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The Influence of Hurricane Winds on Caribbean Dry Forest Structure and Nutrient Pools[1]

Skip J. Van Bloem[2], Peter G. Murphy

Department of Plant Biology, Michigan State University, East Lansing, Michigan 48824, U.S.A.

Ariel E. Lugo, Rebecca Ostertag[3], María Rivera Costa, Ivelisse Ruiz Bernard

International Institute of Tropical Forestry, United States Department of Agriculture Forest Service, Ceiba 1201, Jardín Botánico Sur, Río Piedras, Puerto Rico 00926-1119, U.S.A.

Sandra Molina Colón

Centro de Investigationes Científicas Rev. Tosello Giangiacomo, Pontificia Universidad Católica de Puerto Rico, Ponce, Puerto Rico 00717, U.S.A.

and

Miguel Canals Mora

Bosque Seco de Guánica, Departamento de Recursos Naturales y Ambientales, Guánica, Puerto Rico 00653, U.S.A.

ABSTRACT

In 1998, we measured the effects of Hurricane Georges after it passed over long-term research sites in Puerto Rican dry forest. Our primary objectives were to quantify hurricane effects on forest structure, to compare effects in a large tract of forest versus a series of nearby forest fragments, to evaluate short-term response to hurricane disturbance in terms of mortality and sprouting, and to assess the ability of hurricanes to maintain forest structure. We sampled damage from 33 plots (1.3 ha) across a 3000-ha tract of forest as well as in 19 fragments. For stems with 2.5-cm minimum diameter, 1004 stems/ha (12.4%) suffered structural damage, while 69 percent of the undamaged stems were at least 50 percent defoliated. Basal area lost to structural damage equaled 4.0 m^2/ha (22%) in south-facing native forests. Structural damage and defoliation increased with stem diameter and were more common in certain dry forest species. South-facing forests and those on ridgetops incurred more damage than north-facing forests or those comprised primarily of introduced species. Stem mortality was only 2 percent of all stems after 9 mo. Structural damage did not necessarily result in stem mortality. Hurricane-induced mortality was not associated with stem height or diameter, but was ten times greater than background mortality. Basal sprouting was proportional to the amount of structural damage incurred in a stand. Forest fragments experienced the same patterns of hurricane effects as the reference forest. The low, dense structure of Caribbean dry forest can be maintained by hurricane damage to larger stems and induction of basal sprouting to generate multistemmed trees.

RESUMEN

En 1998 medimos los efectos del Huracán George después de que paso por sitios localizados en Puerto Rico y dedicados a la investigación a largo plazo. Nuestros objetivos fueron cuantificar los efectos de huracanes en la estructura del bosque y comparar estos efectos en un bosque específico con una serie de fragmentos de bosque que se encontraban en la proximidad a nuestra área de estudio. La evaluación de la respuesta rápida del bosque seco debido a los efectos de huracanes se exploro en términos de la mortalidad y regeneración, así como se estudió la habilidad de los huracanes de mantener la estructura del bosque. Para este estudio de muestreo, 33 parcelas con daños (1.3 ha) a lo largo de una sección de 3000 ha de bosque así como en 19 fragmentos de bosque. En tallos con $\geq$2.5 cm de diámetro, 1004 tallos/ha (12.4%) sufrieron daño estructural, mientras que el 69 porciento de los tallos no dañados fueron al menos en un 50 por ciento defoliadas. Perdidas en área basal debido al daño estructural fue equivalente a 4.0 m^2/ha (22%). Bosques con pendientes en dirección sur y aquellos en los topes de las colinas presentaron mas daños que bosques con pendientes orientadas hacia el norte o aquellos que estaban constituidos principalmente de especies introducidas. Mortalidad en los tallos fue solamente un 2 porciento después de 9 meses, así como también se encontró que el daño estructural no contribuyó a la mortalidad de tallos. Mortalidad inducida por el huracán no se encontró asociada con el diámetro o altura de los tallos o bien su diámetro, pero fue 10 veces más grande que la mortalidad de control. Los fragmentos de bosques experimentaron el mismo comportamiento que el bosque de referencia.

Key words: Caribbean; disturbance; forest structure; hurricane; litterfall; mortality; nutrients; Puerto Rico; subtropical dry forest; wind.

THE STRUCTURE OF WEST INDIAN DRY FORESTS differs markedly from those elsewhere in the neo-tropics. Compared to tropical dry forests or seasonal forests in temperate zones, subtropical dry forests (*sensu* Holdridge 1967) have fewer canopy layers, no emergent trees, and, especially in the West Indies, have high stem densities resulting from numerous multistemmed trees (Murphy & Lugo 1986a, Dunphy *et al.* 2000, Quigley & Platt 2003). Differences in structure among dry forests have been attributed to climatic factors such as low annual rainfall and high potential evapotranspiration, as well as a suite of disturbances—including human impacts such as grazing and cutting (Murphy & Lugo 1986a, Kelly *et al.* 1988, Murphy *et al.* 1995, Gonzalez & Zak 1996, Molina Colón 1998), natural

[1] Received 30 June 2003; revision accepted 27 October 2004.
[2] Corresponding author. Current address: Universidad de Puerto Rico, Departamento de Agronomía y Suelos, P. O. Box 9030, Mayagüez, PR 00681-9030, U.S.A.; e-mail: svanbloem@uprm.edu
[3] Current address: Biology Department, University of Hawaii at Hilo, Hilo, HI 96720, U.S.A.

disturbances such as salt spray (Smith & Vankat 1992), trade winds (Lawton 1982), and hurricanes (Lugo *et al.* 1983, Kelly *et al.* 1988, Reilly 1991). Fire, although common in some dry tropical woodlands, is not an important ecological factor in closed canopy dry forests of the West Indies (Murphy & Lugo 1986b). However, the difficulty in teasing apart causal factors of forest structure after the fact is illustrated by studies in the Solomon Islands, where species composition was initially attributed to hurricane disturbance but, after further analysis, to logging by humans (Burslem *et al.* 2000). Although hurricanes are common in the subtropics and widely studied in moist and wet forests (cf. Biotropica 23(4a) 1991 and recent reviews: Everham & Brokaw 1996, Whigham *et al.* 1999), their effects have been less completely studied in dry forests. In this study, we report the effects of Hurricane Georges on dry forests in southwestern Puerto Rico.

If climate alone determined forest structure, the driest forests (based on potential evapotranspiration) would be expected to have the least basal area and biomass. Stem density may also be higher in the driest forests if basal sprouting is caused by droughts killing terminal buds. However, in independent projects, both Murphy and Lugo (1986a) and Quigley and Platt (2003) found that Guánica Forest, Puerto Rico, had structural characteristics that could not be explained by climate alone. Murphy and Lugo (1990) reviewed the structure of 12 mature tropical and subtropical dry forests across a rainfall gradient from 603 to 1800 mm/yr. Of the 12 forests, Guánica Forest had the only fifth highest temperature to precipitation ratio (2.9; T:P ratio acts as a surrogate for potential evapotranspiration, which is seldom reported), yet it was the shortest (9 m canopy height), with the least aboveground biomass (53 Mg/ha), and the second lowest basal area (17.8 m^2/ha). In Guánica Forest, 42 percent of all trees were multistemmed, leading to a stem density of 12,000 stems/ha (Murphy & Lugo 1986a). Quigley and Platt (2003) compared structural characteristics of seasonal forests from the equator to 40°N in the Western Hemisphere and found that forests at 20–30°N, including those in Puerto Rico, had greater stem densities and lower basal areas than those found elsewhere. These results suggest that other factors—such as hurricane disturbance—supplement the effects of drought stress in structuring dry forest. Similarly de Gouvenain and Silander (2003) noted that lowland tropical rainforests affected by hurricanes tended to be shorter, and, in African locations, stem density also increased.

Aside from damaging stems, hurricanes can rapidly redistribute resources and alter community composition and function. Hurricane winds lead to canopy thinning through the loss of leaves—transferring substantial biomass and nutrients to the forest floor. In Hawaii, hurricane litterfall was 1.4 times greater than normal annual levels (Herbert *et al.* 1999). In two wet forests and a cloud forest in Puerto Rico, hurricane litterfall ranged from 1.2–1.9 times greater than normal annual litterfall (Lodge *et al.* 1991). In Mexican dry forests, hurricane litterfall was about 1.3−2.0 times as much as the average of the previous four years (Whigham *et al.* 1991). These large inputs of litter change spatial and temporal resource availability and serve as important nutrient pulses (Lodge *et al.* 1994).

Another poorly understood aspect of hurricane disturbance is its interaction with forest fragmentation. Fragmented forests have more edge to face hurricane winds than do larger tracts of continuous forest and might therefore be more vulnerable to damage. Only 23.2 percent of the dry forest area of SW PR remains forested, contained in a collection of over 600 fragments (Ramjohn 2004). Therefore, the region provides a good location to evaluate the effects of hurricanes on forest fragments.

The main objectives of this study were to (1) provide a description of hurricane effects on Puerto Rican dry forest; (2) compare effects of hurricane winds in a large tract of forest with those in nearby forest fragments; (3) measure short-term responses of trees to hurricane winds in terms of sprouting and mortality; and (4) assess the potential of hurricanes to maintain the unique dry forest structure of the West Indies.

METHODS

The site and the event.—Guánica Forest is located in SW Puerto Rico (17°58′N, 65°30′W). Rainfall averages 860 mm/yr and mean annual temperature is 25.1°C (Murphy & Lugo 1986a). The rainy season is bimodal, split between spring rains in March–April and fall rains from August to December corresponding to the hurricane season. The amount and distribution of rain within years and seasons is highly variable (Murphy *et al.* 1995). The forest canopy reaches 5 m height on south-facing slopes and ridgetops (Murphy & Lugo 1986a), and 9 m in valleys (Molina Colón 1998). Emergents are absent and taller trees are always found in valley areas, leading to a more uniform canopy. Considered one of the best preserved examples of Caribbean dry forest (Ewel & Whitmore 1973), Guánica Forest has been extensively studied over the last 25 yr (Lugo *et al.* 1978; Lugo & Murphy 1986; Murphy & Lugo 1986a, 1990; Murphy *et al.* 1995; Lugo *et al.* 1996; Molina Colón 1998; Dunphy *et al.* 2000; Genet *et al.* 2002a,b; Quigley & Platt 2003; Ramjohn 2004). The forest was set aside for protection in 1917 and its boundaries expanded in the 1930s to include all the plots within this study. Forest structure before Hurricane Georges had been shaped by multiple factors, including human activity (Molina Colón 1998, Lugo *et al.* 2002). Surrounding Guánica Forest are a collection of dry-forest fragments that vary in land-use history, size, age, and dominant tree cover (Lugo *et al.* 1996, Genet *et al.* 2002a, Ramjohn 2004). Most fragments exist in a matrix of agriculture or pasture, but some are surrounded by residential areas.

The flora of Guánica Forest provides a good basis to study regional effects of hurricane disturbance. Of the 18 species for which we had at least 10 trees in our plots, only one (*Pictetia aculeata* (Vahl) Urban) is endemic to Puerto Rico, 17 are found elsewhere in the Caribbean, 10 in Florida, 10 in Central America, and 5 in South America.

The eye of Hurricane Georges passed over Guánica Forest on September 21–22, 1998. Sustained winds blew at 176−184 km/h and gusted up to 240 km/h (Bennett & Mojica 1998), making this a Category 3 hurricane (Saffir–Simpson Index). It took about 18 hr to

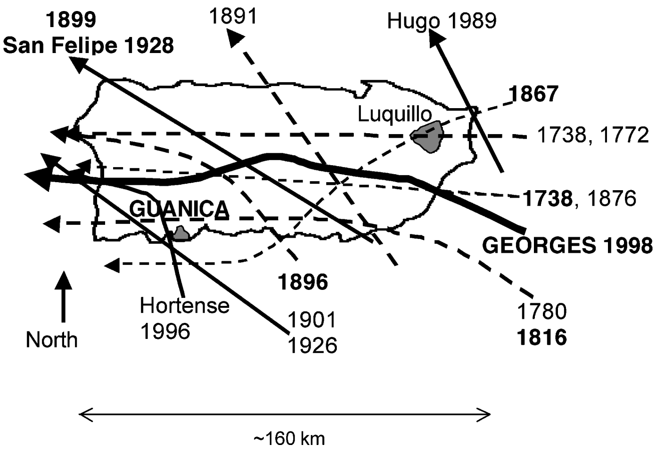

FIGURE 1. Hurricane tracks with year of occurrence of the 15 storms most likely to have affected Guánica Forest. Hurricane Georges is the thickest line across the center. Bolded years are hurricanes likely to have had the strongest effects on Guánica Forest. Solid lines are known hurricane tracks. Dashed lines are best-estimate trajectories based on Salivia (1972), Neuman *et al.* (1993), and Miner-Solá (1996). Hortense was a low-level storm that, according to local reports, had little impact on the forest. Luquillo Forest and Hurricane Hugo included for reference.

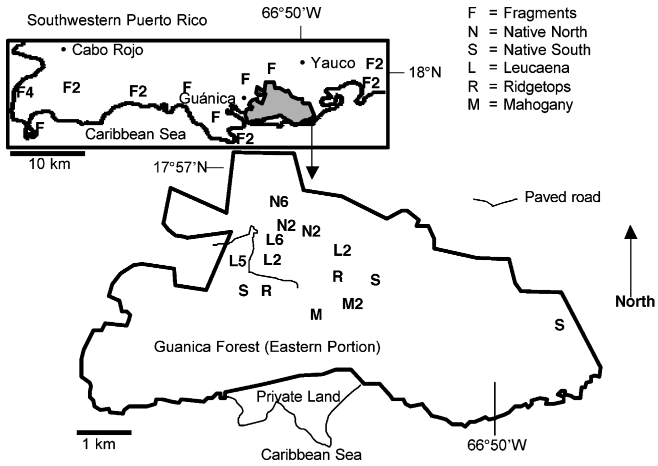

FIGURE 2. Locations of study plots in Guánica Forest and nearby fragments (inset) in southwestern Puerto Rico. Forest types indicated by symbols in legend. Numbers next to symbols denote multiple plots of a type in the area.

cross over the forest and maximum winds lasted about 4 hr. Georges was a relatively dry hurricane (Bennett & Mojica 1998), depositing 151 mm of rainfall, about equal to the September average (Murphy *et al.* 1995).

Between 1700 and 2004, the eyes of 37 hurricanes traversed some portion of PR, a return interval of one hurricane every 8 yr (Quiñones 1992). Only 15 approached the dry forest area (Fig. 1), including the last two – Hortense in 1996 and Georges in 1998—an average return interval of 20 yr. Not all of the 15 hurricanes affected the forest equally. Historical records report that seven of the 15 hurricanes were at least category 3 in the Guánica area, therefore most likely to influence forest structure. Thus, strong hurricanes have an average return interval of 43 yr. Hortense was a category 1 hurricane with less than 100 mm of rainfall in the Guánica area (Bennett 1996) and resulted in very little damage to the forest (A. E. Lugo & M. Canals Mora, pers. obs.). Prior to Georges, the structure of Guánica Forest was probably last affected by Hurricane San Felipe in 1928.

PLOTS AND TERMINOLOGY USED IN THIS STUDY.—We compiled data for this study from a variety of different plots established prior to September 1998 for other research projects. Following the hurricane, we pooled all available data to provide a more comprehensive explanation of hurricane effects than would have been possible otherwise. We measured hurricane effects in 33 experimental plots in Guánica Forest (Fig. 2). These plots were located in semi-deciduous forest (Murphy & Lugo 1986a, Molina Colón 1998) but differed in size, time studied, and land-use history (Table 1). Twenty-eight of the plots were established before the hurricane to study long-term forest growth, structure, and regeneration (Lugo & Murphy 1986, Murphy & Lugo 1986a, Murphy *et al.* 1995, Molina Colón 1998). Following the hurricane, we established one plot in each of three old *Swietenia mahagoni* Jacq. plantations and two new plots on ridges after extensive field surveys revealed that ridges received the greatest damage. Total area sampled was 1.3-ha spread across an area of 3162 ha in the eastern portion of Guánica Forest. However, much more of the forest was inspected as we conducted field surveys, leading us to conclude that our results were representative of the forest as a whole.

We also sampled hurricane effects in 19 forest fragments within 31 km of Guánica Forest (Fig. 2; Genet *et al.* 2002a,b; Ramjohn 2004). Fragments ranged in size from 0.01 to 75.6 ha and had species assemblages comparable to the native forest plots. The fragments faced various directions and occurred over the same elevation range as Guánica Forest. Hurricane effects were measured along 2-m wide transects, the lengths of which varied by fragment size. Transects started on the north and south edges of fragments and ran toward the center. Total area sampled in the 19 fragments was 0.68 ha.

Land-use history of Guánica Forest resulted in two types of forest: (1) those dominated by native species, and (2) those that consisted primarily of naturalized species (*i.e.*, *Leucaena leucocephala* (Lam.) deWitt and *Prosopis juliflora* (SW.) DC.). We refer to these types of forest as "native forest" and "Leucaena forest" (Table 1). Leucaena forest plots had been used for a baseball field, agriculture, and housing sites until about 65 years ago (Molina Colón 1998). Native forest plots either had no signs of human disturbance or some selective cutting prior to the 1930s for subsistence charcoal production (Murphy & Lugo 1986a, Molina Colón 1998). The native forest plots on the north side of Guánica Forest occurred in the lee of hurricane winds, while those on the south side faced Georges' strongest winds (Bennett & Mojica 1998). Thus, we use "native-north" and "native-south" to highlight the influence of aspect on hurricane effects.

TABLE 1. *Description of sites in SW Puerto Rico used to assess hurricane effects. All sites except the fragments were in Guánica Forest.*

Forest type	No. of plots	Sampled area (m^2)	Aspect	Elevation (m)	No. of stems ≥ 2.5 cm	Date established	Prior land use
Leucaena[a]	5	2000	Flat	175	359	1996	Baseball field
Leucaena[a]	5	2000	Flat	100	390	1996	Houses
Leucaena[a]	5	2000	Flat	100–175	455	1996	Agriculture
Native-north[a]	5	2000	North	100	667	1996	Charcoal pits
Native-north[a]	5	2000	North	100	591	1996	Mature[e]
Native-south[b]	1	690	South	175	456	1981	Charcoal pits/mature
Native-south[c]	2	1800	South	55–185	1430	June 1998	Mature[e]
Ridgetop[c]	2	200	None	175–200	162	Nov 1998	Mature[e]
Mahogany[c]	3	300	South	100–150	126	Oct/Nov 1998	Mahogany plantation
Fragments[d]	19	6790	All	5–175	[f]	Jan 1999	Forest fragments

[a]Molina Colón (1998).
[b]Murphy and Lugo (1986).
[c]This study.
[d]Ramjohn (2004).
[e]Mature forest stands did not show signs of major or recent human disturbance.
[f]Only dead or damaged stems in transects were measured in fragments.

Since many trees were multistemmed, we use "tree" to refer to single-trunked individuals *and* entire clumps. When discussing individual trunks, regardless of whether growing singly or clumped, we use "stem." Thus, there will be more stems than trees at each site. Effects were seldom uniform among stems in a clump.

STEM MEASUREMENTS FOR FOREST STRUCTURE.—Within each plot, we tagged all stems ≥2.5-cm diameter at breast height (DBH). Species identifications were based on Little and Wadsworth (1964) and Little *et al.* (1974). Stem height and DBH were measured on all trees between June and September 1998. Height was measured to the nearest 0.25 m using a telescoping pole. DBH was measured at 1.3 or 1.4 m depending on who established the plot (Murphy & Lugo 1986a, Molina Colón 1998). In the fragments, we measured the height and DBH of damaged (but living) and hurricane-killed stems only.

ASSESSMENT OF EFFECTS.—We assessed effects on each tagged stem in the native-south forest plots and in two of the three mahogany plots within 10 days of the storm. Assessment of other plots and fragments was completed by February 1999. Hurricane impacts on stems were divided into six categories: uprooted, snapped, large branches broken, leaning, defoliated only, and no visible effect. The first four categories indicate severe structural damage to a stem and are collectively referred to as such. "Large branches broken" indicated that ≥25 percent of the secondary or tertiary branches were snapped off. For our purposes, secondary branches had diameters ≥ 50 percent of DBH and tertiary branches had diameters 25−50 percent of DBH. Branch loss was not evaluated for the native-north or *Leucaena* plots, precluding their inclusion in some of our analyses. Leaning stems were bent to an angle >30° from vertical at some point along the trunk, but lacked signs of uprooting or breakage. We compared the direction of fall for snapped, uprooted, and leaning stems to the direction of the strongest winds based on meteorological reports (Bennett & Mojica 1998).

We estimated defoliation visually for each tree using six classes: 100 percent (no leaves at all), 95 percent (one to a few leaves remaining), 75, 50, 25, and 0 percent (all leaves present). New leaf growth prevented assessment of defoliation in plots sampled after late-November 1998 and in all fragments. Thus, analyses of defoliation patterns were restricted to the native-south plots and two mahogany plots.

LITTERFALL.—We collected litterfall in thirty 50 × 70 cm wire baskets haphazardly placed in the 1.44-ha native-south forest plot. We emptied the baskets the day before the hurricane and on September 26, 1998–4 d after the hurricane. We checked baskets again in early October, but <1 g of new litterfall was present in any basket, suggesting that all litter had fallen out of the canopy by Sept. 26. Thus, we considered the litterfall samples to have been created during the 18 hours it took the hurricane to traverse the site.

We also collected standing litter on the forest floor 12 d after the hurricane in the 1.44-ha native-south plot. A 15 × 15 cm template was randomly located in the vicinity of the litter baskets ($N =$ 26). All material within this area was collected and sorted into four categories: leaves, brown wood, green wood, and miscellaneous. We distinguished brown wood from green wood based on flexibility. By the twelfth day, green and brown leaves could not be distinguished. Leaves included all leaf parts, and wood included stems, branches and woody vines. The miscellaneous category included any material that did not fit into other categories, including reproductive parts and small fragments of leaves or wood.

Nutrient stocks in standing litter and litterfall are expressed here on a content basis (kg/ha). Tissues were dried at 65°C to a constant weight and ground in a Wiley mill (18 mesh) before analysis. Ground samples were digested with H_2O_2 and concentrated

HNO_3 (Luh Huang & Schulte 1985), and concentrations of P, K, Ca, and Mg were determined on a Beckman Spectra Span V plasma emission spectrometer. Because forest floor samples often harbor soil particles, we express all standing litter mass values on an ash-free basis. Forest floor nutrients were analyzed using bulked samples ($N = 6$), except for green wood, which was not present in all samples ($N = 4$). Forest floor N was determined using duplicate samples in a CE Instruments NC2100 analyzer. Litterfall N was determined on duplicate samples using a LECO CNS 2000 analyzer.

Short-term response.—We determined mortality for stems with DBH ≥ 2.5 cm. Stems were considered dead if they had no leaves, no sprouts, and dried bark as of June 1999 (9 months post-hurricane) when the plots were resampled. Multistemmed trees were considered dead only if all stems were dead. Mortality was not assigned to mode of damage in the native-north or Leucaena forests. Mahogany plots were not revisited, so mortality was not assessed there.

We recorded sprouting from roots and trunks below breast height to evaluate the potential for hurricanes to generate multi-stemmed trees. We counted sprouts on each of the living, tagged stems in the native-south and ridgetop plots in September or November 1998 to determine the number of sprouts existing before the hurricane. In June 1999, we counted new sprouts and noted their point of origin on the stem. New sprouts were distinguished from old sprouts by bark coloration and lignification. Summary data are presented here. Patterns of sprout survival after two years were reported elsewhere (Van Bloem *et al.* 2003).

Statistical analyses.—Plots were pooled by forest type. Categorical data (height, DBH, damage type) were analyzed using χ^2 statistics. Categories were pooled when sample sizes were too small to produce valid χ^2s—these instances are noted in the results. For analysis of species effects, we only included species that had ≥25 individuals in our samples. We used a null hypothesis of equal damage or mortality across all categories (locations, stands, or stem size).

We used regression to compare snap heights to stem diameter, sprouting rates to structural damage rates, and rate of structural damage to wood density (reported for species we examined in Molina Colón 1998). For all tests, $\alpha = 0.05$ and we verified normal distribution of data sets with Kolmogorov-Smirnov tests.

RESULTS

Forest-wide effects.—In Guánica Forest as a whole, structural damage was present on 12.4 percent of stems (1004 stems/ha) as a result of Hurricane Georges. Both hurricane winds and falling limbs or stems caused structural damage to stems. Details of stem damage are presented below. The median rate of defoliation was 50 percent. Overall, 74.6 percent of stems were at least 25 percent defoliated and 69 percent were at least 50 percent defoliated. New leaves began to appear within two weeks for many species, particularly *Coccoloba diversifolia* Jacq., *Bourreria succulenta* Jacq., *Pisonia albida* (Heimerl) Britton, *Guettarda krugii* Urban, and *Pictetia aculeata*.

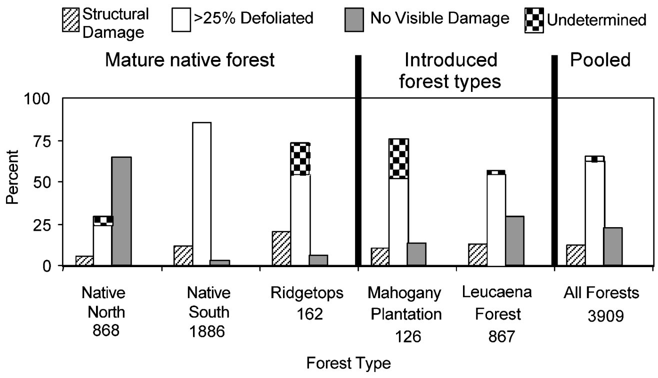

FIGURE 3. Hurricane effects on stems for different forest types within Guánica Forest, Puerto Rico. Structural damage includes uprooting, snapping, breakage of large branches, or leaning. "Undetermined" refers to stems that lacked structural damage but were sampled after significant refoliation had occurred. Most of the stems in this category probably had been defoliated. Numbers below forest type labels indicate the total number of stems sampled in each forest type. "All forests" is pooled data for the five forest types.

Effects by forest type.—Severity of defoliation and stem damage varied by forest type and topographic setting ($\chi^2 = 1357$; 8 df; $P < 0.0001$; Fig. 3). Structural damage was greatest on ridgetops (20%). Native-north forest, in the lee of the strongest winds, had the highest percent of stems without visible hurricane effects and the lowest amount of structural damage (Fig. 3). The basal area of stems suffering structural damage was 4.0 m^2/ha in native-south plots and 3.5 m^2/ha in ridgetops, 22 and 19 percent, respectively, of total live prehurricane basal area. Ridgetops lost less basal area than native-south forests because the average stem diameter in ridgetops was lower before the storm. The mode of structural damage varied by forest type and topography (Fig. 4). Ridgetops generally had higher rates of each mode of structural damage than other forest stands, with the exception of snapping, which affected the greatest number of stems in native-south forests. Although having low damage overall, Leucaena forest had the highest proportion of snapped stems.

Hurricane effects by stem size.—Throughout the dry forest region of Puerto Rico, stems in all height and DBH classes sustained structural damage and the size classes with the most stems (3–6 m in height and 2.50–4.99 cm in DBH, Murphy & Lugo 1986a) had the greatest number of stems damaged. Proportionally, stem damage increased with stem diameter in native-south forest ($\chi^2 = 26.60$; 4 df; $P < 0.0005$; diameter classes >12.5 cm pooled), but not in native-north or Leucaena forests (Fig. 5A). Native-north forests had the least damage of all forest types in all diameter classes. In plots where all modes of damage were measured (*i.e.*, native-south, ridgetops, and mahogany plantations), stems ≥7.5-cm DBH incurred proportionally more damage than smaller stems (Fig. 5B), but damage was not related to stem height (Fig. 5B). Unlike other studies (Putz et al. 1983), no relationship existed between damage and height:diameter ratios.

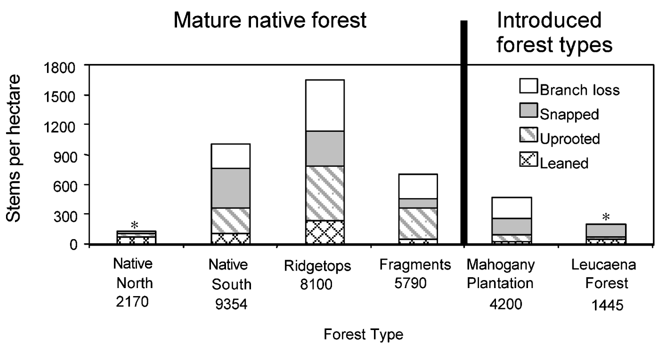

FIGURE 4. Stem density of various modes of structural damage in different stands of Puerto Rico dry forest. Sample included all stems ≥ 2.5-cm DBH. Numbers below forest type labels indicate total stem density of each forest type. *Branch loss not estimated for native-north or Leucaena sites; structural damage densities are therefore underestimated.

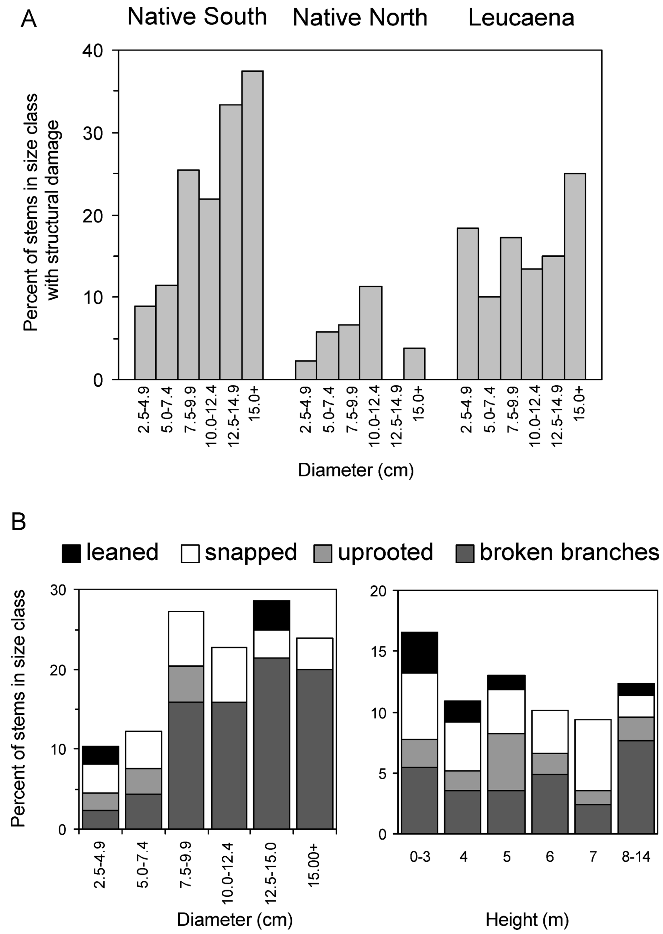

FIGURE 5. (A) Proportion of structural damage incurred by stems within diameter classes for three forest types in Guánica Forest. Broken branches not assessed in native-north or Leucaena forests. (B) Stems incurring various modes of structural damage as a proportion of all stems in each diameter or height class. Data included stems only from native-south, mahogany, and ridgetop sites because broken branches were not assessed for native-north or Leucaena forest.

The type of damage was related to stem size (Fig. 5B). Both taller and wider stems were more likely to have broken branches while shorter, thinner stems more often leaned. Snap height was not related to stem diameter ($R^2 = 0.03$). Stems that were poorly rooted or damaged at or near root level before the hurricane were nearly always snapped or uprooted after the hurricane. Taller, wider stems were also more likely than short, narrow stems to be defoliated (χ^2 for height = 70.432; 5 df; $P < 0.0001$; height classes ≥7 m pooled; χ^2 for DBH = 31.475; 3 df; $P = 0.0076$; ≥10-cm DBH classes pooled). The strongest hurricane winds came from the southeast (Bennett & Mojica 1998) resulting in northwesterly fall directions of stems in Guánica Forest and fragments (Fig. 6).

Surveys in fragments included only damaged stems along a transect, so proportional damage could not be assessed among size classes. However, patterns of stem damage in fragments and Guánica Forest were similar. Total density of damage was 703 stems/ha in fragments and 1004 stems/ha in Guánica Forest. The proportion of damaged stems in the 2.5–4.9-cm DBH class differed by only 8 percent between the fragments and Guánica Forest (52–60 percent, respectively) and by ≤5 percent in all other size classes.

Species effects.—Rates of both defoliation and structural damage differed by tree species. However, defoliation rates were not related to functional traits such as successional status or leaf phenology (Table 2). Pioneers accounted for 80 percent of species with above-average stem damage rates (Table 2). As in other studies of hurricane effects (Putz *et al.* 1983, Zimmerman *et al.* 1994, Asner & Goldstein 1997), no relationship existed between wood density and structural damage.

Litter and nutrients.—Total litterfall averaged 7.5 Mg/ha during the 18-h period of Hurricane Georges or 1.6 times the annual rate reported by Lugo and Murphy (1986). Compared to nonhurricane years, the litterfall pulse was 499 times average daily September litterfall and 17 times the average September monthly rate (Murphy *et al.* 1995). Leaf litterfall totaled 55 percent of annual estimates for the semi-deciduous Guánica Forest, corresponding to the median 50 percent defoliation estimate. Wood litterfall from Hurricane Georges was >11 times than measured for the year 1981. In October 1998, leaves comprised 46 percent, and wood 33 percent, of the total standing litter mass (Table 3). Post hurricane wood litter stocks more than doubled those found in 1981, a nonhurricane year (Lugo & Murphy 1986).

Nutrient content (kg/ha) of standing litter and litterfall immediately after Hurricane Georges exceeded that measured in 1981, primarily due to wood (Table 3). Hurricane leaf litterfall deposited 100 percent of annual N and 170 percent P, despite equaling only 55 percent of annual leaf litterfall. Wood litterfall contained 9.6 times the amount of N and 13.8 times the amount of P deposited in a nonhurricane year (Table 3). Total N, P, and K stocks on the forest floor after the hurricane were 71–320 percent higher than in

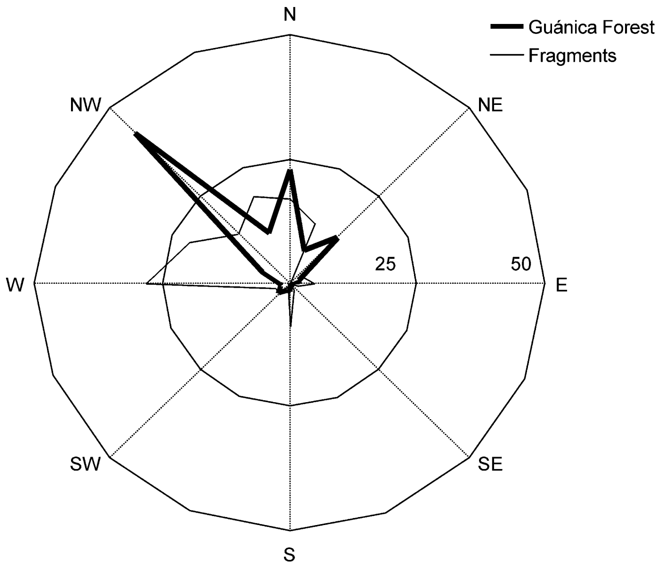

FIGURE 6. Stem-fall directions of snapped, uprooted, and leaning stems in Guánica Forest and nearby forest fragments. Totals are pooled from both Guánica Forest and the fragments. Strongest winds from Hurricane Georges came from the southeast. The radial scale is number of stems. The direction of fall was measured for 259 fallen stems in total; 119 from Guánica Forest and 140 from fragments.

1981 (Table 3). The total standing stocks of Ca (930 kg/ha) and Mg (37.7 kg/ha) after the hurricane were each five times greater than hurricane litterfall inputs. Ca and Mg stocks in 1998 were 47 and 8 percent, respectively, of stocks found in the top 5 cm of soil in 1981 (forest floor Ca and Mg were not measured at that time, Lugo & Murphy 1986).

SHORT-TERM RESPONSE.—After nine months, mortality ranged from 1.3–2.2 percent for trees, and 0.7–7.4 percent for stems (Table 4). Total tree and stem mortality averaged 1.7 and 2.0 percent, respectively. There were no species effects, nor was mortality related to stem DBH or height classes (Table 5). The dead stems in ridgetop and native-south plots included 40 percent of the snapped stems, 21 percent of uprooted stems, 4.5 percent with large branches broken, 8.5 percent that were at least 95 percent defoliated, and 1.5 percent of stems incurring less defoliation. No stems that leaned or lacked visible effects died. Thus, the severity of damage increased the odds of mortality, but not all damaged stems died because many of them resprouted from stumps or roots.

New sprouts appeared below breast height on 29–63 percent of stems in Guánica Forest, far outnumbering the prehurricane sprouting rate of 3.5 percent. Stems on ridgetops sprouted most. The proportion of stems sprouting correlated with the proportion having structural damage ($r = 0.94$; $P = 0.017$), but even undamaged stems without signs of defoliation sprouted at eight times the prehurricane rate (Van Bloem *et al.* 2003). In addition to the sprouts measured, many stems also sprouted above breast height. These higher sprouts would not contribute to increased stem density, basal area, or multistemmed growth forms common to Guánica Forest, but would fill in the small canopy gaps opened by the hurricane.

TABLE 2. *Hurricane effects on representative tree species in Guánica Forest. Defoliation was assessed in native-south forests and mahogany plantations within 2 weeks for species with ≥25 total trees. Median defoliation rate was 50 percent. Damage was assessed in all forest types for species with ≥25 total stems. Average damage rate was 12.4 percent. Designation of species as evergreen, deciduous, and pioneer from Little and Wadsworth (1964), Little et al. (1974), and Molina Colón (1998).*

Species	Successional status	Total trees	Percent ≥ 50 percent defoliated	Leaf habit
Defoliated trees				
Guettarda krugii		42	91	Deciduous
Bursera simaruba	Pioneer	65	86	Deciduous
Krugiodendron ferreum		25	84	Evergreen
Coccoloba diversifolia		83	83	Evergreen
Exostema caribaeum	Pioneer	90	78	Deciduous
Pictetia aculeata	Pioneer	97	75	Deciduous
Amyris elemifera		115	73	Evergreen
Eugenia foetida		94	73	Evergreen
Swietenia mahagani		37	51	Deciduous
Gymnanthes lucida		257	43	Evergreen
		Total stems	Percent damaged	
Damaged stems				
Pilosocereus royenii	Pioneer	47	63.8	
Erythroxylum rotundifolium		35	37.1	
Bursera simaruba	Pioneer	113	30.1	
Pisonia albida	Pioneer	52	25.0	
Erithalis fruticosa	Pioneer	37	21.6	
Eugenia foetida		184	12.5	
Exostema caribaeum	Pioneer	130	12.3	
Krugiodendron ferreum		39	10.2	
Amyris elemifera		204	10.1	
Bourreria succulenta	Pioneer	54	9.3	
Bucida bucerus		65	9.2	
Swietenia mahagani		54	7.4	
Thouinia portoricensis		148	7.4	
Gymnanthes lucida		452	7.1	
Crossopetalum rhacoma		30	6.7	
Coccoloba diversifolia		320	6.3	
Coccoloba microstachya		190	5.8	
Guettarda krugii		187	5.3	
Pictetia aculeata		218	2.8	
Pithecellobium unguis-cati	Pioneer	44	2.3	
Tabebuia heterophylla		138	1.1	
Eugenia xerophytica		55	0.0	

TABLE 3. *Biomass and nutrient content of litterfall and standing litter in the 1.44-ha native-south forest plot. Mass values of standing litter are expressed as means (standard errors) and are corrected for ash-free dry mass.*

		(kg/ha)				
Component	Dry mass (g/m^2)	N	Ca	P	K	Mg
October 1998 standing litter[a]						
Leaves	845 (126)	160	370	3.8	39.5	19.6
Brown wood	573 (65)	69	195	1.4	18.8	5.0
Green wood	30 (16)	3	7	0.1	1.5	0.4
Misc.[b]	356 (38)	92	358	2.3	21.7	12.7
Total	1833 (148)	324	930	7.6	81.5	37.7
July 1981 standing litter[a,c]						
Leaves	1033 (56)	165	–	3.7	17.0	–
Wood	244 (1)[d]	24	–	0.5	2.3	–
Total	1277 (56)	189	–	4.2	19.3	–
September 1998 litterfall						
Leaves	238.7	43.8	44.4	1.2	17.5	4.5
Wood	509.5	40.3	140.7	1.1	21.0	3.1
1981–82 Annual litterfall[c]						
Leaves	433.7	44.3	–	0.7	35	–
Wood	45.6	4.2	–	0.08	1.0	–

[a] $N = 26$.

[b] Miscellaneous category includes small leaf fragments, fruits, and flowers.

[c] July 1981 standing litter and 1981–82 leaf litter values from Lugo and Murphy (1986); $N = 30$, missing nutrient values were not reported therein.

[d] Calculated from data reported in Murphy and Lugo (1986) and Lugo and Murphy (1986a).

DISCUSSION

The effects of Hurricane Georges suggest that hurricane disturbance can be an important force in creating and maintaining the structure of West Indian dry forests. The hurricane reduced the number of large-diameter stems in windward sites by snapping or uprooting but without necessarily causing mortality of these trees due to subsequent resprouting. Low mortality and abundant sprouting would, over time, lead to increased stem density and multistemmed trees without changing species composition (Van Bloem 2004).

HURRICANE EFFECTS ON GUÁNICA FOREST IN CONTEXT OF PREVIOUS STUDIES.—Hurricane effects have been studied in nine tropical and subtropical dry forests, including this study, but comparing hurricane effects from different storms or forests is difficult because the combined effects of storm intensity and duration cannot be easily standardized. However, Everham and Brokaw (1996) and Whigham *et al.* (1999) reviewed the effects of catastrophic winds on various temperate and tropical forests, providing a context into which our results can be placed.

In general, mortality and damage were low in dry forests (Table 6). Guánica Forest (12.4%) was near the middle of the range (7–32%) in stem damage, but lost the most basal area (21%). As suggested by Whigham *et al.* (1999), mortality and basal area loss were lower in dry forests than in wet forests, as was structural damage, with the exception of the S. Florida site (Table 6).

Guánica Forest incurred disproportionate damage to larger-diameter stems—a general trend for dry forests hit by category 3 or stronger hurricanes. Hurricanes affected larger diameter trees in Jamaica (Wunderle *et al.* 1992), St. John (Reilly 1991), and Sri Lanka (Dittus 1985). In Guadalupe, stems of 7.5−15-cm DBH (compared to average stand DBH of 7 cm) were most affected while those >15 cm were less affected. Everham and Brokaw (1996) proposed a unimodal pattern of damage relative to stem diameter with the most damage in intermediate-size stems. This was not the trend in dry forests but large-diameter stems can be quite rare in these forests. For example, our samples included only 86 stems larger than 15-cm DBH, and only 26 stems > 20 cm. Therefore, dry forests may represent only the increasing part of the curve.

In Guánica Forest, stem size influenced the mode of damage incurred (Fig. 5B). Tall, wide-diameter stems would be most exposed

TABLE 4. *Hurricane-related mortality of trees and stems ≥ 2.5-cm DBH in four types of forest in Guánica Forest 9 mo after Hurricane Georges.*

	Mortality percent[a]				
Site	Trees[a]	Stems[a]	Total trees live and dead	Total stems live and dead	Area sampled (m^2)
Native-south	1.6[b]	2.7	850	1886	2490
Native-north	2.2	1.6	836	1223	4000
Ridgetops	2.0	7.4	102	162	200
Leucaena	1.3	0.7	853	1172	6000
Total	1.7	2.0	2641	4443	12690

[a] There were no significant differences in tree mortality among sites ($\chi^2 = 2.262$; $P = 0.45$; 3 df). Stem mortality differed among sites ($\chi^2 = 36.664$; $P < 0.0005$; 3 df).

[b] Tree mortality reported here is only for the two 1.0-ha sites in native-south stands (sampled area was 1800 m^2) because multistemmed trees in the 1.44-ha native-south site were not assessed for mortality. Stem mortality includes all native south stands.

TABLE 5. *Percent stem mortality by size class for height and DBH for all stems in native-north, native-south, ridgetop, and Leucaena plots. Mortality was not assessed in mahogany plantations.*

	Height (m)							
	3–3.9	4–4.9	5–5.9	6–6.9	7–7.9	8–8.9	≥9.0	Total
Total stems	447	865	843	738	364	196	213	3690[a]
Mortality (%)	2.7	2.5	3.2	2.0	1.4	1.0	1.9	2.0

	DBH (cm)						
	2.5–4.9	5.0–7.4	7.5–9.9	10.0–12.4	12.5–14.9	≥15.0	Total
Total stems	2192	1482	464	153	64	86	4441[a]
Mortality (%)	2.4	1.8	1.3	1.3	1.6	1.2	2.0

[a]Totals for height and DBH are not equal because heights were not measured on all live stems. Mortality was not associated with size class. For height: $\chi^2 = 6.165$; $P = 0.19$; 4 df; 7–9-m height classes pooled. For DBH: $\chi^2 = 4.021$; $P = 0.13$; 2 df; 7.5–15-cm DBH classes pooled.

to hurricane winds, but potentially the best anchored. Branch loss on these stems would reduce wind resistance before snapping or uprooting occurred (Vogel 1994). Uprooting was absent in larger stems, suggesting that their root systems were strong enough to withstand winds. Leaning stems were most common in small size classes because thin, flexible stems bent without breaking. Only the distribution of snapped stems across diameter classes followed the unimodal pattern predicted by Everham and Brokaw (1996). Although hurricane-force winds came from directions ranging from southwest to east (Bennett & Mojica 1998), tree-fall directions indicated that the strongest hurricane winds created the most damage (Fig. 6), a commonly observed pattern (Boose *et al.* 1994). In Guánica Forest, the majority of stems fell between north and northwest. In the fragments, tree fall directions were more variable, but still concentrated between north and west, reflecting the position of the fragment in relation to the trajectory of the storm and the mitigating effects of topography.

As in other forests, aspect and forest type influenced damage severity (Everham & Brokaw 1996). Native-north forest incurred substantially less damage than native-south stands. The low damage rates in mahogany plantations and Leucaena forests can be attributed to a combination of factors. First, dominance by trees of a single species and age leads to a continuous canopy resistant to wind. Second, the mahogany plantations were in valleys and the Leucaena forests were on flat land and therefore relatively sheltered. Neither introduced forest type was found on ridges or south facing

TABLE 6. *Comparison of mortality and structural damage caused by hurricanes in various tropical forests.*

Forest life zone	Location	Hurricane (category[a]) year	Percentage of stem mortality (mo after)	Percentage of structural damage (min stem size cm)	Percent loss of basal area	Stem size with most structural damage	Reference
Subtropical dry	Guánica, PR	Georges (3) 1998	2.0 (9)	12.4 (2.5)	22	>7.5-cm DBH	1
Subtropical dry	St John, US Virgin Is.	Hugo (4) 1989		25 (5)		Taller and wider	2
Subtropical dry	Sri Lanka	na (3) 1978	14 (42)	32 (na)		Taller	3
Subtropical dry	Yucatan, Mexico	Gilbert (5) 1988	11.2 (17)	27.6 (10)			4
Subtropical dry	Jamaica	Gilbert (3) 1988		5 (3)			5
Subtropical dry[b]	Dominica	David (4) 1979		4 (10)	7	No trend	6
Subtropical dry	Florida	Andrew (4) 1992	11.5 (4)	85 (2)		Intermediate width	7
Tropical dry	Guadalupe	Hugo (4) 1989	15.8 (16)	21 (3.8)	14	7.5–15-cm DBH	8
Tropical wet	Various	Category 3–5	1–58 (na)	4.5–80 (4–5)[c]	10–58		9

[a]Category based on the Saffir Simpson Index.

[b]These sites sheltered from hurricane winds. Plantations and palm brakes excluded.

[c]For limits defining range, other wet forest studies used 10 cm minimum diameters. Missing data were not reported or calculated in original sources. References: 1 – this study; 2 – Reilly (1991); 3 – Dittus (1985); 4 – Whigham *et al.* (1991); 5 – Wunderle *et al.* (1992); 6 – Lugo *et al.* (1983); 7 – Slater *et al.* (1995); 8 – Imbert *et al.* (1996); 9 – from Everham and Brokaw (1996). Reports of hurricane effects on dry forests of Tonga (Woodroffe 1983), Guam (Kerr 2000), Mauritius (King 1945, Sauer 1962), and Belize (Stoddart 1962) did not quantify damage rates or mortality.

slopes and it was therefore impossible to determine whether their lower damage rates were due to topography or forest type.

RESISTANCE, RESILIENCE AND THE POTENTIAL EFFECTS OF NUTRIENTS.—Guánica Forest contained species that exhibited either resistance (displayed by low rates of damage) or resilience (low mortality and high sprouting) to hurricane winds, which resulted in only minor changes in species composition. Resistance was increased by the prevalence of multistemmed trees because the likelihood of mortality was lower and wind-speed effects on any one stem in a clump were reduced (Vogel 1994). Resistance may also be related to nutrient supply (DeAngelis *et al.* 1989). Following a hurricane in Hawaii, trees in nutrient-limited moist forests resisted damage, breaking less than those in fertilized plots. Conversely, fertilized trees responded with higher post-hurricane growth rates and productivity (Herbert *et al.* 1999). Similarly, Guánica Forest's structural resistance may be related to water or phosphorus limitation, both of which are in short supply (Lugo & Murphy 1986). Trees in resource-limited environments tend to invest high amounts of carbon into physical structure built for strength and longevity (Chapin 1980).

Unable to undergo retranslocation, hurricane leaf litter provided a nutrient pulse to the forest floor equal to average annual inputs with two-thirds of the rainy season remaining. Studies in wet forests have shown that pulses of dead wood resulted in short-term (<5 yr) immobilization of nutrients in microbial pools and decreased forest productivity (Zimmerman *et al.* 1994, Scatena *et al.* 1996). However, dry forest soils rarely remain wet throughout the entire rainy season and wet-dry cycles can release a significant portion of immobilized nutrients by plasmoptysis of microbes (Kieft *et al.* 1987, Lodge *et al.* 1994, Jaramillo & Sanford 1995, Campo *et al.* 1998). Some portion of the hurricane nutrient pulse may therefore have been available for plant uptake, aiding sprout development and refoliation (Lugo & Murphy 1986, Cornejo *et al.* 1994, Cuevas & Lugo 1998).

EFFECTS OF FRAGMENTATION.—Overall damage rates in forest fragments of the region were similar to Guánica Forest. Throughout the dry forest zone, larger-diameter stems incurred proportionally higher structural damage than smaller stems. Most fragments were located on sites that are highly marginal for cultivation or grazing due to slope or thin, rocky soils (Lugo *et al.* 1996). These sites, like ridgetops in Guánica Forest and slopes in Luquillo Forest (Wadsworth & Englerth 1959; Basnet *et al.* 1992, 1993; Scatena & Lugo 1995), provided poor anchorage for trees and resulted in uprooting being the most common type of structural damage in fragments.

SHORT-TERM RESPONSE.—Whereas hurricane disturbance resulted in >20 percent stem mortality in moist or wet tropical forests (Everham & Brokaw 1996), mortality was low in Guánica and other dry forests (Table 6). Catastrophic stem mortality (CSM: mortality resulting directly from a disturbance) was only 2 percent after 9 mo for stems of $\geq$2.5-cm DBH. Mortality was unrelated to stem size, but this was not surprising considering that larger stems have root systems able to support a flush of new sprouts. The 2 percent mortality rate would lead to an average loss of 240 stems/ha and 0.4 m^2/ha basal area (Murphy & Lugo 1986a). We conservatively estimated CSM because delayed mortality can continue for at least 4 yr after a hurricane (Dittus 1985, Lugo & Scatena 1996) as heavily damaged or defoliated stems may die as a result of subsequent stresses such as seasonal or more prolonged droughts (Lugo & Waide 1993, Walker 1995). Although hurricane mortality in stems did not show an association with size class, if delayed mortality caused by CSM is related to structural damage or to degree of defoliation, then larger stems may eventually die in higher proportions.

Over time, however, it is unlikely that CSM will impact as many total stems as background stem mortality (BSM: mortality due to senescence or competition). BSM in Guánica Forest has been calculated at 0.3 percent/yr (P. G. Murphy, pers. obs.). Although CSM from Hurricane Georges was nearly seven times greater than BSM, a hurricane as strong as Georges would have to cross the forest once every ten years to kill the same the number of stems, or four times as often as has historically occurred (Salivia 1972, Quiñones 1992, Miner-Solá 1996).

Whigham *et al.* (1999) predicted that sprouting would be an important response in dry forests, particularly when mortality and damage rates were low. Furthermore, they predicted that sprouting would be greater on damaged stems and that the sprouting response would result in minimal changes in species composition of the forest. The prevalence of sprouting following Hurricane Georges largely followed these predictions except that sprouting occurred regardless of mode or severity of structural damage, even on undamaged stems (Van Bloem *et al.* 2003). Survival of sprouts would generate multistemmed trees and result in the dense, clumped growth form of West Indian dry forest. Although the cohort of new sprouts experienced some mortality, 88 percent survived 2 yr after the hurricane (Van Bloem *et al.* 2003) and, in some cases, sprout growth exceeded 2 m in height. With a forest-wide sprouting rate of 33 percent, it would take only two hurricanes per tree generation to achieve the current proportion of multistemmed trees (42%), assuming sprouting effects were roughly additive, or a single hurricane in heavily impacted areas, such as the ridgetops. Based on typical growth rates (Murphy *et al.* 1995), and the size of some stems in multistemmed trees, it appears that many stems could have arisen as a response to a hurricane in 1928 (Fig. 1). Although we recognize that alternative explanations exist (*e.g.*, cutting and drought), our observations support hurricane disturbance as a plausible explanation for the maintenance of high stem densities seen in Guánica Forest and throughout dry forests of the West Indies. This conclusion reflects the observation that lowland tropical rainforests also tend to be shorter and denser in hurricane-prone locations (de Gouvenain & Silander 2003).

Whigham *et al.* (1999) noted that "there are few examples where it has been shown that the structure and dynamics of the forest are strongly influenced by periodic hurricane events as much or more than by background canopy gaps." Dry forests of the West Indies may be an exception. As demonstrated in Guánica Forest, hurricanes disproportionately damaged larger stems and promoted sprouting at or near the base of trees, even on undamaged stems.

Damage rates were primarily determined by stem diameter and topographic exposure to wind. Damaged stems did not necessarily die. Sprouting minimized mortality and changes in species composition, and increased the potential to add new stems to the forest. Post-hurricane mortality rates were elevated over background mortality, but would affect fewer stems over time. A collection of forest fragments incurred the same rate and type of structural damage as Guánica Forest, suggesting that the spatial extent of a forest stand did not influence hurricane effects. The effects of Hurricane Georges on the structure of Guánica Forest were comparable to other cases of hurricane disturbance in dry forests, but were less than those reported for most wet tropical forests. Climate characteristics alone fail to explain dry forest structure in the West Indies and, as hurricanes are common in the region (Neumann *et al.* 1993), we conclude that the unique West Indian dry forest structure arises at least in part from recurring hurricane disturbance.

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