BIOTROPICA 37(1): 16–24 2005

Factors Affecting Mortality and Resistance to Damage Following Hurricanes in a Rehabilitated Subtropical Moist Forest[1]

Rebecca Ostertag[2,3,4], **Whendee L. Silver**[3,4] and **Ariel E. Lugo**[4]

[3]Department of Environmental Science, Policy, and Management, 151 Hilgard Hall, University of California, Berkeley, CA 94720-3110, U.S.A.

[4]International Institute of Tropical Forestry, Ceiba 1201, Jardín Botánico Sur, Río Piedras, PR 00926-1119, U.S.A.

ABSTRACT

The ability to resist hurricane damage is a property of both individuals and communities, and can have strong effects on the structure and function of many tropical forests. We examined the relative importance of tree size, species, biogeographic origin, local topography, and damage from previous storms in long-term permanent plots in a rehabilitated subtropical moist forest in Puerto Rico following Hurricane Georges in order to better predict patterns of resistance. Severe damage included uprooted trees, snapped stems, or crowns with greater than 50 percent branch loss. Hurricane induced mortality after 21 mo was 5.2 percent/yr, more than seven times higher than background mortality levels during the nonhurricane periods. Species differed greatly in their mortality and damage patterns, but there was no relationship between damage and wood density or biogeographic origin. Rather, damage for a given species was correlated with mean annual increment, with faster growing species experiencing greater damage, suggesting that growth rate may reflect a variety of life history tradeoffs. Size was also predictive of damage, with larger trees suffering more damage. Trees on ridges and in valleys received greater damage than trees on slopes. A strong relationship was noted between previous hurricane damage and present structural damage, which could not solely be explained by the patterns with size and species. We suggest that resistance of trees to hurricane damage is therefore not only correlated with individual and species characteristics but also with past disturbance history, which suggests that in interpreting the effects of hurricanes on forest structure, individual storms cannot be treated as discrete, independent events.

RESUMEN

La habilidad de resistir daños causados por un huracán es una propiedad común de individuos y comunidades, y puede tener efectos marcados en la estructura y función de muchos bosques tropicales. Con el fin de predecir mejor los patrones de resistencia, nosotros examinamos la importancia relativa del tamaño de los árboles, las especies, el origen biogeográfico, la topografia local y el daño por tormentas pasadas en parcelas permanentes de largo plazo en un bosque rehabilitado subtropical húmedo en Puerto Rico, luego del paso del huracán Georges. Las daños severos incluyeron árboles con raíces socavadas, tallos rotos y/o doseles con pérdida de ramas mayor del 50 por ciento. La mortalidad inducida por el huracán después de 21 meses fue de 5.2 por ciento por año, siete veces superior que los niveles de mortalidad ocurridos durante períodos sin huracanes. Las especies difirieron mayormente en su mortalidad y patrones de daño, pero no hubo relación entre el daño causado y la densidad de la madera u origen biogeográfico. Más bien, el daño causado para una cierta especie estaba correlacionado con el incremento del promedio anual, con las especies de rápido crecimiento experimentando mayor daño, lo cual sugiere que la tasa de crecimiento puede reflejar variedad en las concesiones de historia de vida de las especies. El tamaño de los árboles también fue indicativo del daño, con los árboles más grandes sufriendo mayor daño. Los árboles en las cimas y en los valles recibieron mayor daño que los árboles en las pendientes. Se observó una fuerte relación entre el daño causado por huracanes pasados y el actual daño estructural, el cual no pudo ser explicado solamente por los patrones de tamaño y especies. Nosotros sugerimos que la resistencia de los árboles al daño causado por el huracán se correlaciona no sólo con las características individuales y de las especies, sino también con el historial de daños anteriores, lo cual sugiere que en la interpretación de los efectos de huracanes en la estructura del bosque, una tormenta individual no se puede tratar como un evento independiente y discreto.

Key words: disturbance; mean annual increment; mortality; resilience; resistance.

THE ABILITY TO AVOID DAMAGE DUE TO NATURAL DISTURBANCES, defined as resistance, and the ability to recover after disturbances, defined as resilience, are important properties of individual species as well as communities (Holling 1973, Walker *et al.* 1999, Gunderson 2000). Differences in resistance and resilience among individual trees will alter competitive hierarchies and will therefore have strong effects on future forest structure. Hurricanes are an important natural disturbance in many tropical forests that act to define forest structure and function, particularly through variation in their intensity and frequency. Hurricane winds can lead to defoliation and large nutrient inputs to the forest floor, structural damage, decreased biomass, and mortality (*e.g.,* Lugo *et al.* 1983; Whigham *et al.* 1991; Walker 1991, 1995; Weaver 1994; Lugo & Scatena 1996; Ostertag *et al.* 2003). These disturbances can also alter resource availability and heterogeneity, providing opportunities for regeneration, species invasion, and alteration of successional pathways (Guzmán-Grajales & Walker 1991, Everham *et al.* 1996, Harrington *et al.* 1997).

Posthurricane surveys have shown that trees differ in their resistance to damage and in their mortality rates (Walker 1991, Zimmerman *et al.* 1994), but predicting damage and mortality has proven difficult because multiple factors may determine how a tree responds to hurricane winds and these factors may operate at differing spatial and temporal scales. The level of damage a tree experiences may relate to its size (Lugo *et al.* 1983, Walker 1991, Herbert *et al.* 1999), position on the landscape (Bellingham 1991, Boose *et al.* 1994, Weaver 1999), or to species-specific characteristics such as architecture, wood density (Zimmerman *et al.* 1994), or biogeographical origin (MacDonald *et al.* 1991). For example, after Hurricane Hugo in Puerto Rico, pioneer species, characterized by low wood densities, suffered greater damage than many nonpioneer trees (Zimmerman *et al.* 1994). Nonnative species displayed more damage than native species after a hurricane in the Mascarene Islands, and it was hypothesized that this result was because those species were not adapted

---

[1] Received 2 March 2004; revision accepted 22 August 2004.

[2] Current address: Department of Biology, University of Hawaii at Hilo, 200 W. Kawili St. Hilo, HI 96720; e-mail: ostertag@hawaii.edu

to the disturbance regime (MacDonald *et al.* 1991). This suggestion that biogeographic origin affects damage resistance was also made for provenances of *Pinus caribaea* and *P. oocarpa*, after noting in plantations in Puerto Rico that provenances from locations with higher hurricane frequencies had lower mortality rates and less mechanical injury (Liegel 1984). Complicating these factors, however, is the previous damage to an individual tree and the length of time between storms. Other research (Sauer 1962, Putz & Sharitz 1991, Elmqvist *et al.* 1994, Peterson 2000) provide some circumstantial evidence that previously damaged trees are more susceptible to future damage, but this question has not been addressed on an individual tree level on tagged trees followed through multiple storms. We had a rare opportunity to examine all of these factors in parallel, after the passage of Hurricane Georges in 1998, which had particularly strong effects in a subtropical moist forest in the northeastern portion of Puerto Rico. This forest experienced a hurricane 9 yr previously, in an area in which trees were tagged, measured, and hurricane damage was quantified. Our objective was to examine the influence of hurricanes on forest structure and function by quantifying multiple factors including the relative importance of species, biogeographic origin, local topography, size, and previous damage as factors affecting resistance to hurricane damage and life history tradeoffs. We hypothesized that tree damage is strongly related to tree size, topography, and species characteristics but does not differ between native and nonnative species. We also hypothesized that previous damage from earlier hurricanes, although partially related to species and size characteristics, will in itself also be a useful predictor of future damage.

METHODS

SITE AND STORM DESCRIPTIONS.—The Cubuy Annex of the Luquillo Experimental Forest (LEF), Puerto Rico (18°17′N, 65°53′W) was once pasture but was reforested in the mid-to-late 1930s with single and mixed species plantings and natural regeneration (Marrero 1947). Today it is a diverse closed canopy secondary forest containing 75 tree species (Silver *et al.* 2004). The canopy is uneven with many of the larger diameter trees ranging in height from 15 to 30 m. The life zone is classified as subtropical moist forest (Ewel & Whitmore 1973), with elevations ranging from 300 to 550 m. Soils are generally highly weathered Ultisols derived from volcanoclastic material.

Monitoring of this forest began in 1959 when the U.S. Forest Service established 116 permanent circular plots, which were of 0.04 ha in size and spaced 100 m apart (from center to center) in a 9 ha area of contiguous forest. At that time, only merchantable trees that were greater than 9.1 cm diameter at breast height (DBH) (DBH at 1.37 m above the ground) and of appropriate form were tagged and identified. These surveys were expanded in 1992 when all trees that were greater than 9.1 cm DBH were tagged and identified. Large trees >24.1 cm DBH outside of the 0.04 ha plots were also tagged, up to 16.05 m from the center of the plot. In this study, we searched for all trees within the 0.04 ha plots as well as these larger tagged trees so that we would have a representative range of sizes and species.

This forest was hit by two hurricanes within a 9-yr period. On 18 September 1989, Hurricane Hugo hit northeastern Puerto Rico, including the LEF. This hurricane was a Category 4 storm on the Saffir–Simpson scale with sustained winds of 166 km/h and gusts of 194 km/h (Scatena & Larsen 1991). Hurricane Georges made landfall on the southeastern coast of Puerto Rico on 21 September 1998 and traversed the island from east to west. The island-wide overall statistics for hurricane were sustained winds of 184 km/h, gusts of 241 km/h, and a Category 3 storm on the Saffir–Simpson Scale (Ostertag *et al.* 2003). Although Hugo was an overall more powerful storm than Georges, all indications are that the Cubuy forest area was damaged more severely by Georges. Evidence of this comes from Zimmerman *et al.* (1995), who surveyed a nearby site in the Cubuy region in which they noted minimal damage and estimated peak sustained winds of 115 km/h. In addition, the Cubuy area was farther from the eye path in Hurricane Hugo (see Zimmerman *et al.* 1995), and during Hurricane Georges a different wind direction placed this forest much closer to the eye of the second hurricane (for a map of the eye of the storm, see USGS Fact Sheet 040-99, http://water.usgs.gov/pubs/FS/FS-040-99/pdf/fs-040-99.pdf).

TREE DAMAGE AND GROWTH MEASUREMENTS.—During the 1992 forest survey described above, measurements on the effects of Hurricane Hugo were also taken in all 116 plots. Unfortunately, the data were collected 3 yr after the hurricane, and it is likely that these methods underestimated defoliation damage because this would be less evident after 3 yr, while evidence of snaps, uproots, or major branch damage remain. We used the same methodology as in the 1992 survey and took tree damage measurements in 1999 and 2000 (at 6 and 21 mo after Hurricane Georges).

To compare the effects of the two hurricanes, we focused on a subset ($N = 21$) of the 116 plots. Fifteen of these plots were being used for a previous study (Silver *et al.* 2004) and the additional plots were chosen for the accessibility and to increase the range of tree species sampled. The plots were spread out across the original 9 ha area and contained a variety of key species. A total of 976 tagged trees were located and measured in 1999 and in 2000, these trees were checked for mortality only.

In both the 1992 and 1999 sampling, tree status was classified as live, recently dead (due to the hurricane), or old dead (dead before most recent hurricane). Each tree was also classified by crown class (dominant, codominant, intermediate, or suppressed); when the top of the tree had snapped off, crown class was estimated based on the debris on the forest floor. Every live tagged tree was measured for DBH (DBH at 1.37 m) allowing for mean annual increment of diameter growth to be calculated based on the 7-yr growth period from 1992 to 1999. Mortality was calculated as (no. of trees dead) × 100/total no. of trees/7 yr. Wood density values were taken from a pantropical survey (Reyes *et al.* 1992).

Damage to trees was quantified by noting damage type (snap, uproot, defoliation and branch damage, or no visible damage). Snap height (done only in 1999) and angle of uproot were also noted. Whenever possible, branch damage was assessed. A category of no branch damage was used for trees that had no visible defoliation or loss of branches. However, trees in all other categories experienced defoliation but differed in the degree of branch damage. Light damage was defoliation and branch loss of small terminal branches that affected <25 percent of crown. Moderate damage affected 25–50 percent of crown and consisted of loss of fine and larger diameter branches, and heavy damage affected >50 percent of crown and was loss of very large branches. This same classification

TABLE 1. *Mortality of trees at each sampling period for the most abundant tree species (>20 individuals) and total number of trees of all species in the Cubuy annex of LEF. Mortality from Georges was measured at 6 and 21 mo and calculated as the number of dead trees divided by total sample size at that time period. Sample sizes changed slightly between the two measuring periods because some trees could not be found at both periods. The background mortality rate was calculated as the species that were alive in the 1992 forest survey but were categorized as old dead (i.e., dead before the hurricane) in the 1999 survey. Species are listed from high to low total mortality with nonnative species in bold.*

	Trees at 6 mo after Georges		Trees at 21 mo after Georges		Trees before Georges			
	N	Mortality (percent/yr)	*N*	Mortality (percent/yr)	*N*	No. of live in 1992	No. of dead before hurricane	Background mortality (percent/yr)
Calophyllum antillanum	136	14.7	136	14.7	149	136	13	1.2
Roystonea boriquena	39	10.3	37	9.3	39	39	0	0.0
Tectona grandis	139	10.1	139	3.3	147	139	8	0.8
Syzygium jambos	42	9.5	42	2.7	42	42	0	0.0
Hymenaea courbaril	24	0.0	24	2.4	24	24	0	0.0
Tabebuia heterophylla	268	0.7	268	1.3	268	258	10	0.5
Andira inermis	58	0.0	57	1.0	58	58	0	0.0
Mangifera indica	28	0.0	27	0.0	28	28	0	0.0
All species	930	7.5	928	5.2	976	930	46	0.7

was also used for the royal palm, *Roystonea boriquena*, a conspicuous component in this forest. Because the palm does not have branches it was evaluated as to whether it was missing <25 percent, 25–50 percent, or >50 percent of its leaves.

STATISTICAL ANALYSES.—Relationships for independence between categorical variables were evaluated using *G*-tests, which are log-likelihood ratio tests, where $G = 2 \ln$ (likelihood ratio), and where the *P*-value is based on a χ^2 distribution (Sokal & Rohlf 1995). Data were analyzed using JMP (SAS Institute 1995). *G*-tests were done to examine how both tree mortality and tree damage were affected by the following categorical variables: DBH class in 10-cm increments, crown class, local topography, and damage in the previous hurricane (Hugo) based on the 1992 measurements. In the 1992 sampling only one tree was listed as having light defoliation, and so this tree was combined with the no damage category. In addition, because there were few snaps and uproots in the 1992 data, we also combined these categories. In translating DBH into categories, we grouped all trees ≥40 cm due to the paucity of very large trees in this developing forest.

To facilitate comparisons across groups with differing sample sizes, we created a "damage index," which is percentage of trees with heavy branch damage, snaps, or uproots in a given class. This damage index thus concentrates on trees with severe crown loss or stem and root breakage and is comparable to one of the components calculated by Bellingham *et al.* (1995) that was used to group species into different degrees of resistance and recovery. The damage index was used to compare across species, size classes, crown classes, topography, and previous damage. When used to compare species, the damage index was only calculated for species in which there were 20 or more individuals; when used to compare the other variables, there were hundreds of individuals making up the percentage. The damage index represents the severity of damage relative to the total number of individuals within that category (*e.g.*, a damage index of 33 for a species would mean that one-third of the individuals had severe damage in Hurricane Georges).

RESULTS

MORTALITY FROM HURRICANE GEORGES.—Mortality 6 mo after Hurricane Georges was only 7.5 percent/yr, but decreased to 5.2 percent/yr at 21 mo. This storm-related mortality was over seven times greater than the background mortality of 0.7 percent/yr for trees from the 1992 to 1999 period (Table 1). Mortality varied greatly by species: the nonnative species *Mangifera indica* had the lowest rate and the native species *Calophyllum antillanum* had the highest rate (Table 1).

Trees that uprooted or snapped were much more likely to die after 21 mo, while those trees with none, light, or medium amounts of defoliation were more likely to survive ($G = 183.2$, df $= 5$, $P < 0.0001$, Table 2). Overall 3.2 percent of defoliated trees, 37.7 percent of snaps, and 41.9 percent of uprooted trees died within 21 mo of the storm. Although the type of damage affected the probability of death, mortality was independent of other characteristics such as crown class, DBH class, topography, or damage in the previous hurricane.

RESISTANCE TO DAMAGE FROM HURRICANE GEORGES.—Of the trees that were not killed in the storm, only about 9 percent of trees had no damage (Table 2). Species varied greatly in their resistance to damage

TABLE 2. *Observed number of live and dead trees (and expected values in parentheses) suffering various types of hurricane damage. Trees were classified by whether they showed evidence of branch damage (light, medium, or heavy canopy damage), snap of trunk, or complete or partial uprooting. Snapped or uprooted trees died more often than would be expected.*

	Branch damage					
	None	Light	Medium	Heavy	Snap	Uproot
Dead	1 (6.2)	1 (23.8)	4 (14.0)	16 (18.7)	46 (10.1)	14 (2.6)
Live	73 (67.9)	287 (264.2)	165 (155.0)	210 (207.3)	76 (111.9)	18 (29.4)

TABLE 3. *Percentage of the most abundant tree species (>20 individuals) suffering various types of hurricane damage. Trees were classified by whether they showed evidence of branch damage (light, medium, or heavy canopy damage), snap of trunk, or complete or partial uprooting. Species are listed according to their damage index, which is the sum of heavy canopy damage, snaps, and uprooted trees. Mean annual increment was also calculated for each species, except for the palm which does not have secondary growth. Nonnative species are in bold.*

		Branch damage						
	None	Light	Medium	Heavy	Snap	Uproot	Damage index (percent)	Mean annual increment (cm/yr)
Hymenaea courbaril	0.0	16.7	4.2	50.0	20.8	8.3	79.2	0.381
Calophyllum antillanum	2.2	10.3	19.1	36.8	22.8	8.8	68.4	0.232
Syzygium jambos	7.1	26.2	9.5	28.6	28.6	0.0	57.1	0.220
Roystonea boriquena	5.3	21.1	18.4	36.8	18.4	0.0	55.3	
Mangifera indica	17.9	10.7	17.9	42.9	10.7	0.0	53.6	0.328
Andira inermis	17.9	25.0	16.1	25.0	16.1	0.0	41.1	0.103
Tectona grandis	11.6	40.6	22.5	10.9	10.9	3.6	25.4	0.220
Tabebuia heterophylla	9.4	48.9	24.4	13.9	2.3	1.1	17.3	0.101
All species	8.1	31.5	18.5	24.7	13.7	3.5	41.9	0.176

(Table 3). Overall, the damage index across species was 41.9 percent, but was as low as 17.3 percent for *Tabebuia heterophylla* and as high as 79.2 percent for *Hymenaea courbaril*. Tree damage was not correlated with wood density ($P > 0.4$) and did not appear related to biogeographic origin of species, as both the native and nonnative species spanned the range in terms of damage index. Rather, the damage index of a species was positively correlated with mean annual diameter growth increment (Spearman's rho = 0.81; $P < 0.03$), with species with faster diameter growth rates experiencing greater amounts of damage. This result suggests a life history tradeoff between growth rate and damage (Table 3), although it is influenced by tree size because growth rate is not a constant variable. When correlating basal area increment with damage index, the relationship was not significant. However, when using all variables in a stepwise multiple regression, damage index was related most strongly to basal area increment and average DBH of the species ($y = 92{,}628$ BAI (m^2) $- 6.7$ AVERAGE DBH (cm) $+ 116.5$; $R^2 = 91.9$ percent). Thus, in the multiple regression, the damage index of a species was greater for species that were of smaller size in the forest and were fast growing.

Across all trees, most trees fell in a NW direction (275–30°) or a SW direction (170–240°), with a few trees falling E (85–102°). Since the major path of the storm was from east to west, these treefall likely reflect in part average wind orientation, as demonstrated by Boose *et al.* (1994). Average snap height was 5.1 m, with 26 trees snapping between 0 and 2 m, 26 trees between 2.1 and 4 m, 32 trees between 4.1 and 6 m, 29 trees between 6.1 and 8 m, 9 trees between 8.1 and 10 m, and 6 trees snapping at heights > 10 m.

Damage was not independent of DBH class ($G = 65.1$, df $= 15$, $P < 0.0001$). Heavy branch damage was less common than expected for smaller trees (<20 cm), but higher than expected for trees in larger size classes. Uproots were also common for trees in the 30–40 cm range. Overall, damage index increased with tree size (Fig. 1a). Damage was also related to crown class ($G = 90.5$, $P < 0.0001$). Dominant trees, which were emergent in the canopy, tended to have more medium-to-heavy defoliation, but those trees did not snap or uproot as much as shorter trees. Suppressed trees appeared to have less damage in general (Fig. 1b).

Damage was also not independent of topography ($G = 19.6$, df $= 10$, $P < 0.04$). Slopes tended to have fewer uproots and less heavy branch damage than expected, flat ridge areas had more uproots and fewer snaps than expected, while valleys tended to be higher than expected in all three types of major damage. The percentage of trees with heavy damage growing on slopes was lower than for trees growing on ridgetops or in valleys (Fig. 1c).

Previous storm damage in Hurricane Hugo had a large effect on damage in Hurricane Georges (Fig. 1d). Trees that were classified as snapped or uprooted in 1992 data set were more likely than expected to snap or uproot after Hurricane Georges ($G = 28.9$, df $= 15$, $P < 0.02$). In addition, those trees with previous heavy crown damage were also more likely to experience the same heavy crown damage again. However, we also found that trees with no previous damage were also susceptible to damage (Fig. 1d), suggesting that other variables contributed to resistance. Our other analyses show that larger trees and trees of certain species tended to be damaged more than others. These factors alone, though, cannot account for the previous damage results. For example, in six out of eight species, the damage index was greater for trees that had previous damage (Table 4), suggesting that species composition alone did not determine these damage patterns. Similarly, trees <40 cm DBH that received heavy branch damage, snaps, or uproots in the previous hurricane were more likely to sustain this type of damage again than trees that did not receive any damage in the earlier storm (Table 4). Thus, although some species and larger size classes were more likely to be damaged in Hurricane Georges, previous hurricane damage also contributed to hurricane damage in this storm—and to some extent its contribution is independent of diameter class or species.

COMPARISON OF DAMAGE BETWEEN THE TWO HURRICANES.—Although measurements were taken at different time periods after the hurricanes, some comparisons can be made between the two storms, taking this time difference into account. Mortality was lower after Hurricane Hugo

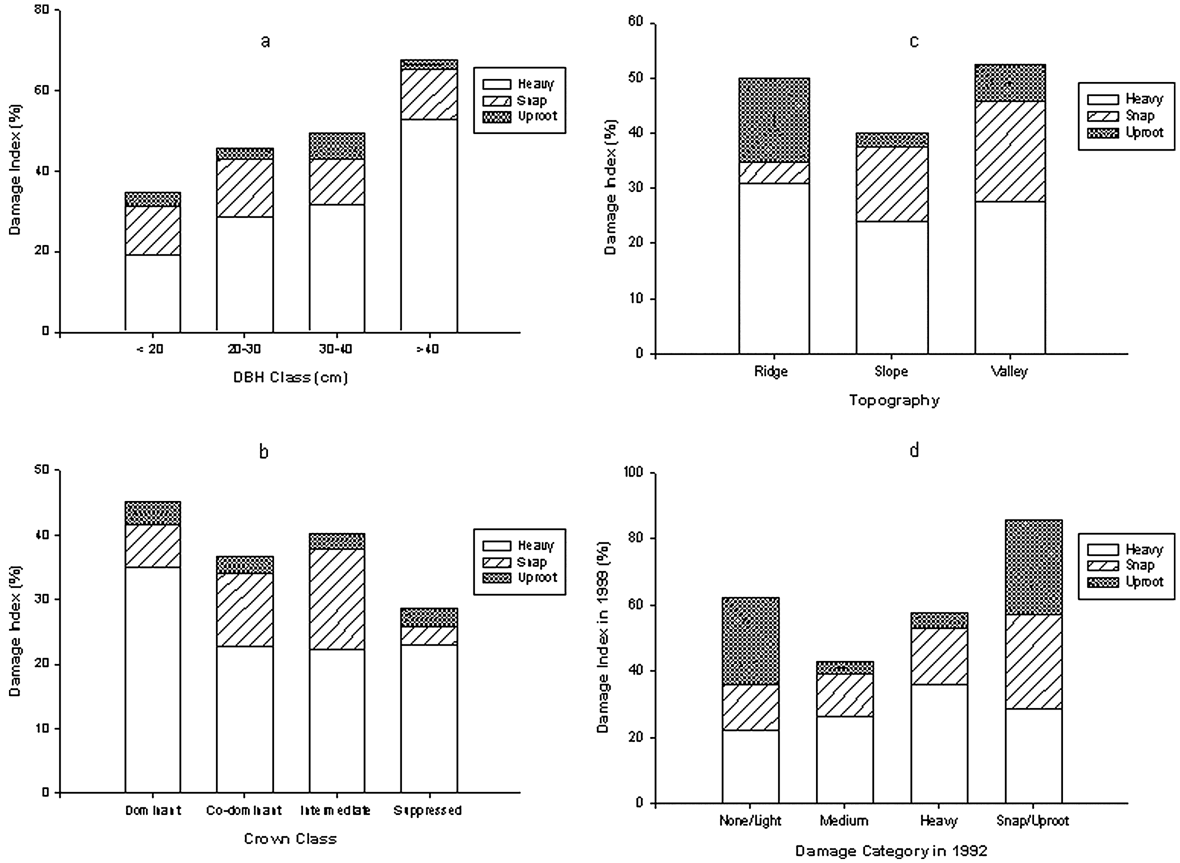

FIGURE 1. Damage index in relation to various forest or individual tree characteristics. The damage index was calculated as the percent of trees that uprooted, snapped, or had >50 percent canopy branch damage of all the trees in that class. (a) Damage index in relation to tree size. (b) Damage index in relation to crown class. (c) Damage index in relation to topography, as determined for each tree during the 1992 survey. (d) Damage index from Hurricane Georges in relation to tree damage in Hurricane Hugo, which hit this area 9 yr earlier. Trees were classified into damage categories in 1992, and the previous damage is related to the amount of damage in the second storm.

and the 1992 damage indices were always lower than the ones from Hurricane Georges (Table 5). In addition, other factors affecting damage were similar between the two storms, suggesting that we have identified the important predictor variables. In both storms, larger diameter trees had more damage and canopy dominants tended to have more heavy branch damage. Topography had no significant effect in the first storm but trees on slopes had less damage in the second storm (Table 5). Species comparisons could not be made because dead trees in 1992 were not identified by species. However, all evidence suggests that the second hurricane did more damage to the forest.

DISCUSSION

The ability of trees to resist severe wind damage is one important aspect of a species' life history, which along with regeneration abilities and the characteristics of the disturbance regime, will help define the structure of the community (Lugo & Scatena 1996). Given that Scatena and Larsen (1991) suggest that a Category 4 storm hits Puerto Rico on average every 50–60 yr, most trees will experience several high-intensity storms over their lifetime. Damage and recovery from storms will be associated with interactions between storm variables and the specific environmental characteristics of a site. Our results suggest that resistance to damage will be related to tree size, topographic position, species characteristics, and past disturbance history.

Mortality of trees is an important statistic to consider because tree death will significantly alter light availability and offer opportunities for structural change. Mortality from this hurricane was elevated sevenfold above background mortality levels, which is a common result of severe storms in the tropics (Bellingham *et al.* 1992, Lugo & Waide 1993, Lugo & Scatena 1996, Weaver 1998a). When multiple measurements are made, mortality is noted to occur for several years after the storm (Whigham *et al.* 1991, 1999; Walker 1995; Frangi & Lugo 1998; Weaver 1999). Mortality in our study was related exclusively to the type of damage rendered, with most mortality coming from snapped or uprooted trees.

In contrast, the severity of damage to trees that survived the hurricane was related to a variety of size and life history characteristics. Similar to other studies, we found that tree diameter and canopy position influence the type and severity of damage, with larger trees generally experiencing greater damage of all types (Fig. 1a; Lugo *et al.* 1983, Putz & Brokaw 1989, Brokaw & Walker 1991, Basnet *et al.* 1992,

TABLE 4. *The effect of previous hurricane damage is to some degree independent of species, tree size, and topography. The table shows the damage index both for trees that received no damage during Hurricane Hugo (data recorded in 1992) and trees that received either heavy branch damage, snapped, or uprooted in the earlier hurricane. Note that for six of eight species trees that had previous damage had a higher damage index than trees that did not have previous damage. In addition, trees <40 cm DBH and trees in all topographic positions had higher values if they had been damaged in the previous storm.*

	No damage in 1992	Damage in 1992
Species		
Calophyllum antillanum	39.0	100.0
Roystonea boriquena	71.2	100.0
Tectona grandis	57.9	33.3
Syzygium jambos	82.4	60.0
Hymenaea courbaril	23.1	60.0
Tabebuia heterophylla	54.1	66.7
Andira inermis	12.5	41.7
Mangifera indica	11.4	41.7
DBH class (cm)		
<20	31.7	47.8
20–<30	41.1	67.7
30–<40	55.0	66.7
≥40	84.6	63.6
Local topography		
Ridge	30.8	100.0
Slope	30.1	48.3
Valley	47.8	80.0

Table 5. *Comparisons between Hurricane Hugo data (measured 3 yr after the storm) and Hurricane Georges (measured 9 mo after).*

	Hugo	Georges
Storm characteristics		
Mortality (percent/yr)	1.3	5.2
Major direction of treefalls	90–270	170–30
Damage indices		
DBH class (cm)		
<20	10.1	34.4
20–<30	14.9	45.6
30–<40	17.9	49.2
≥40	44.4	67.5
Crown class		
Dominant	9.6	45.1
Codominant	7.3	36.5
Intermediate	9.2	40.2
Suppressed	19.0	28.6
Topography		
Ridge	17.2	50.0
Slope	14.1	40.0
Valley	13.5	52.5

Zimmerman *et al.* 1994, Weaver 1998a, Peterson 2000, Platt *et al.* 2000), although there are exceptions (Bellingham 1991, Putz & Sharitz 1991, Bellingham *et al.* 1995, Harrington *et al.* 1997, Burslem *et al.* 2000). Slopes tended to have less damage (Fig. 1c; Basnet *et al.* 1992, Weaver 1998b), but this varies to some degree with the landscape heterogeneity and range of topographic variables (Bellingham 1991, Bellingham *et al.* 1992). Exposure has been shown by modeling exercises using digital elevation maps to also strongly affect tree damage (Boose *et al.* 1994), but we lack the meteorological information to conduct a similar type of analysis.

As expected, we noted strong differences in resistance to damage among species. However, relating damage to species characteristics was more challenging. We found no clear patterns in damage between native and nonnative species, in contrast to other studies (Tables 1 and 3). These studies were largely observational on only a few species, noting that a nonnative species (sometimes in plantations or dominant in a stand) had large amounts of damage (*e.g.*, MacDonald *et al.* 1991, Basnet *et al.* 1992, Harrington *et al.* 1997). In addition, the three nonnative species are all of Asian origin and are likely to be subject to cyclones in some part of their range. Similar to Bellingham *et al.* (1995), we also did not find patterns relating wood density with damage, but we used compiled published numbers rather than measuring on the trees at our site. Zimmerman *et al.* (1994) did find a relationship between wood density and damage when they used many more species, but another study showed that elastic modulus was more correlated with damage than wood density (Asner & Goldstein 1997).

We noted a life history tradeoff between diameter growth rate and resistance to damage on a species basis. Because growth rate integrates variables such as architecture, elastic modulus, successional status, and wood density, we suggest that this may be an appropriate scale to address this question. For example, *Tabebuia heterophylla* had the slowest growth rate (Table 3), very low mortality (Table 1), and the lowest damage index (Table 3). Coupled with its wind-dispersed seeds, it is not surprising that this species is the most abundant tree in the area (more than 25 percent of all stems measured), and it has been noted to be dominant in abandoned pasture sites in another study in the region (Zimmerman *et al.* 1995). Species dominance, however, may be influenced by the fact that this a rehabilitated forest and the plantings may have altered natural densities. Species such as *Hymenaea courbaril*, *Mangifera indica*, and *Calophyllum antillianum* had high damage indices and relatively fast growth rates (Table 3).

These species differences can be put in the context of the damage and responsiveness syndromes defined by Bellingham *et al.* (1995) and elaborated on by Batista and Platt (2003). Although this scheme was developed for understanding community structure in natural forests, it is relevant with our species-specific approach to damage in our mixed forest. They grouped species into four categories based on whether they had low or high damage from a hurricane (resistance) and their posthurricane growth rates (responsiveness). Species with low damage and fast posthurricane recovery are called Usurpers; species with low damage and slow recovery are called Resistant; species with high damage and fast recovery are Resilient; and species with high damage and slow recovery are Susceptible. Although our growth rate information cannot be broken down as pre- and posthurricane given that we had two storms over our measuring period, we suggest that with its slow growth rate and low damage index, *Tabebuia heterophylla* would fit in the Resistance syndrome and those species with high damage and fast growth rates would likely fit in the Resilience syndrome. A species such as *Tectona grandis*, with its low damage but fairly high growth rate may fit the Usurper syndrome. Species in these three categories are more likely to persist in areas with a high frequency of hurricanes, and provides a conceptual framework for understanding species differences (Batista & Platt 2003). A Usurper species is distinguished from a Resistant one by its ability to grow fast after a hurricane (*i.e.*, take advantage of altered resource availability). Given that we cannot examine pre- and posthurricane growth rate separately we cannot adequately distinguish between these two categories. However, if the tradeoff between growth rate and resistance holds for other tropical forests, we would predict that Resistant species would be more prevalent than Usurper species. Our results are also supported by a study of two tree species in Nicaragua after Hurricane Joan; *Vochysia ferruginea* had rapid growth rates and high mortality while *Qualea paraensis* had much slower growth rates but very little mortality (Boucher *et al.* 1994). The same pattern was seen in several temperate and tropical studies that compared slow- and fast-growing trees (Foster 1988, Elmqvist *et al.* 1994) and with species varying in shade tolerance (Merrens & Peart 1992). These tradeoffs may be further influenced by site characteristics such as nutrient availability. In a Hawaiian forest *Metrosideros polymorpha* trees fertilized with the limiting nutrient phosphorus suffered more canopy damage but also recovered faster after the hurricane and were therefore considered more functionally resilient (Herbert *et al.* 1999). Trees with higher nutrient levels had higher leaf area indices before the storm but were able to recover due to a faster rate of photosynthesis per unit leaf area and aboveground net primary productivity (Herbert *et al.* 1999). We suggest that life history tradeoffs, implicit in these hurricane syndromes, should be further considered when thinking about community resistance.

By following the effects of two hurricanes on the same individual trees, we noted that previous damage helped predict damage in subsequent storms. Putz and Sharitz (1991) hypothesized that earlier damage had a positive effect on current damage, but their study was based on visual surveys done after the second storm. Similarly, Peterson (2000) noted effects of previous damage in an area struck by two tornadoes and Elmqvist *et al.* (1994) saw more damage in a second hurricane but did not follow individual trees. Here, we supported this hypothesis and demonstrated that damage from earlier storms influenced resistance largely independent of tree size or species (Table 4). This result has important implications for understanding community structure. Most trees will probably experience several hurricanes within their lifespan, and resistance to storm damage is likely to decrease with each storm, as recovery may alter properties such as tree architecture, resistance to pathogens, and growth rate. In areas prone to hurricanes, trees in the Resistant or Usurper syndromes would be most likely to persist over the long-term. If hurricane frequency or intensity does increase due to global change, as some predict (Emanuel 1987), then species composition will likely change in favor of species with high resistance to damage. In addition, canopy structure may also be affected by multiple storms; in an analysis of tropical forests worldwide, there was a significant negative correlation between hurricane frequency and canopy height (de Gouvenain & Silander 2003). Frequent hurricanes will likely select for slow growing species that are resistant to damage, and create forests with trees more concentrated in protected landscape positions and trees of smaller diameter and shorter canopy heights.

In conclusion, our results suggest that although there is great variation between storms, resistance to disturbance is strongly related to individual characteristics such as size and spatial position on the landscape, species characteristics such as diameter growth rate, and past disturbance history. Although forests are remarkably resilient after wind disturbance, and generally defoliated trees recover within months of the storm, hurricanes are important structuring events in Caribbean forests, which increase mortality rates above background levels, providing the potential for new recruitment. For trees that do not die in hurricanes, there is a tradeoff between diameter growth and damage from disturbances. Trees with slow growth rates tend to be more resistant to damage, which will interact with storm frequency and which over the long-term may have strong effects on species composition. In addition, because previous damage affects tree resistance in the next storm, individual storms cannot be treated as discrete, independent events.

ACKNOWLEDGMENTS

The authors thank Ivelisse Ruíz Bernard, Gustavo Guzman, Marco Guzman Marquez, Lehida Meléndez Morales, Eva Suazo Burgos, and Miriam Colón Casiano for help in the field. Fred Scatena, Andy Thompson, and Megan McGroddy helped this project succeed in countless ways. This research was done in cooperation with the University of Puerto Rico as part of the USDA Forest Service contribution to the National Science Foundation Long-Term Ecological Research Program at the Luquillo Experimental Forest (Grant # BSR-8811902) to the Institute of Tropical Ecosystems Studies and the International Institute of Tropical Forestry (USDA Forest Service). This work was also supported by a grant from the A. W. Mellon Foundation to W. Silver and done under the California Agricultural Experiment Station projects # 6363-MS (WLS).

LITERATURE CITED

Asner, G. P., and G. Goldstein. 1997. Correlating stem biomechanical properties of Hawaiian canopy trees with hurricane wind damage. Biotropica 29: 145–150.

Basnet, K., G. E. Likens, F. N. Scatena, and A. E. Lugo. 1992. Hurricane Hugo: Damage to a tropical rain forest in Puerto Rico. J. Trop. Ecol. 8: 47–55.

Batista, W. B., and W. J. Platt. 2003. Tree population responses to hurricane disturbance: Syndromes in a south-eastern USA old-growth forest. J. Ecol. 91: 197–212.

Bellingham, P. J. 1991. Landforms influence patterns of hurricane damage: Evidence from Jamaican montane forests. Biotropica 23: 427–433.

———, V. Kapos, N. Varty, J. R. Healey, E. V. J. Tanner, D. L. Kelly, J. W. Dalling, L. S. Burns, D. Lee, and G. Sidrak. 1992. Hurricanes need not cause high mortality: The effects of Hurricane Gilbert on forests in Jamaica. J. Trop. Ecol. 8: 217–223.

———, E. V. J. Tanner, and J. R. Healey. 1995. Damage and responsiveness of Jamaican montane tree species after disturbance by a hurricane. Ecology 76: 2562–2580.

Boose, E. R., D. R. Foster, and M. Fluet. 1994. Hurricane impacts to tropical and temperate forest landscapes. Ecol. Monogr. 64: 369–400.

Boucher, D. H., J. H. Vandermeer, M. A. Mallota, N. Zamora, and I. Perfecto. 1994. Resistance and resilience in a directly regenerating rainforest: Nicaraguan trees of the Vochysiaceae after Hurricane Joan. For. Ecol. Manag. 68: 127–136.

Brokaw, N. V. L., and L. R. Walker. 1991. Summary of the effects of Caribbean hurricanes on vegetation. Biotropica 23: 442–447.

Burslem, D. F. R. P., T. C. Whitmore, and G. C. Brown. 2000. Short-term effects of cyclone impact and long-term recovery of tropical rain forest on Kolombangara, Solomon Islands. J. Ecol. 88: 1063–1078.

De Gouvenain, R. C., and J. A. Silander, Jr. 2003. Do tropical storm regimes influence the structure of tropical lowland rain forests? Biotropica 35: 166–180.

Elmqvist, T., W. E. Rainey, E. D. Pierson, and P. A. Cox. 1994. Effects of tropical cyclones ofa and val on the structure of a Samoan lowland rain forest. Biotropica 26: 384–391.

Emanuel, K. A. 1987. The dependence of hurricane intensity on climate. Nature 326: 485–486.

Ewel, J. J., and J. L. Whitmore. 1973. The ecological life zones of Puerto Rico the U.S. Virgin Islands. USDA Forest Service Research Paper ITF-18. Institute of Tropical Forestry, Rio Piedras, PR.

Everham, III, E. M., R. W. Myster, and E. Vandegenachte. 1996. Effects of light, moisture, temperature, and litter on the regeneration of five tree species in the tropical montane wet forest of Puerto Rico. Am. J. Bot. 8: 1063–1068.

Foster, D. R. 1988. Species and stand response to a catastrophic wind in central New England, U.S.A. J. Ecol. 76: 135–151.

Frangi, J. L., and A. E. Lugo. 1998. A flood plain palm forest in the Luquillo Mountains of Puerto Rico five years after Hurricane Hugo. Biotropica 30: 339–348.

Gunderson, L. H. 2000. Ecological resilience—in theory and application. Annu. Rev. Ecol. Syst. 31: 425–439.

Guzmán-Grajales, S. M., and L. R. Walker. 1991. Differential seedling responses to litter after Hurricane Hugo in the Luquillo Experimental Forest, Puerto Rico. Biotropica 23: 407–413.

Harrington, R. A., J. H. Fownes, P. G. Scowcroft, and C. S. Vann. 1997. Impact of Hurricane Iniki on native Hawaiian *Acacia koa* forests: damage and two-year recovery. J. Trop. Ecol. 13: 539–558.

Herbert, D. A., J. H. Fownes, and P. M. Vitousek. 1999. Hurricane damage to a Hawaiian forest: Nutrient supply rate affects resistance and resilience. Ecology 80: 908–920.

Holling, C. S. 1973. Resilience and stability of ecological systems. Ann. Rev. Ecol. Sys. 4: 124.

Liegel, L. H. 1984. Assessment of hurricane rain/wind damage in *Pinus caribaea* and *Pinus oocarpa* provenance trials in Puerto Rico. Commonw. For. Rev. 63: 47–53.

Lugo, A. E., M. Applefield, and D. J. Pool. 1983. The impact of Hurricane David on forests of Dominica. Can. J. For. Res. 13: 201–211.

———, and F. N. Scatena. 1996. Background and catastrophic tree mortality in tropical moist, wet, and rain forest. Biotropica 28: 585–599.

———, and R. B. Waide. 1993. Catastrophic and background disturbance of tropical ecosystems at the Luquillo Experimental Forest. J. Biosci. 18: 475–481.

Marrero, J. 1947. A survey of the forest plantations in the Caribbean National Forest. MF Thesis, University of Michigan, Ann Arbor, Michigan.

MacDonald, I. A. W., C. Thébaud, W. A. Strahm, and D. Strasberg. 1991. Effects of alien plant invasions on native vegetation remnants on La Réunion Mascarene Islands, Indian Ocean. Environ. Conserv. 18: 51–61.

Merrens, E. J., and D. R. Peart. 1992. Effects of hurricane damage on individual growth and stand structure in a herdwood forest in New Hampshire, U.S.A. J. Ecol. 80: 787–795.

Ostertag, R., F. N. Scatena, and W. L. Silver. 2003. Forest floor decomposition following hurricane litter inputs in several Puerto Rican forests. Ecosystems 6: 261–273.

Peterson, C. J. 2000. Damage and recovery of tree species after two different tornadoes in the same old growth forest: A comparison of infrequent wind disturbances. For. Ecol. Manag. 135: 237–252.

Platt, W. J., R. F. Doren, and T. V. Armentano. 2000. Effects of Hurricane Andrew on stands of slash pine (*Pinus elliottii* var. *densa*) in the everglades region of south Florida (USA). Plant Ecol. 146: 43–60.

Putz, F. E., and N. V. L. Brokaw. 1989. Sprouting of broken trees on Barro Colorado Island, Panama. Ecology 70: 508–512.

Putz, F. E., and R. R. Sharitz. 1991. Hurricane damage to old-growth forest in Congaree Swamp National Monument, South Carolina, U. S. A. Can. J. For. Res. 21: 1765–1770.

Reyes, G., S. Brown, J. Chapman, and A. E. Lugo. 1992. Wood densities of tropical trees. USDA Forest Service, Southern Forest Experiment Station, General Technical Report SO-88, New Orleans, Louisiana.

SAS Institute. 1995. JMP introductory guide, version 3.1. SAS Institute, Cary, North Carolina.

Sauer, J. D. 1962. Effects of recent tropical cyclones on the coastal vegetation of Mauritis. J. Ecol. 50: 275–290.

Scatena, F. N., and M. C. Larsen. 1991. Physical aspects of Hurricane Hugo in Puerto Rico. Biotropica 23: 317–323.

Silver, W. L., L. M. Kueppers, A. E. Lugo, R. Ostertag, and V. Matzek. 2004. Carbon sequestration and plant community dynamics following reforestation of tropical pasture. Ecol. Appl. 14: 1115–1127.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry: The principles and practice of statistics in biological research. 3rd edition. W. H. Freeman and Co., New York.

Walker, L. R. 1991. Tree damage and recovery from Hurricane Hugo in Luquillo Experimental Forest, Puerto Rico. Biotropica 23: 379–385.

———. 1995. Timing of post-hurricane tree mortality in Puerto Rico. J. Trop. Ecol. 12: 315–320.

———, A. Kinzig, and J. Landgridge. 1999. Plant attribute diversity, resilience, and ecosystem function: The nature and significance of dominant and minor species. Ecosystems 2: 95–113.

Weaver, P. L. 1994. Effects of Hurricane Hugo on trees in the Cinnamon Bay Watershed, St. John, U. S. Virgin Islands. Caribbean J. Sci. 30: 255–261.

———. 1998a. The effects of environmental gradients on hurricane impact in Cinnamon Bay Watershed, St. John, US Virgin Islands. *In* F. Dallmeier and J. A. Comisky (Eds.). Forest biodiversity in North, Central, and South America, and the Caribbean, pp. 333–348. Unesco and Parthenon Publishing Group, Paris.

———. 1998b. Hurricane effects and long-term recovery in a subtropical rain forest. *In* F. Dallmeier and J. A. Comisky (Eds.). Forest biodiversity in North, Central, and South America, and the Caribbean, pp. 249–270. Unesco and Parthenon Publishing Group, Paris.

———. 1999. Impacts of Hurricane Hugo on the dwarf cloud forest of Puerto Rico's Luquillo Mountains. Caribbean J. Sci. 35: 101–111.

Whigham, D. F., M. B. Dickinson, and N. V. L Brokaw. 1999. Background canopy gap and catastrophic wind disturbances in tropical forests. *In* L. R. Walker (Ed.). Ecosystems of disturbed ground, pp. 223–252. Elsevier, Amsterdam.

———, I. Olmsted, E. C. Cano, and M. E. Harmon. 1991. The impact of Hurricane Gilbert on trees, litterfall, and woody debris in a dry tropical forest in the northeastern Yucatan Peninsula. Biotropica 23: 434–441.

Zimmerman, J. K., T. M. Aide, M. Rosario, M. Serrano, and L. Herrera. 1995. Effects of land management and a recent hurricane on forest structure and composition in the Luquillo Experimental Forest, Puerto Rico. For. Ecol. Manag. 77: 65–76.

———, E. M. Everham, III, R. B. Waide, D. J. Lodge, C. M. Taylor, and N. V. L. Brokaw. 1994. Responses of tree species to hurricane winds in the subtropical wet forest in Puerto Rico: Implications for tropical tree life histories. J. Ecol. 82: 911–992.