tiges et la biomasse que pour le nombre d'espèces, après plus de 40 ans. En outre, d'autres études connexes menées dans des types de forêts semblables ont montré que les ouragans et les coupes intensives induisent des réactions de croissance comparables. Cette étude s'avère être d'intérêt régional puisque la forêt humide de basse montagne de Puerto Rico partage des conditions environnementales semblables ainsi que les mêmes essences forestières avec les montagnes des Antilles.

Mots-clés: forêt humide de basse montagne, ouragans, suivi des forêts, structure, dynamique forestière, Puerto Rico.

ABSTRACT

LONG-TERM CHANGES IN STRUCTURE AND COMPOSITION FOLLOWING HURRICANES IN A PRIMARY LOWER MONTANE RAIN FOREST IN PUERTO RICO

Ridges within the lower montane rain forests (sensu Beard) of the Caribbean Basin are dominated by *Dacryodes excelsa*, a tree species known as tabonuco in Puerto Rico and gommier in the Lesser Antilles. Periodically, hurricanes traverse the islands causing changes in structure, species composition, and dynamics of forests. The chronology of post-hurricane vegetation change from 1946 to 2010 on a 0.4 ha ridge plot ~380 m in elevation in the Luquillo Experimental Forest of northeastern Puerto Rico showed: (1) defoliation, breakage, and uprooting by wind accompanied by immediate mortality resulting in a loss in forest structure, including stem numbers, tree height, and biomass; (2) delayed mortality of some impacted trees, along with prompt, abundant ingrowth of *Cecropia schreberiana*, and other secondary species, increasing the number of stems within the forest; (3) a post-hurricane increase in diameter growth and biomass accumulation for ~20 years, followed by a decline in both rates; (4) a high post-hurricane survival and increase in dbh increment of *Dacryodes excelsa*; (5) a post-hurricane increase in species richness for ~20 years when primary and secondary species grow together, followed by a decline due to competition; (6) asymptotic conditions for stems, biomass, and number of species after more than 40 years. In addition, related studies in the same forest type showed that hurricanes and thinning evoke comparable growth responses. This study should be of regional interest because Puerto Rico's lower montane rain forest shares similar environmental conditions as well as tree species with the mountainous Antilles.

Keywords: lower montane rain forest, hurricanes, forest monitoring, structure, forest dynamics, Puerto Rico.

RESUMEN

CAMBIOS A LARGO PLAZO DE ESTRUCTURA Y COMPOSICIÓN DE UN BOSQUE PRIMARIO PLUVIAL MONTANO BAJO TRAS EL PASO DE HURACANES EN PUERTO RICO

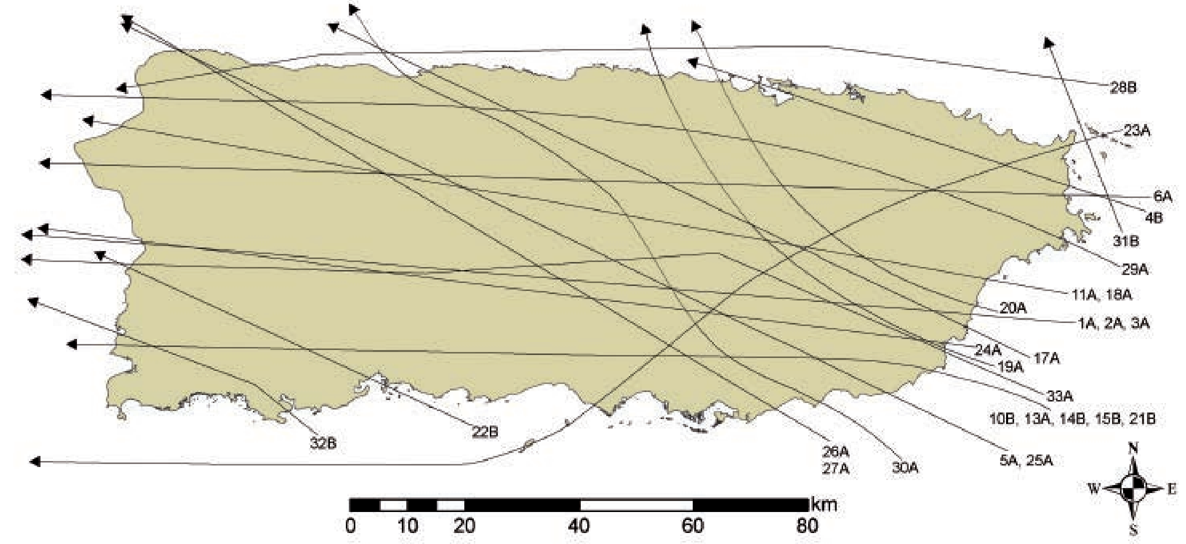
Dacryodes excelsa, especie de árbol conocido como tabonuco en Puerto Rico y gommier en las Antillas Menores, domina en las cumbres del bosque pluvial montano bajo (según Beard) del archipiélago del Caribe. Periódicamente, los huracanes atraviesan las islas causando cambios en la estructura, composición de especies y dinámica de los bosques. La cronología de cambios post-huracanes en la vegetación entre 1946 y 2010 en una parcela de 0.40 hectárea a unos 380 metros de altitud en el Bosque Experimental de Luquillo, en el noreste de Puerto Rico, evidenció: (1) defoliación, rotura y caída de árboles causadas por el viento; todo ello acompañado por la mortalidad inmediata ocasionando un destructuración forestal, con pérdidas de densidad y altura de árboles , así como de biomasa; (2) una mortalidad diferida de ciertos árboles dañados, con un rápido y abundante reclutamiento de *Cecropia schreberiana* y otras especies secundarias, lo que aumenta el número de tallos del bosque; (3) un aumento post-huracán del incremento de crecimiento de diámetros y la acumulación de biomasa durante unos veinte años, seguido de un descenso de ambas tasas; (4) una alta supervivencia post-huracán y un aumento en el incremento del diámetro de parte de *Dacryodes excelsa*; (5) un aumento post-huracán de la riqueza de especies durante los primeros 20 años en los que las especies primarias y secundarias crecen juntas, seguido por un consecuente ocaso debido a la competencia; (6) y por fin, condiciones de evolución asintóticas para los tallos, la biomasa y el número de especies después de más de 40 años. Además, algunos estudios relacionados con el mismo tipo de bosque demostraron que los huracanes y las entresacas de árboles provocan respuestas de crecimiento comparables. Este estudio resulta ser de interés regional porque el bosque pluvial montano bajo de Puerto Rico comparte similares condiciones ambientales y las mismas especies de árboles con las Antillas montañosas.

Palabras clave: bosque pluvial montano bajo, huracanes, monitoreo forestal, estructura, dinámica forestal, Puerto Rico.

Introduction

Forest monitoring provides resource information needed to develop forest management policies and practices, planning activities, and programs. The U.S. Forest Service and collaborators have carried out studies in the Luquillo Mountains for nearly a century, including at least five separate timber surveys of stocking and timber volumes between 1905 and 1948 (WADSWORTH, 1951, 1970). In 1939, the International Institute of Tropical Forestry, first called the Tropical Experiment Station, was established to conduct research on forest management, protection, and utilization, along with soil and water conservation in Puerto Rico and the U.S. Virgin Islands. Since 1943, the Institute's staff has set up ~620 plots of different sizes totaling 67 ha in primary and secondary stands within the Luquillo Experimental Forest (hereafter called El Yunque). The plots, established for a variety of reasons, are located between 200 and ~1000 m in elevation and contained ~134 000 trees at first measurement (WEAVER, 2012). Nearly 80% of the plots were permanently marked, and some of the earliest plots were re-measured. In 1980, the Institute initiated an inventory program to monitor the island's secondary forests, subsequently adding plots in El Yunque (BRANDEIS *et al.*, 2007).

Hurricanes, also called typhoons, are strong tropical cyclones that form in the South Atlantic, the Caribbean Basin, the Gulf of Mexico, and in the eastern Pacific Ocean. Their trajectories pass over the Antilles, the Caribbean and Gulf coasts of Central America and Mexico, the southern and eastern United States, the East Indies, Southeast Asia, Australia, and Madagascar, where they recurrently affect vegetation and human settlements. Hurricanes that traverse the Caribbean basin occur from June through November. Those that pass near or over Puerto Rico typically originate near the Cape Verde Islands off western Africa and enter the island from the southeast. Since 1700, apparent and confirmed trajectories of 31 hurricanes of varying intensity passed within 50 km of the *forest*, including four over the mountains (figure 1; SALIVIA, 1972; WEAVER, 2012). Based on these data, hurricanes may be expected to pass directly over the forest once every 78 years and within 50 km once every 10 years. Five hurricanes heavily impacted the mountains during the 20th century: San Felipe (1928), the island's legendary storm; San Nicolas (1931), passed along the coast north of the forest; San Cipriano (1932), with a trajectory directly over El Yunque; Hugo (1989), the first major hurricane after a hiatus of 57 years; and Georges (1998). Santa Clara (1956*),* with winds barely classed as hurricane force, had its greatest impact in the middle of the island.



Legend for major hurricanes in Puerto Rico since 1700[1, 2]

Key	Year	Name	Key	Year	Name	Key	Year	Name	Key	Year	Name
1-A	1738	Santa Rosa II	10-B	1805	San Vicente II	18-A	1827	San Jacinto II	26-A	1899	San Ciriaco
2-A	1738	San Leoncio III	11-A	1807	San Jacinto	19-A	1835	San Hipólito	27-A	1928	San Felipe II
3-A	1751	San Agapito	12-B/?	1809	San Esteban III	20-A	1837	N.S. de los Angeles	28-B	1931	San Nicolás
4-B	1766	San Jenaro	13-A	1813	San Liborio II	21-B	1851	San Agapito II	29-A	1932	San Cipriano II
5-A	1766	San Marcus	14-B	1814	San Liborio III	22-B	1852	San Llorenzo	30-A	1956	Santa Clara (Betsy)
6-A	1772	San Agustín	15-B	1816	San José de Cupertino	23-A	1867	San Narciso	31-B	1989	Hugo
7-B/?	1772	San Ramón II	16-A/?	1819	San Mateo III	24-A	1876	San Felipe I	32-B	1996	Hortense
8-B/?	1780	San Antonio	17-A	1825	Santa Ana	25-A	1893	San Roque III	33-A	1998	Georges
9-B/?	1785	San Lupo									

[1] Key: A = hurricane vortex passed over island with hurricane force winds; B = hurricane vortex passed over part of the island or offshore, with hurricane force winds on part of the island; A/? and B/? = uncertain trajectory (i.e., San Ramón II in 1772 passed northeast of the island). Trajectories in 1899 and later are known; pre-1899 trajectories were sketched from descriptions except those classed as A/? or B/?.

[2] Sources: Neumann et al. 1988, Salivia 1972.

Figure 1
Hurricane map: Hurricane trajectories over Puerto Rico since 1700. El Yunque forest lies in the northeastern part of the island centered at the intersection of hurricanes: 6A, San Agustín (1772); 23A, San Narciso (1867); and 29A, San Cipriano II (1932). The trajectory of hurricane 4B, San Jenaro (1766), passed just northeast of the forest. During the past three centuries, most hurricanes have entered Puerto Rico from the southeast (WEAVER, 2012).

The purpose of this paper is to document the 64-year history of changes induced by hurricanes on plot TR-1 (i.e. tabonuco ridge plot), the best maintained permanent plot in Puerto Rico's lower montane rain forest (LMRF) (photograph 1). Relatively recent summaries of high wind and hurricane effects in temperate and tropical forests worldwide already exist (EVERHAM & BROKAW, 1996; LUGO, 2008). This report highlights rare, long-term data with comparisons limited to other long-term plots (i.e. ≥30 years) in the same forest.

Setting

The 11 300 ha El Yunque contains four main forest types common to the mountainous West Indies (BEARD, 1949; WADSWORTH, 1951): LMRF (locally tabonuco forest) between 120 and 600 m in elevation; montane rain forest (locally colorado forest) between 600 and 900 m; dwarf forest from ~900 m to the summits as high as 1074 m; and palm brake scattered mainly on steep windward slopes and in ravines above 450 m. All forests combined contain 225 tree species, 16 of which were classed earlier as El Yunque endemics (LITTLE & WOODBURY, 1976). Nearly 170 *tree* species were tallied within the LMRF (LITTLE, 1970).

The best developed stands are on low, well-drained ridges, where *Dacryodes excelsa* (photograph 1), a mature canopy dominant known as tabonuco in Puerto Rico or gommier in the Lesser Antilles, is abundant and attains ›30 m in height and ›1 m in dbh (i.e. tree diameter at 1.4 m above the ground) (LITTLE & WADSWORTH, 1964). Two other canopy species, *Manilkara bidentata*, and *Sloanea berteroana*, also attain large sizes but are less common than *D. excelsa* (BRISCOE & WADSWORTH, 1970; CROW, 1980). *Cecropia schreberiana* and *Schefflera morototoni*, both secondary species, regenerate in openings and rapidly grow into the canopy. Understory species such as *Cordia borinquensis*, *Micropholis garciniifolia,* and *Prestoea montana* are relatively common and vary by site. The latter two species sometimes reach mid-canopy.

Mean rainfall in El Yunque is 3860 mm/yr, ranging from an average of 3540 mm/yr in the LMRF to 4850 mm/yr in dwarf forest (GARCIA-MARTINÓ *et al.*, 1996). Mid-elevations in the Mameyes watershed, where the study plot is located, are wetter than the average for LMRF (EWEL & WHITMORE, 1973). The mean annual temperature for is 22 °C with little seasonal variation, and the soils are deep, well drained clays (USDA NATURAL RESOURCES CONSERVATION SERVICE, 2002). On TR-1, typical LMRF tree species grow in association with a few species from higher elevations.

Methods

Four plots of different sizes and a group of 417 plots called the pilot management study were established within the LMRF between 1943 and 1957 (table I). The original purpose of the first three plots was to determine species composition, tree sizes, and typical dbh growth rates in a forest type not previously studied by the U.S. Forest Service. The fourth plot and the pilot study were set up to determine the effect of thinning on the productivity of timber species.

Measurement and analyses of the plots were initially done at 5-yr intervals whereas later studies were carried out opportunistically. Attempts to compare results among LMRF plots are limited by measurement schedules and protocols, elevation, topography, hurricanes, and past silviculture. Studies within the first three plots during the late 1970s revealed systematic changes in species composition and tree size that were attributed to past hurricane disturbance (CROW, 1980; WEAVER, 1983). Subsequently, later studies considered hurricane effects during analyses.

TR-1, set up at 380 m elevation on a northeastern ridge within the Mameyes watershed, was re-measured eight times through 2010. All trees ›4 cm in dbh and rooted within the plot were identified, measured to the nearest 0.1 cm, and permanently tagged. Mortality was noted but ingrowth (i.e. recruitment) into the minimum dbh class, was not measured until 1977, and not tagged until 1988. Tree

Table I.
Long-term plots established ›50 years ago in lower montane rain forest (locally tabonuco forest) within El Yunque. TR-1 is the study plot. Results from the remaining plots were compared with the study plot.

Plots¹	Plots (no.)	Elev (m)	Area (ha)	Trees (no.)	Species (no.)	Characteristics²
TR-1	1	~380	0,40	713	46	1946; ridge, no human disturbance
EV-3	1	~380	0,72	955	53	1943; mixed topography, very lightly thinned
TS-3	1	570	0,40	949	48	1946; slope, no human disturbance
Tcu	1	450	0,10	493	42	1947; cutover (thinned) secondary forest
Pilot³	417	200-600	~0.08	2808	29	1957; thinned secondary + undisturbed plots

[1] Plot names: TR-1, tabonuco ridge; EV-3, El Verde tabonuco forest; TS-3, upper tabonuco slope; Tcu, cutover tabonuco forest; Pilot study, experimental thinnings in secondary tabonuco forest. Tabonuco forest (Wadsworth 1951) = lower montane rain forest (Beard 1949).
[2] Dates for plot estabishment and type of silvicultural treatment. Minimum recorded dbh was 4 cm for all plots except the pilot study where 9.0 cm was used. Only crop trees of timber species were measured in the pilot study whereas all species were measured in the other studies. Boundary problems were evident on EV-3 for work carried out after 1976.
[3] Pilot study: 417 variable radius plots set up in three separate areas of secondary forest and one area of primary forest. Individual plots average ~0.08 ha in size.

heights were first estimated in 1988 using an optical rangefinder. Species names follow local texts (LIOGIER, 1985-97; see also LITTLE & WADSWORTH, 1964; LITTLE *et al.*, 1974).

Data analyses were carried out for stems, total above-ground dry-weight biomass (hereafter biomass), and species richness. Stem numbers included residuals (i.e. stems surviving from the first measurement in 1946) and total stems (i.e. residuals plus ingrowth). Major primary canopy species, major secondary species, and select understory species were analyzed separately to show their trends over time. Mean tree heights and mean dbhs for total stems and for residuals were determined for several measurement dates. Mean dbh growth rates were compared at alpha = 0.05 for all surviving *D. excelsa* trees for periods ‹21 years post-hurricane (i.e. 1946-1951 plus 1989-2010) vs. ›21 years post-hurricane (i.e. 1951-1988) using a standard t-test (STEEL & TORRIE, 1960).

Biomass was determined for broadleaf species using:

$$Y = 4.73 - 2.86\,D + 0.58\,D^2, \text{ with } r^2 = 0.89$$

where D = dbh in cm and Y = biomass in kg (WEAVER &GILLESPIE, 1992). Biomass for the sierra palm (*P. montana*) was estimated by:

$$Y = 6.4X - 10.0, \text{ with } r^2 = 0.96$$

where X = height in m and Y = biomass in kg (FRANGI & LUGO, 1985).

Results

Forest Structure and Growth

The greatest number of total stems was 713 (1761/ha) in 1946 and the fewest was 374 (924/ha) in 2000 (table II). Residual stems had declined by 10% as of 1951, by 41% in 1977, 49% in 1988, 64% in 1994, and 73% in 2000; by 2010, ~77% of the stems first recorded in 1946 had died (figure 2). Ingrowth composed 12% of the total stems in 1977, 21% in 1988, 48% in 1994, 51% in 2000, increasing to 70% by 2010 (figure 2). Ingrowth rates (in stems/ha/yr) averaged 6.5 from

Table II.
Number of stems by indicator species on permanent plot TR-1 from 1946 to 2010.[1, 2]

Species	Stand 1946	Ing. 46-88	Mort. 46-88	Stand 1988	Ing. 88-00	Mort. 88-00	Stand 2000	Ing. 00-10	Mort. 00-10	Stand 2010	Res. 2010
Major secondary species											
Cecropia schreberiana Mig.	19	0	18	1	131	105	27	24	12	39	0
Schefflera morototoni (Aubl.) Maguire	30	0	15	15	6	11	10	10	1	19	3
Subtotals	49	0	33	16	137	116	37	34	13	58	3
Major canopy species											
Dacryodes excelsa Vahl	86	2	14	74	1	13	62	0	4	58	58
Manilkara bidentata (A. DC.) Chev.	10	8	0	18	17	10	25	14	1	38	7
Sloanea berteroana Choisy	34	11	23	22	20	15	27	22	4	45	4
Subtotals	130	21	37	114	38	38	114	36	9	141	69
Selected understory species											
Cordia borinquensis Urban	49	3	40	12	4	6	10	0	2	8	4
Micropholis garciniifolia Pierre	48	1	12	37	2	11	28	1	2	27	23
Ocotea spathulata Mez	42	2	27	17	1	16	2	0	1	1	1
Prestoea montana (R. Grah.) Nichols.	78	22	25	75	24	45	54	18	8	64	14
Melastomatcaeae[3]	81	3	56	28	1	21	8	136	3	141	0
Subtotals	298	31	160	169	32	99	102	155	16	241	42
Remaining 49 species	236	58	123	176	71	123	121	25	30	114	48
Totals (all 59 species above)	713	110	353	475	278	376	374	250	68	554	162

[1] Plot size = 1 acre. To convert tabular data to estimates in stems/ha multiply by 2.47.
[2] Ing. = ingrowth (recruitment); Mort. = mortality; Res. = residuals, or survivors of stems first recorded in 1946.
[3] Probably *Miconia tetrandra* and possibly *Tetrazygia* sp. before 1988; after 1988, *Miconia tetrandra*.

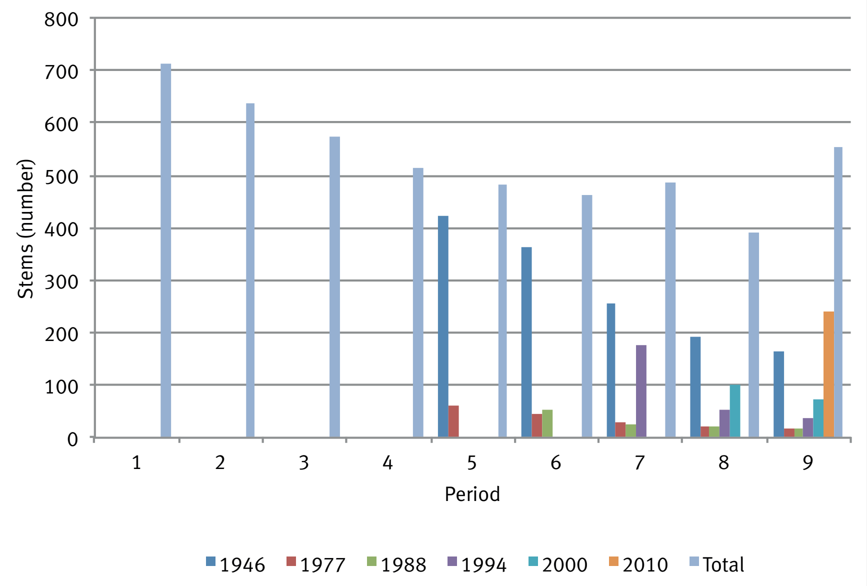


Figure 2.
Record of stem numbers: Periods 1, 2, 3, and 4, respectively, show 713 stems in 1946, and survivors of those stems as of 1951, 1956, and 1966. Ingrowth from all previous periods was first tallied in 1977 (period 5), which shows 423 survivors from 1946 (dark blue) plus 60 surviving ingrowth (red), yielding 483 total stems (light blue). Ingrowth is color-coded by period as shown below the graph. Periods 6, 7, 8, and 9, respectively, show the number of surviving stems from 1946 at the beginning (dark blue), surviving ingrowth from past periods in sequential order (various colors), followed lastly by new ingrowth for the particular period, and the sum total of stems (light blue). By 2000 (end of period 8), total stems had declined to a low of 390 (193 residuals plus 197 surviving ingrowth. By 2010, post-Georges recovery had increased total stems to 553 (165 residuals plus 338 surviving ingrowth).

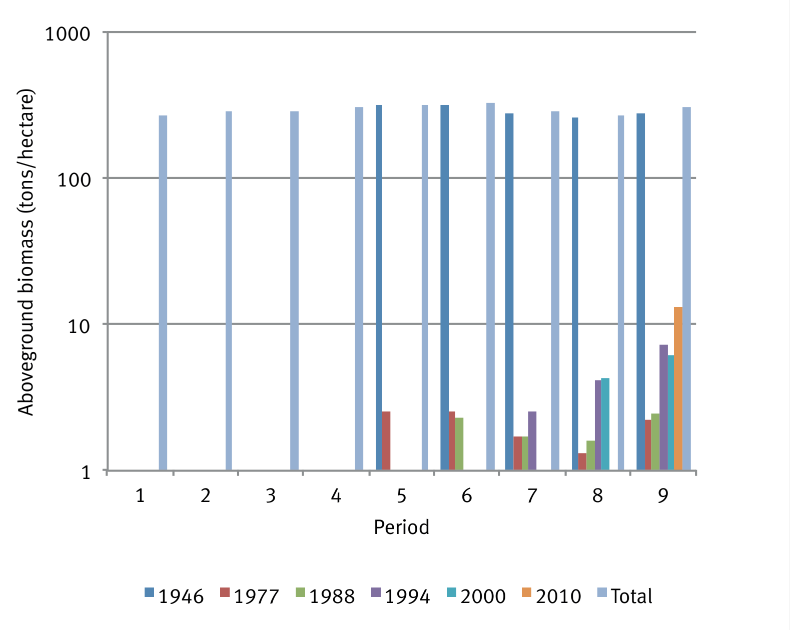


Figure 3
Record of aboveground biomass: Periods 1, 2, 3, and 4, respectively, show 266.3 t/ha in 1946, and net biomass growth on surviving stems as of 1951, 1956, and 1966. Ingrowth from all previous periods was first tallied in 1977 (period 5), which shows 319.1 t/ha on residuals in 1977 (dark blue) plus 2.5 t/ha on ingrowth (red) yielding a total of 321.6 t/ha (light blue). Biomass on ingrowth is color-coded by period as shown below the graph. Periods 6, 7, 8, and 9, respectively, show the amount of surviving biomass from 1946 at the beginning (dark blue), surviving biomass on ingrowth from past periods in sequential order (various colors), followed lastly by new biomass ingrowth for the particular period, and the sum of total biomass (light blue). By 2000 (end of period 8), total biomass had declined to 369.0 t/ha (257.7 t/ha on residuals plus 4.3 t/ha on ingrowth). By 2010, post-Georges recovery had increased total biomass to 307.5 t/ha (276.4 t/ha on residuals plus 31.5 t/ha on surviving ingrowth).

1946 to 1988, 57.2 from 1988 to 2000, and 61.8 from 2000 to 2010 (table II). Mortality rates (in stems/ha/yr) averaged 20.8 from 1946 to 1988, 77.4 from 1988 to 2000, and 16.8 from 2000 to 2010 (table II).

The mean estimated height for residual stems, total stems, and residual *D. excelsa* varied within a range of 2.5 m between 1988 and 2010 (table III). Mean dbh for residual stems and for residual *D. excelsa* continuously increased from 1946 to 2010. In comparison, mean dbh for total stems increased from 1946 to 1988 and fluctuated thereafter (table IV). Post-hurricane dbh growth rates for *D. excelsa* slowed significantly after 21 years: a mean of 0.24±0.01cm/yr (n=289) for ‹21 years vs. 0.14±0.01 cm/yr (n=308) for ›21 years.

Total biomass was lowest in 1946, peaked in 1988, and declined again by 2000 (table V). Biomass accumulation averaged 1.34 t/ha/yr from 1946 to 1988 and -4.46 t/ha/yr between 1988 and 2000 (table V). Biomass for the three major canopy species ranged from 49 to 58% of the stand in all years. Biomass for the five understory species ranged from 11 to 18%, and for both secondary species ‹5% in all years. The biomass on all surviving residual stems, as a proportion of total stand biomass, declined gradually from 99% in 1977, through 98% in 1988 and 2000, to 90% in 2010 (figure 3).

Species Composition

A total of 59 species, or one-third of those tallied within the LMRF, were recorded at some time on the plot (table VI). Ten species were lost and six gained between 1946 and 2010. The lost species, none with ›3 individuals, totaled only 17 stems. Species on the plot declined from 46 in 1946 to 40 in 1977, and then fluctuated between 40 and 43 species except for a record low of 37 in 2000 (figure 4). Of the original 46 species recorded in 1946, 38 survived until 1988, and 29 through 2010 (figure 4).

Long-term survival varied by species. Slightly ›50% of all mature canopy dominants survived the entire measurement period: 67% of the

D. excelsa and 70% of the *M. bidentata*, but only 12% of the *S.berteroana* (table II). Understory species averaged 14% survival, and ranged from 2% for *Ocotea spathulata* to 48% for *M. garciniifolia*. Of the secondary species, all *C. schreberiana* died and only 6% of the *S. morototoni* survived.

Regeneration also varied by species. By 2010, the three mature canopy dominants had increased by an average of 8%, with *M. bidentata* and *S. berteroana* accounting for virtually all of the ingrowth (table II). *D. excelsa* recruited only three new stems in 64 years and the only one surviving in 2010 entered the plot in 2000. None of the understory species increased in numbers. Ingrowth for *M. garciniifolia* and *P. montana*, however, did help to maintain 56 and 82% of their original populations. Secondary species increased by an average 18% due mainly to the abundant ingrowth of *C. schreberiana*.

Yokahú Tower and Hurricane Hugo: Yokahú tower, located in lower montane rain forest, was completed by 1963 to provide a convenient site for viewing different forest types within El Yunque. The effects of Hurricane Hugo (September 18, 1989), the island's first major hurricane in 57 years, were evident throughout El Yunque. Photograph P. L. Weaver.

Table III.
Comparison of estimated mean tree heights on permanent plot TR-1 before and after hurricanes Hugo in 1989 and Georges in 1998.

Year[1]	1946 residuals[2] (meters)	Total stems[3] (meters)	*Dacryodes excelsa*[2] (meters)
1988	13.6±0.32 (362)	11.8±0.30 (461)	18.4±0.85 (74)
1994	12.3±0.39 (254)	9.3±0.28 (486)	16.6±0.90 (68)
2000	12.9±0.42 (191)	9.4±0.30 (380)	17.0±0.87 (62)
2010	14.3±0.56 (166)	9.6±0.23 (554)	19.1±0.93 (58)

[1] Height was not estimated in years before 1988.
[2] Means ± SE (no. stems). Residuals = survivors from 1946.
[3] Total stems includes residuals (survivors) from 1946 plus ingrowth.

Table IV.
Comparison of mean tree diameters (dbh) on permanent plot TR-1 from 1946 to 2010.

Years	1946 residuals[1] (centimeters)	Total stems[1, 2] (centimeters)	*Dacryodes excelsa*[1, 3] (centimeters)
1946	12.7±0.47 (713), 4.1-97.8	12.7±0.47 (713), 4.1-97.8	27.2±2.41 (87), 4.1-97.8
1951	14.2±0.52 (639), 4.1-100.1	14.2±0.52 (639), 4.1-100.1	28.7±2.47 (85), 4.1-100.1
1956	15.2±0.57 (575), 4.1-101.6	15.2±0.57 (575), 4.1-101.6	29.2±2.47 (81), 4.1-101.6
1966	16.9±0.65 (513), 4.1-105.7	16.9±0.65 (513), 4.1-105.7	31.0±2.66 (79), 4.1-105.7
1977	19.0±0.77 (425), 4.1-110.5	17.5±0.70 (483), 4.1-110.5	32.6±2.75 (75), 4.6-110.5
1988	20.6±0.88 (362), 4.3-111.1	17.6 ±0.75 (461), 4.1-111.1	34.4±2.83 (73), 4.6-111.1
1994	23.2±1.14 (254), 4.7-94.3	15.4±0.71 (486), 4.1-94.3	34.8±2.84 (67), 4.7-94.3
2000	25.7±1.43 (191), 5.1-95.0	17.0±0.87 (380), 4.1-95.0	37.4±3.02 (61), 7.4-94.5
2010	28.3±1.69 (166), 5.3-97.1	14.3±0.66 (554), 4.1-97.1	40.8±3.22 (58), 7.8-97.1

[1] Means ± standard errors (number of stems), plus range of diameters.
[2] Total stems includes residuals (survivors) from 1946 plus ingrowth.
[3] Residual stems only.

Discussion

Monitoring on TR-1 encompasses a complete disturbance cycle from 14 years after San Cipriano to 12 years after Georges. A report written immediately after San Felipe for low elevations in the Luquillo district indicated massive defoliation, snapping of trees, and uprooting of trunks, followed by an abnormally high post-storm seed production (BATES, 1929). The time elapsed for foliage recovery varied by tree species, ranging from 4 to 6 months. Aerial photos of the study plot taken in 1936 showed a closed canopy suggesting a similar response.

From 1932 to 1989, the plot experienced a long period of relative calm. In 1989 and 1998, hurricanes again battered the forest causing immediate impacts (photograph 2).The Institute's scientists and collaborators quickly responded to assess impacts, including: (1) tree damage with regard to storm trajectory, wind speed, tree species, tree size, and site aspect and topography; (2) losses of basal area and biomass, fine root mortality, litterfall, and litter decomposition; (3) rapid post-storm recovery characterized by re-sprouting, seedling regeneration, and growth of herbaceous cover; and (4) changes in species richness, composition, basal area and biomass growth rates, reorganization of above ground biomass, nutrient use efficiency, and productivity. The results of these relatively short-term studies, some conflicting, have already been summarized (WALKER, *et al.*, 1991, 1996; WEAVER, 2012).

Forest Structure and Growth

The maxima for stem density and species richness on TR-1 occurred in the late 1940s and early 1950s after *C. schreberiana* and *S. morototoni* had grown into post-hurricane openings along with other species. Between the early 1950s and 1988, competition among survivors reduced stem numbers, limiting most ingrowth to small gaps caused by background mortality (table II). From 1989 to 2000, the recurrence of storms initially reduced total stems to a record low (table II, figure 2). By 2010, post-Georges ingrowth, much of it by *C. schreberiana*, raised the total stems to nearly 80% of the 1946 tally. The increase in stem numbers *will likely* continue for another decade.

Table V.
Total aboveground biomass of selected species, including residuals from 1946 and ingrowth, for all recorded stems on permanent plot TR-1 by year.

Species	**Estimated total aboveground biomass by year of measurement (t/ha)**									**% range of grand totals[1]**
	1946	**1951**	**1956**	**1966**	**1977**	**1988**	**1994**	**2000**	**2010**	
Major secondary species										
Cecropia schreberiana	2,1	3,4	3,8	3,8	2,7	0,8	4,9	2,0	5,3	0.7-1.7
Schefflera morototoni	3,7	5,9	7,8	10,3	12,4	11,8	5,4	2,9	5,0	1.1-3.9
Subtotals	5,8	9,4	11,6	14,1	15,1	12,6	10,3	4,9	10,3	1.8-4.7
Major canopy species										
Dacryodes excelsa	138,6	146,1	143,0	156,3	158,7	167,1	151,7	154,9	171,2	49.4-57.6
Manilkara bidentata	0,3	0,4	0,5	0,7	0,9	1,3	1,4	1,6	3,2	0.1-1.0
Sloanea berteroana	5,9	6,7	7,8	2,9	1,3	1,1	1,0	1,0	2,0	0.3-2.7
Subtotals	144,8	153,2	151,3	159,9	161,0	169,6	154,0	157,5	176,4	50.0-58.5
Selected understory species										
Cordia borinquensis	1,3	1,2	1,1	0,9	0,5	0,5	0,4	0,3	0,4	0.1-0.5
Micropholis garciniifolia	18,7	17,8	17,1	18,0	16,7	17,3	16,1	15,6	15,6	5.1-7.0
Ocotea spathulata	6,0	6,1	4,4	4,6	3,2	2,8	0,4	0,0	0,1	0-2.2
Prestoea montana	16,3	16,5	15,5	15,7	16,2	15,5	12,1	10,9	13,2	4.1-6.1
Melastomataceae[2]	4,8	5,6	6,5	8,4	10,2	7,3	1,7	1,6	4,4	0.6-3.2
Subtotals	47,0	47,2	44,5	47,6	46,9	43,3	30,8	28,4	33,7	10.6-17.6
Remaining 49 species[3]	68,8	74,9	80,0	89,6	98,7	97,1	89,2	78,2	87,2	25.8-31.4
Grand totals	266,3	284,6	287,5	311,2	321,6	322,5	284,3	269,0	307,5	100,0

[1] Percent range = lowest and highest selected species biomass divided by grand total biomass from 1946 to 2010.
[2] See Melastomataceae footnote in Table II.
[3] Remaining species: 36 originally recorded in 1946 plus survivors of 13 species recorded as ingrowth in 1977 or later.

Table VI.
Number of stems by species on TR-1 from 1946 to 2010.[1]

Species	Stand 1946	Ing. 46-88	Mort. 46-88	Stand 1988	Ing. 88-00	Mort. 88-00	Stand 2000	Ing. 00-10	Mort. 00-10	Stand 2010	Res. 1946
Alchornea latifolia Sw.	11	0	5	6	0	4	2	0	0	2	2
Alchorneopsis floribunda (Benth.) Muell.	3	0	0	3	1	1	3	5	0	8	2
Andira inermis (W. Wr.) DC.	3	0	1	2	0	0	2	0	0	2	2
Antirhea obtusifolia Urban	1	1	0	2	0	0	2	0	1	1	1
Beilschmiedia pendula (Sw.) Hemsl.	1	0	0	1	0	1	0	0	0	0	0
Buchenavia tetraphylla (Aublet) R. Howard	5	0	1	4	0	0	4	0	1	3	3
Byrsonima spicata (Cav.) HBK	2	0	1	1	0	1	0	0	0	0	0
Byrsonima wadsworthii Little	3	0	0	3	0	2	1	0	0	1	1
Casearia sylvestris Sw.	2	0	2	0	0	0	0	0	0	0	0
Cassipourea guianensis Aubl.	1	2	0	3	3	4	2	0	1	1	0
Cecropia schreberiana Mig.	19	0	18	1	131	105	27	24	12	39	0
Cordia borinquensis Urban	49	3	40	12	4	6	10	0	2	8	4
Croton poecilanthus Urban	1	0	0	1	0	1	0	0	0	0	0
Cyathea arborea (L.) J.E. Smith	4	0	4	0	0	0	0	2	0	2	0
Cyrilla racemiflora L.[2]	6	0	2	4	0	0	4	0	0	4	4
Dacryodes excelsa Vahl	86	2	14	74	1	13	62	0	4	58	58
Daphnopsis philippiana Krug & Urban	2	2	2	2	0	2	0	0	0	0	0
Eugenia borinquensis Britt.[2]	3	0	0	3	0	1	2	0	1	1	1
Garcinia portoricensis (Urban) Alain	10	12	3	19	8	14	13	3	3	13	3
Guarea glabra Vahl	1	1	0	2	0	0	2	1	0	3	1
Guatteria caribaea Urban	1	0	0	1	0	1	0	0	0	0	0
Hedyosmum arborescens Sw.	3	0	3	0	0	0	0	0	0	0	0
Henriettea squamulosa (Cogn.) Judd[2]	37	6	24	19	3	12	10	4	3	11	3
Hirtella rugosa Pers.	25	9	6	28	2	15	15	1	0	16	10
Homalium racemosum Jacq.	5	0	0	5	0	3	2	0	0	2	2
Inga laurina (Sw.) Willd.	11	0	5	6	0	4	2	0	0	2	2
Laplacea portoricensis (Krug & Urban) Dyer	20	0	17	3	0	3	0	2	0	2	0
Magnolia splendens Urban[2]	10	0	6	4	0	2	2	0	0	2	2
Manilkara bidentata (A. DC.) Chev	10	8	0	18	17	10	25	14	1	38	7
Margaritaria nobilis L.f.	1	0	0	1	0	0	1	0	0	1	1
Matayba domingensis (DC.) Radlk[2]	8	0	1	7	0	3	4	0	3	1	1
Meliosma herbertii Rolfe	13	5	6	12	2	6	8	2	0	10	5
Micropholis garciniifolia Pierre[2]	48	1	12	37	2	11	28	1	2	27	23
Myrcia deflexa (Poir) DC.	1	0	1	0	0	0	0	0	0	0	0
Myrcia splendens (Sw.) DC.	3	0	3	0	0	0	0	0	0	0	0
Ocotea leucoxylon (Sw.) Mez	1	0	1	0	1	0	1	2	1	2	0
Ocotea spathulata Mez[2]	42	2	27	17	1	16	2	0	1	1	1
Prestoea montana (R. Grah.) Nichols	78	22	25	75	24	45	54	18	8	64	14
Psychotria berterioana DC.	24	1	24	1	17	4	14	6	11	9	0
Sapium laurocerasus Desf.	1	0	1	0	0	0	0	2	0	2	0
Schefflera morototoni (Aubl.) Maguire	30	0	15	15	6	11	10	10	1	19	3
Sloanea berteroana Choisy	34	11	23	22	20	15	27	22	4	45	4
Solanum rugosum Dunal	1	0	1	0	0	0	0	0	0	0	0
Tabebuia heterophylla (DC.) Britt.	9	2	7	4	3	3	4	3	1	6	0
Tetragastris balsamifera (Sw.) Kuntze	3	0	0	3	0	1	2	0	0	2	2
Miconia tetrandra (Sw.) D. Don[3]	81	1	46	36	20	35	21	121	6	136	0
Subtotals	713	91	347	457	266	355	368	243	67	544	162
New species from 1977-2010											
Ardisia obovata Desv. ex Hamilt.	0	1	0	1	0	1	0	0	0	0	
Chionanthus domingensis Lam.	0	0	0	0	3	0	3	1	2	2	
Coccoloba swartzii Meisner	0	0	0	0	1	1	0	0	0	0	
Ixora ferrea (Jacq.) Benth.	0	5	2	3	0	3	0	0	0	0	
Miconia prasina (Sw.) DC.	0	0	0	0	1	0	1	0	1	0	
Myrcia fallax (A. Rich) DC.	0	1	0	1	1	1	1	1	0	2	
Ocotea moschata (Meissn.) Mez	0	4	3	1	0	0	1	0	0	1	
Oxandra laurifolia (Sw.) A. Rich.	0	1	1	0	0	0	0	0	0	0	
Palicourea crocea (Sw.) Roem. & Schultes	0	0	0	0	2	2	0	0	0	0	
Palicourea croceoides W. Hamilton	0	7	0	7	4	11	0	0	0	0	
Cyathea briophila (R. Tryon) Proctor	0	0	0	0	0	0	0	2	0	2	
Drypetes glauca Vahl	0	0	0	0	0	0	0	1	0	1	
Cyathea portoricensis Spreng ex Kuhn	0	0	0	0	0	0	0	2	0	2	
Subtotals	0	19	6	13	12	19	6	7	3	10	
Totals	713	110	353	470	278	374	374	250	70	554	

[1] Ing. = ingrowth; Mort. = mortality; Res. = residuals, or survivors of the original stand in 1946.
[2] Species most common in wetter forest types at higher elevations in the Luquillo Experimental Forest.
[3] See Melastomataceae footnote in table II.

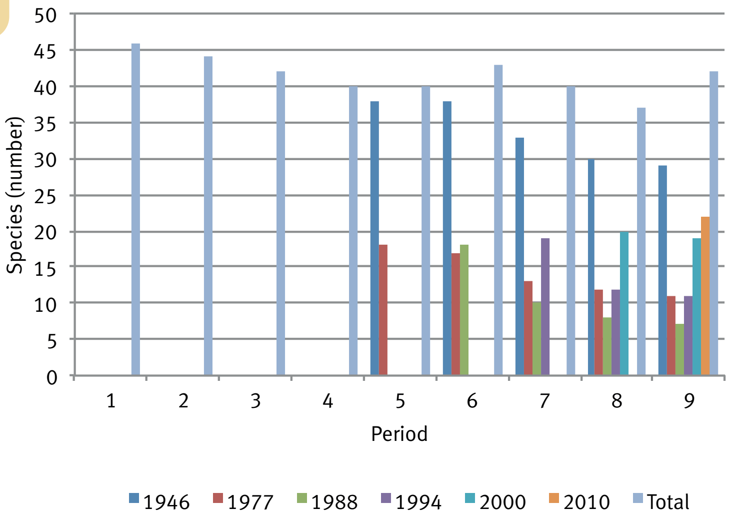


Figure 4.
Record of species' numbers: Periods 1, 2, 3, and 4, respectively, show 46 species in 1946, with a decline in the original number of species in 1951, 1956, and 1966. Ingrowth from all previous periods was first tallied in 1977 (period 5), which shows 38 residual species in 1977 (dark blue) plus 2 new ingrowth species (red) yielding a total 40 species (light blue). The number of new species is color-coded by period as shown below the graph. Periods 6, 7, 8, and 9, respectively, show the number of surviving species from 1946 at the beginning (dark blue), surviving species on ingrowth from past periods in sequential order (various colors), followed lastly by the number of new species in ingrowth for the particular period, and the sum of total species (light blue). By 2010 (end of period 9), post-Georges recovery showed 29 residual species (dark blue) plus surviving ingrowth species by period. Because some surviving species were tallied in more than one period, the net number of ingrowth species is 13, yielding a total of 42 distinct species (light blue).

Foliage profiles (i.e. measurements indicating the percent of vegetation cover in height intervals above the ground) showed that the average canopy height of LMRF tallied near the *El Verde plot* shortly after Hurricane Hugo had decreased up to 50% (BROKAW & GREAR, 1991). A simple comparison of estimated tree heights on the study plot for 1946 residuals, for total stems, and for *D. excelsa* residuals shows that height differences ranged between 15% and ~30% in different years (table III). Lower height values after Hugo and Georges reflect canopy losses due to the storms.

Biomass approaches minima immediately after hurricanes when trees succumb, or in some cases slightly later because of delayed mortality (i.e. the subsequent death of impacted trees that initially survive the storm). Delayed mortality, first reported in other hurricane prone areas (SAUER, 1962; WHIGHAM *et al.,* 1991), may result from the twisting or flexing of cambium or bark tissues, or possibly injuries to root systems during storms. The standing biomass of 266 t/ha in 1946 was the lowest recorded for the plot (table V, figure 3). Biomass increased during the early 1950s, despite stem losses, because of increment on large residuals. From 1989 to 2000, biomass again declined, with the most rapid loss immediately after Hugo.

D. excelsa survived all of the hurricanes well. The post-hurricane increase in dbh growth for ~20 years results from a temporary increase of available light and reduced competition. Biomass growth after 2000 averaged slightly more than that attained during the late 1940s (table V). If the 14 years of biomass accumulation after the first pair of storms paralleled the growth documented during 10 years after the second pair, one might assume that standing biomass on the study plot was at its lowest point shortly after San Cipriano. The minimal biomass recorded in 1946 (table V, figure 3) and the continual long-term increase in dbh for *D. excelsa* residuals (table IV) support this idea.

The lightly thinned El Verde plot and the upper slope plot showed post-hurricane trends between 1946 and 1976 that parallel those on TR-1 (table I). By the 1970s, biomass accumulation at El Verde had slowed, and both stem density and species richness were less than during the 1940s (CROW, 1980). Subsequent unpublished work at El Verde by A.P. Drew (deceased) showed a low for stem density in 1990 after Hugo, followed by an increase (LUGO, 2008). Moreover, plot basal area and biomass appeared to climb through 2006, despite hurricanes Hugo and Georges. On the upper slope plot, post-hurricane observations from 1946 to 1976 showed that stem numbers decreased by 14% whereas basal area and biomass increased by 5% (WEAVER, 1983).

Species Composition

TR-1 has a distinct mix of tree species for its elevation within the LMRF (table VI). Although *Henriettea squamulosa* and *M. garciniifolia* grow within the type, they are more common in the montane rain and dwarf forests (WADSWORTH, 1951; WEAVER, 1983, 2010a); likewise, *Cyrilla racemiflora*, *Magnolia splendens*, and *O. spathulata*, are more common in montane rain forest but also grow at high elevations in LMRF like the upper slope plot at 570 m (WADSWORTH, 1951; WEAVER, 1983). *Eugenia borinquensis*, normally absent in LMRF, abounds in dwarf forest and is common in montane rain forest (WEAVER, 2010a). *P. montana*, common in El Yunque, dominates palm brakes, often with ~60% of the stems and basal area. It also grows abundantly in ravines (WEAVER, 1983, 2010b).

Gradient sampling in LMRF showed that stem density, tree height, biomass, and species richness all declined from ridges and upper slopes to ravines; moreover, several tree species showed preferences for ridge, slope, or ravine topography (WEAVER, 2010b). The study plot's mix of tree species may be the product of recurrent disturbance on a prominent, well-drained ridge in a very wet part of the forest. Classification of El Yunque's forests into ecological life zones separates the watersheds containing TR-1 and El Verde according to rainfall (EWEL & WHITMORE, 1973). Previous studies elsewhere in the Caribbean, attributed differences in forest structure and composition within the LMRF to aspect, elevation, and topography (SHREVE, 1914; BEARD, 1949).

Cecropia schreberiana trees persist between storms within palm brakes, along ravines and riparian areas, and in treefall gaps throughout El Yunque. The species is most abundant after hurricanes when its dormant seeds germinate in response to canopy openings; it is, however, uncommon in abandoned pastures at lower elevations around the forest (BROKAW, 1998). *S. morototoni* reproduces less abundantly and grows less rapidly in dbh, but survives for longer periods between storms (table II). *M. bidentata* and *P. montana* maintain their populations through regeneration in shade or small openings (tables II, IV; BANNISTER, 1970; YOU & PETTY, 1991).

In comparison, the low recruitment of *D. excelsa* probably reflects its preference for convex topography (tables II, V). Its persistence on ridges has been attributed to better soil drainage, better anchorage among boulders, and root grafting, all of which make the trees more resistant to wind throw (BASNET *et al*., 1993). In Dominica, the measured crown-to-bole ratios of dominant *D. excelsa* were observed to be relatively small (BELL, 1976). Moreover, before Hurricane Hugo, the LMRF canopy was described as smoother and with fewer and smaller treefall gaps than were evident in Panamanian rain forest (BROKAW *et al.,* 2004). In summary, the LMRF on Caribbean islands appears adapted to hurricanes with its "little-developed emergent story, small crowns, small crown-to-stem ratio, many stems, and small photosynthetic surface per stem, accompanied by slow stem growth rates, gradual limb loss, and in situ decomposition of standing trunks" (ODUM, 1970). As observed, the gradual mortality of upright stems within the type (CROW, 1980; ODUM, 1970) should produce smaller gaps than those found in hurricane-free environments like Panama.

The trajectory in species richness during the 64-year period appears little affected by the lack of ingrowth records between 1951 and 1966. Hurricanes may temporarily reduce species richness on a plot, notably occasional or rare species, as witnessed by the low total in 2000. The number of species within the entire forest, however, remains stable. Within 12 years of Georges, the stand had recruited several new species (figure 4). After ~20 years, competition again tends to reduce species' numbers locally as the less tolerant ones gradually diminish.

The El Verde plot provides a reliable post-hurricane history from 1943 to 1976 for several species that were recorded on TR-1. *D. excelsa*, *M. bidentata*, and *P. montana* increased in stem numbers and basal area during the period whereas *S. berteroana* initially increased but later declined (CROW, 1980). *C. schreberiana and S. morototoni were common during the 1940s but later declined.* After Hugo, *C. schreberiana*, *S.morototoni*, and *M. bidentata* increased as they did on TR-1. Also, *D. excelsa* continued to increase through 2006 (LUGO, 2008) in contrast to its slow decline on TR-1 (table III). This difference may be largely due to topography (i.e. TR-1 ridge vs. El Verde mixed topography) although other factors may contribute (table I). Species diversity on El Verde gradually declined from the mid-1940s through 2005, with only a slight increase after Hugo (DREW *et al*., 2009). On the upper slope plot, mature forest species like *D. excelsa*, *M. bidentata*, and *S. berteroana* remained stable or increased in stem numbers between 1946 and 1976 whereas secondary species like *Alchorneopsis portoricensis*, *C. schreberiana*, and *S. morototoni* all declined considerably (WEAVER, 1983).

Years of forest monitoring: Dr. Frank H. Wadsworth, director of the Institute of Tropical Forestry from 1956 to 1979, explains the results of thinning in secondary lower montane rain forest to visitors from the World Wildlife Fund, InterAmerican University, and U.S. Forest Service offices in Washington and Atlanta. Dr. Wadsworth began to establish long-term plots in El Yunque in 1943 to learn about species composition and dbh growth rates.
Photograph P. L. Weaver.

Experimental Thinning in LMRF

Hurricanes create gaps within forests that stimulate growth on surviving trees and help the regeneration of secondary species; similarly, thinning is designed mainly to stimulate the growth of crop trees (photograph 3) but often facilitates undesired secondary regeneration. The young cutover plot in LMRF averaged 3 to 10 times more basal area increment for ~30 years than in unmanaged stands (WEAVER, 1983). Likewise, the pilot study showed that dbh increment on liberated trees averaged nearly twice the mean for the same species on uncut plots (CROW & WEAVER, 1977). Mature canopy species, among them *D. excelsa*, *M. bidentata*, and *S. berteroana*, responded best, nearly doubling their growth whereas six species common in secondary forests, including *Byrsonima spicata*, *Homalium racemosum*, *Inga laurina*, and *M. domingensis,* increased by an average of 50%. In comparison, the dbh growth on four early secondary species, including *C. schreberiana* and *S. morototoni,* changed little (WEAVER, 1983). *Miconia tetrandra*, common above 450 m elevation (LITTLE *et al*., 1974), was abundant on TR-1 after all of the hurricanes (table VI). This species also regenerated well after a 1947 thinning of an El Yunque montane rain forest plot at 700 m (WEAVER, 2001).

Río Mameyes: The Río Mameyes, the largest of 10 major streams that originate in the Luquillo Mountains, flows under Puente Roto (Broken Bridge) near the northern forest boundary several days after the passage of Hurricane Hugo. Stream channels throughout the mountains remained temporarily cluttered with fallen trees and soil causing changes in aquatic habitat. Puente Roto probably owes its interesting name to earlier storms when less stable wooden structures spanned the river.
Photograph P. L. Weaver.

Benefits of Monitoring in the LMRF

Permanent plot monitoring within El Yunque helped early investigators determine species' compositions and distributions, typical tree sizes, stem densities, stand volumes, and growth rates in anticipation of timber harvest (WADSWORTH, 1951, 1970). Later, the plot data were used to determine ingrowth and mortality rates, biomass changes, primary productivity, hurricane impacts, and to estimate tree ages (CROW, 1980; WEAVER, 2010a, 2010b). Some plots also revealed the positive effects of thinning on the growth of crop trees (CROW & WEAVER, 1977; WEAVER, 1983). The results of the Institute's studies may prove useful to forest managers in the Caribbean Basin where environmental conditions are similar. Also, continued monitoring of El Yunque's plots, where feasible, combined with the collection of parallel climatic records may assume future importance in assessing the performance of tropical forests as the biome experiences the effects of global change (CLARK & CLARK, 2011).

Conclusions

Environmental factors like aspect, elevation, and topography affect forest structure and composition as do hurricanes and human activity. Tropical storms and hurricanes frequent the Caribbean Basin and their impact causes vegetative responses that are evident for long periods. Indeed, hurricanes are frequent enough so that much of the lower montane rain forest (LMRF) is in some state of recovery from past events. Permanent monitoring on the Tabonuco ridge plot (TR-1) showed responses in forest structure, species composition, and stand dynamics, including:

- A 50% decline in total stems on the plot between 1946 and 2000.
- A nearly 80% loss of stems first recorded in 1946 accompanied by ingrowth equal to 70% of the stems recorded in 2010.
- A continuous increase in diameter on 1946 residual stems and surviving *Dacryodes excelsa.*
- A 70% increase in diameter increment during the post-hurricane period during the first 21 years in relation to the post-hurricane period beyond 21 years.
- An estimated 15 to 30% decline in tree height on surviving 1946 residuals and *Dacryodes excelsa* after hurricanes Hugo and Georges, followed by post-storm recovery.
- A 45 year period (i.e. 1932 to 1977) of continuous biomass accumulation, becoming asymptotic from 1977 to 1989; and then decreasing dramatically by 2000.
- A total of 59 species recorded on the plot, with a maximum of 46 in 1946 and a minimum of 37 in 2000.
- Abundant post-hurricane ingrowth of *Cecropia schreberiana* along with *Schefflera morototoni*, some of which persisted for more than 20 years.
- A standing biomass between 49 and 58% for *Dacryodes excelsa,* compared to less than 5% for *C. schreberiana* and *S. morototoni* throughout the measurement period.

In closing, natural events like hurricanes and the impact of human activities like thinnings produce similar responses for 20 years such as the ingrowth of secondary species and increased diameter increment on liberated trees.

Acknowledgments
Humfredo Mercano, Luis Ortiz, and Iván Vicéns helped with field work. Dr. Frank H. Wadsworth, who established the plots, made comments on the original draft. In addition, three anonymous reviewers of *Bois et Forêts des Tropiques* offered helpful suggestions regarding content and form. This work was done in cooperation with University of Puerto Rico at Río Piedras.

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