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SPECIAL ISSUE

Structural response of Caribbean dry forests to hurricane winds: a case study from Guánica Forest, Puerto Rico

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ABSTRACT

Aim Tropical dry forests in the Caribbean have an uniquely short, shrubby structure with a high proportion of multiple-stemmed trees compared to dry forests elsewhere in the Neotropics. Previous studies have shown that this structure can arise without the loss of main stems from cutting, grazing, or other human intervention. The Caribbean has a high frequency of hurricanes, so wind may also influence forest stature. Furthermore, these forests also tend to grow on soils with low amounts of available phosphorus, which may also influence structure. The objective of this study was to assess the role of high winds in structuring dry forest, and to determine whether soil nutrient pools influence forest response following hurricane disturbance.

Location Guánica Forest, Puerto Rico.

Methods Over 2000 stems in five plots were sampled for hurricane effects within 1 week after Hurricane Georges impacted field sites in 1998. Sprout initiation, growth, and mortality were analysed for 1407 stems for 2 years after the hurricane. Soil nutrient pools were measured at the base of 456 stems to assess association between nutrients and sprout dynamics.

Results Direct effects of the hurricane were minimal, with stem mortality at < 2% and structural damage to stems at 13%, although damage was biased toward stems of larger diameter. Sprouting response was high – over 10 times as many trees had sprouts after the hurricane as before. The number of sprouts on a stem also increased significantly. Sprouting was common on stems that only suffered defoliation or had no visible effects from the hurricane. Sprout survival after 2 years was also high (> 86%). Soil nutrient pools had little effect on forest response as a whole, but phosphorus supply did influence sprout dynamics on four of the more common tree species.

Main conclusions Hurricanes are able to influence Caribbean tropical dry forest structure by reducing average stem diameter and basal area and generating significant sprouting responses. New sprouts, with ongoing survival, will maintain the high frequency of multi-stemmed trees found in this region. Sprouting is not limited to damaged stems, indicating that trees are responding to other aspects of high winds, such as short-term gravitational displacement or sway. Soil nutrients play a secondary role in sprouting dynamics of a subset of species. The short, shrubby forest structure common to the Caribbean can arise naturally as a response to hurricane winds.

Keywords

Forest structure, Guánica Forest, hurricane, phosphorus, Puerto Rico, soil nutrient pools, sprouting, stem mortality, tropical dry forest.

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INTRODUCTION

Although the physiognomy of tropical dry forests is primarily determined by rainfall, there are important structural differences among these forests from region to region that cannot be explained by percipitation. While there is some evidence suggesting that biomass and canopy height are related to either the amount of rainfall or the number of dry months (< 50 mm of rain) in a year (Murphy & Lugo, 1986a, 1995; Holbrook et al., 1995), stem density and the proportion of multiple-stemmed trees cannot be explained by water supply. We have previously compared climatic and structural features of mature dry forests composed of primary tree species (Murphy & Lugo, 1986b, 1990; Van Bloem et al., 2003). We noted that Caribbean dry forests had higher stem density and lower basal area than other locations (Fig. 1), despite being at or near the median in dry months, rainfall and temperature : precipitation
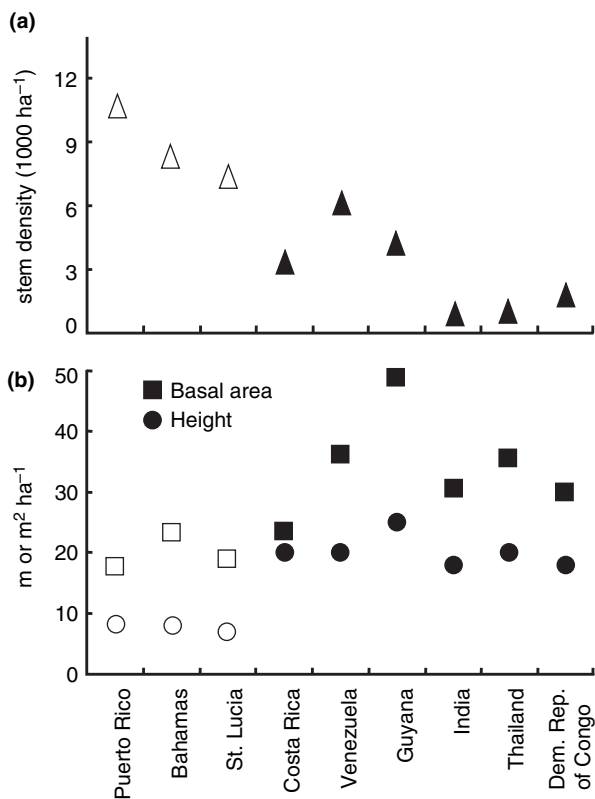

Figure 1 Structural characteristics of mature tropical dry forests. Stem density (a) is higher in the Caribbean sites of Puerto Rico, the Bahamas, and St Lucia (open symbols), while height and basal area (b) are lower. Direct comparison is possible for sites where the minimum stem diameter included in the measurements was similar (2.5 cm). This minimum size was larger for three sites: India (3.0 cm), Thailand (4.5 cm) and DR Congo (not reported). References for locations: Puerto Rico (Murphy & Lugo, 1986b), Bahamas (Smith & Vankat, 1992), St. Lucia (Gonzalez & Zak, 1996), Costa Rica, Venezuela and Guyana (Quigley & Platt, 2003), India (Bandhu, 1970), Thailand (Ogawa et al., 1965) and Zaire (Malaisse, 1978).

ratio. We concluded that other factors superimposed their influence on that of rainfall to determine forest structure. Two such factors could be soil nutrient supply and hurricane winds. Caribbean dry forests frequently grow in coastal zones on calcareous soils or on otherwise poor substrates, leading to high leaf N : P ratios (25) and phosphorus use efficiency (> 6000), which may indicate nutrient limitation (Lugo & Murphy, 1986; Murphy & Lugo, 1995; Tanner et al., 1998). In this paper, we discuss the role of wind in structuring Caribbean dry forest and the role of nutrients in regulating responses. The opportunity to embark on this study was provided by Hurricane Georges when it passed over our field sites near Guánica, Puerto Rico, in 1998.

The annual likelihood that a hurricane will impact Puerto Rico is c. 12–14% (Jarvinen et al., 1984). A severe hurricane (Category 3–5; Saffir-Simpson Index) has a 3–5% chance of striking in a given year. Based on historical accounts and meteorological data, the hurricane return interval for south-west Puerto Rico, where the Guánica Forest is located, is c. 20 years (Salivia, 1972; Miner-Solá, 1996), but spacing between hurricanes is unpredictable and the frequency of Category 3 or stronger storms averages one every 43 years (S. J. Van Bloem et al., 2005). Prior to Hurricane Georges, the last hurricane to pass over the forest was Hurricane Hortense in 1995 (Category 1), which followed a hurricane-free period of 67 years. Hortense resulted in very minor damage to the forest (M. Canals, Director of Guánica Forest, personal communication, and A.E. Lugo, personal observation). Despite their unpredictable occurrence, multiple hurricanes would affect mature trees in their lifetimes. In addition to direct effects on tree stems (e.g. defoliation, breakage and uprooting), hurricanes also alter nutrient cycles, providing a pulse of nutrient-rich litter to the forest floor, and have the potential to cause increased salt deposition on exposed foliage, if vegetation is close to the sea (Grace, 1977).

As dry forests account for the largest proportion of all tropical forests (Murphy & Lugo, 1986a) and are increasingly converted by human activities (Miles et al., 2006), it is important to understand how these forests maintain their physiognomy and how they will respond to disturbance. Recent predictions indicate hurricane frequency or intensity may increase as a result of changing global climate (Michener et al., 1997; Webster et al., 2005), further highlighting the need to understand how dry forests respond to high winds. The objectives of this paper are to: (1) review major effects of hurricane disturbance on tropical dry forest, using Guánica Forest as a case study; (2) describe Guánica Forest's responses to hurricane winds; (3) assess the importance of soil nutrient pools for forest response; and (4) place hurricane effects and responses in Guánica Forest in context with similar studies elsewhere.

MATERIALS AND METHODS

Hurricane Georges was a Category 3 hurricane that crossed over Puerto Rico on 21–22 September 1998. Sustained winds blew at 176–184 km h^{-1} with gusts up to 240 km h^{-1}.

Hurricane-force winds impacted Guánica Forest for c. 4 h. Rainfall from the hurricane was 151 mm in the Guánica area – equal to the average September monthly rainfall.

Guánica Forest is a 4000-ha tract of tropical dry forest located in south-west Puerto Rico. It was originally set aside as a state forest in 1917 and has been expanded since then. The forest is primarily semi-deciduous, with mature stands intermingled with pioneer stands. All the plots used in this study were in mature forest, with no recent history of heavy use by humans, and they have been protected since the 1930s. We established a primary research plot of 1.44 ha in 1981 and added two 1.0-ha plots in June 1998 and two 0.01-ha plots in October 1998. Within the plots, storm damage was assessed on 2048 stems within 1 week of Hurricane Georges. Sprouting patterns were followed on 1407 stems for 23 months after the hurricane. Only stems of ≥ 2.5 cm diameter at breast height (d.b.h.; 1.4 m) were included.

Hurricane effects were classed into three categories: major structural damage (snapping, uprooting, permanent leaning beyond 45° from vertical, or loss of branches with at least one-third trunk diameter), defoliated, or not visibly affected. Leafless stems with dried bark 9 months after the hurricane were presumed dead. Defoliation was estimated visually, using five categories: 100% (completely leafless), 95% (a few leaves remaining), 75%, 50% and 25%. Stems with no sign of defoliation were placed in the unaffected category.

Pre-hurricane sprouting was assessed on 451 stems 2 days before Hurricane Georges. All sprouts arising on a stem below 1.4 m were counted. Sprouts were distinguished from branches by emerging from the trunk at < 45° from vertical and having an overall upright orientation (Dunphy *et al.*, 2000). Root sprouts were also counted. Post-hurricane sprouts were censused in the same manner and distinguished by bark colour. The location of sprouts on each stem was measured, as was the length of the longest sprout.

Soil nutrients were analysed from three bulked sub-samples collected in July 1999 at the base of each tree in the 1.4-ha site ($n = 456$). Sub-samples were collected with a soil probe to 10-cm depth. Samples were placed in cloth bags, air-dried and ground. Total soil carbon and nitrogen were analysed on 100-mg soil sub-samples using dry combustion in a LECO CNS analyzer (LECO Corp., St Joseph, MI, USA). Soil samples were combusted at 1450 °C. Carbon was detected using an infrared beam and nitrogen with thermal conductivity detector. Organic matter was measured as loss on ignition by combusting samples in a muffle furnace at 490 °C. Total concentrations of other elements (Ca, K and P) were determined by digesting 100-mg sub-samples in nitric acid followed by hydrogen peroxide. Using 5-g sub-samples, available calcium was extracted in KCl and available phosphorus and potassium were extracted using a modified Olsen solution (Wilde *et al.*, 1979). Digested total and available element concentrations were determined using an atomic-emission spectrometer.

Statistical analysis was performed with SYSTAT 8.0 (Systat Software Inc., Richmond, CA, USA). Chi-squared tests were used to analyse categorical data. Correlation analyses were used to determine associations between soil nutrients and sprout initiation, growth, or mortality, and between sprout length and tree physiognomy. Pearson correlation coefficients (r) are reported with Bonferroni-adjusted P values for significance levels at α = 0.05.

RESULTS

Mortality and stem damage following Hurricane Georges were low. After 9 months, mortality was < 2%. Nearly 13% of stems overall incurred major structural damage, with more exposed sites on ridges having greater damage rates (20%). Dead and damaged stems accounted for basal area losses of 3.9 m^2 ha^{-1} (21%). Stem damage was biased to stems > 7.5 cm d.b.h. (Fig. 2). Many of the large stems that were uprooted grew in shallow soils or over rocks instead of in crevices. Tall, slender whip-like trees escaped stem damage and precluded a height effect in damage rates.

Sprouting occurred on 48% of stems which had incurred major structural damage, with an average of > 21 sprouts per stem. Notably, sprouting on undamaged and defoliated stems was 25–28% higher than the pre-hurricane sprouting rate (Fig. 3). However, sprouting was not related to the severity of defoliation (Table 1). Basal sprouts accounted for 41% of post-hurricane sprouts. A total of 75% of the sprouts developed below 40 cm height on stems. All species sprouted to varying degrees, those species that produced sprouts with the greatest median length tended to be the ones with the greatest number of mature stems per tree ($r = 0.62$; $P = 0.012$; Fig. 4) and the highest proportion of multiple-stemmed trees ($r = 0.55$; $P = 0.018$). The low pre-hurricane sprouting rate (3.5%) supported observations of only a limited forest response to Hurricane Hortense.

For the forest as a whole, soil nutrient pools had little effect on sprout mortality, initiation, or growth, despite low P availability in soil. Large sample sizes provided significant but small r values (c. 0.3), suggesting weak positive relationships forest-wide between sprout mortality and available P, available Ca, organic matter and N : P, and negative trends with total Ca, pH and C : N. There were no significant forest-wide
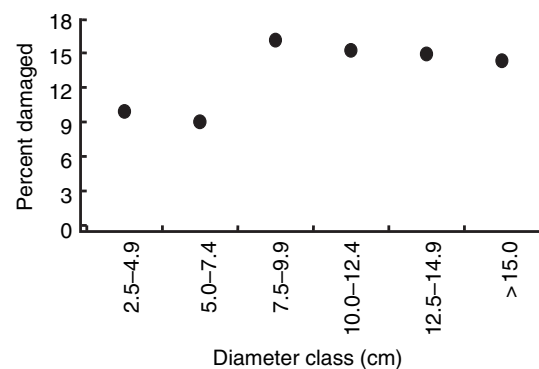

Figure 2 Size bias of major structural damage incurred on stems ≥ 2.5 cm d.b.h. Stems larger than 7.5 cm d.b.h. incurred greater damage ($\chi^2 = 26.60$, d.f. = 5, $P < 0.0005$).
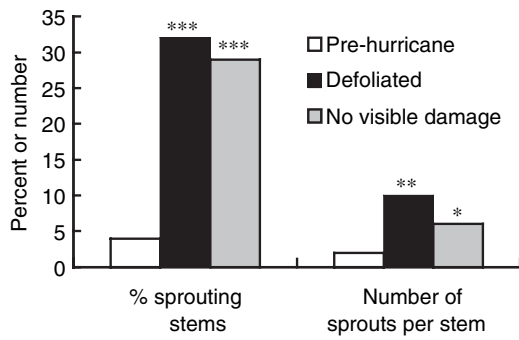
Figure 3 Pre- and post-hurricane sprouting rates on defoliated and undamaged stems. Pre-hurricane sprouts were surveyed 2 days before the hurricane, post-hurricane sprouts 9 months later. Only sprouts developing below breast height were included for analysis. There were 451 stems analysed for pre-hurricane sprouts. Post-hurricane sprouts were compared to pre-hurricane sprouts from 1153 defoliated stems using z tests and from 49 undamaged stems using t tests. ***$P < 0.0002$, **$P < 0.0005$, *$P = 0.024$.

Table 1 Proportion of sprouting stems and mean number of sprouts per stem of defoliated stems 9 months following Hurricane Georges. Standard error of the mean is in parentheses. Pre-hurricane sprout rates were 3.5% and 1.7 (0.3) sprouts per stem. Sprouting patterns were not related to severity of defoliation (d.f. = 5 for both; $\chi^2 = 3.69$; $P = 0.60$ for % sprouting; $\chi^2 = 1.35$; $P = 0.92$ for sprouts per stem)

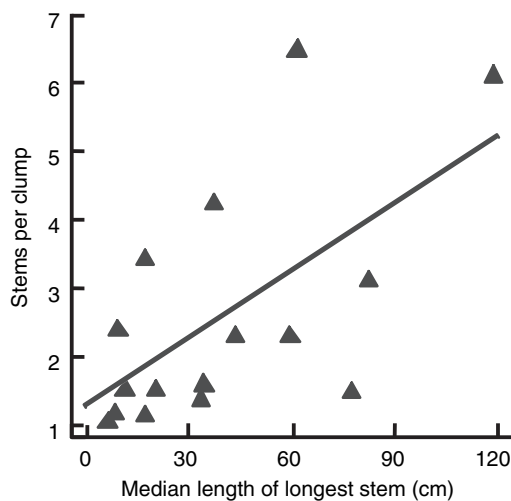| Defoliation rate	n stems	Sprouting (%)	Sprouts per stem
0	79	32	9.9 (1.8)
25	284	27	8.9 (1.9)
50	361	30	10.5 (2.3)
75	303	34	8.7 (1.2)
95	102	41	12.2 (3.1)
100	56	34	12.2 (4.5)

Figure 4 The relationship between median sprout length and the average number of stems per tree for each species, with regression line ($P = 0.012$). Each triangle represents a species with at least 20 individual trees.

Table 2 Correlation between sprout development and soil nutrient pools or nutrient pool ratios for five more commonly sprouting species. No correlations were found between nutrient pools and other common species (see Murphy & Lugo, 1986b, for species composition) or between the species below and other nutrients, pH, or organic matter

Species	Sprout stage	Nutrient	r	P
Bourreria succulenta Jacq.	Growth	C : P	0.790	0.039
Crossopetalum rhacoma Crantz	Initiation	Total P	0.889	0.045
	Mortality	Total P	0.919	0.014
Eugenia foetida Pers	Initiation	C : P	0.498	0.041
		% available P	0.625	0.001
	Mortality	C : P	0.455	0.046
		% available P	0.570	0.004
		N : P	0.473	0.033
Exostema caribaeum (Jacq.) Roem. & Schult.	Initiation	C : N	0.495	0.037
	Mortality	C : N	0.457	0.039
Pictetia aculeata (Vahl) Urb.	Initiation	% available P	0.826	0.037
	Growth	% available P	0.939	0.022

correlations between any nutrient and sprout initiation or growth. However, for five of the more common species, soil nutrient pools appeared to influence some stage of sprouting dynamics (Table 2). Phosphorus, either total, available, or in relation to C or N, was associated with greater sprout initiation (number of sprouts per stem), higher growth, or lower mortality. Only one species responded significantly to any other soil chemistry variable (C : N ratio). No relationships were found between sprouting and total N, Ca, K, or organic matter.

DISCUSSION

An immediate effect of Hurricane Georges on the structure of Guánica Forest was to reduce basal area with the selective removal of poorly anchored, larger-diameter stems by snapping or uprooting. A short term decrease in stem density will be compensated by the development of a new flush of basal sprouts, leading to multi-stemmed trees. The effects and responses of the forest following Hurricane Georges contrasts with the less powerful Hurricane Hortense. Hurricane induced mortality was lower in Guánica Forest than in other Caribbean dry forests. Whigham *et al.* (1991) reported 11.2% mortality in the Yucatan, similar to estimates from Florida and Guadeloupe (Slater *et al.*, 1995; Imbert *et al.*, 1998). Stem damage was in the middle of the range reported (4–85%) with lower values found after hurricanes in Jamaica and Dominica (Lugo *et al.*, 1983; Wunderle *et al.*, 1992), and higher values from Florida, Guadeloupe, St. John, and the Yucatan (Whigham *et al.*, 1991; Slater *et al.*, 1995; Imbert *et al.*, 1998; Weaver, 1999). Although the methods used to study hurricane effects have differed among researchers, making direct comparisons difficult, an

overall conclusion can be made that hurricane disturbance directly restructures forest physiognomy.

After 2 years, many sprouts had reached sub-canopy height (4 m) and sprout mortality was low – only 13.6% (Van Bloem et al., 2003). We attribute low mortality to the ability of sprouts to access a relatively large supply of resources. Light would be available through the thin dry forest canopy (Murphy et al., 1995) and in small gaps. Nutrients would be supplied from retranslocation in mature trees or uptake from well developed root systems, which would also provide water. Although few sprouts had become large enough to include in our minimum diameter class (2.5 cm d.b.h.), continued survival suggests they will eventually attain that size and add to the multi-stemmed physiognomy of the forest. Mature multi-stemmed trees frequently have a cohort of stems that are approximately the same size (Van Bloem, 2004) which may reflect the passage of previous hurricanes. Although cutting or grazing can lead to multi-stemmed trees, neither activity has been present in the forest for the last 70 years. Previous studies have determined that the growth form arises without human intervention (Dunphy et al., 2000), but have not identified the mechanism which elicits sprouting.

That sprouting would occur on broken stems is not surprising, but the frequency of sprouting on undamaged or defoliated stems is unusual. Other studies of post-hurricane sprouting rarely quantify this response because they generally focus on the recovery of damaged stems. Five years following a hurricane in Guadeloupe, 50% of new recruits arose from basal sprouts (Imbert et al., 1998). In rain forest in Luquillo, Puerto Rico, after Hurricane Hugo, only 9% of 'upright' stems sprouted (Walker, 1991). If these values are representative of their forest type, it suggests that dry forests respond to hurricanes by adding new stems through sprouting, while this mechanism is relatively unimportant in wet forests. Sprouting would be hindered in wet forests, with taller, thicker canopies limiting light availability. Bellingham & Sparrow (2000) have suggested that forests trade sprouting capability for recruitment by seedlings. Following the hurricane, few new seedlings became established in Guánica Forest (Van Bloem, 2004), supporting this trade off. In slow-growing dry forests, sprouting is an effective way for trees to maximize leaf area index while covering maximal ground area and minimizing the distance needed to transport water in stems.

We hypothesize that widespread sprouting after a hurricane is only present when sustained winds surpass a threshold between 119 and 180 km h^{-1}. This range corresponds to the difference in wind speed between a Category 1 hurricane (i.e. Hortense, with no sprout response) and a Category 3 hurricane (Georges). Gravitational displacement caused by bending has been shown to result in increased ethylene production at or near the root collar of tree stems (Savidge et al., 1983; Telewski, 2000). Ethylene alters the flow of auxin (Wood, 1985; Eklund & Little, 2000), which could change hormone balances sufficiently to induce sprouting. The amount of time needed to induce an ethylene response has been shown to be as little as

76 s to as long as 2 h (Telewski, 2000). Hurricane winds lasted for 4 h in Guánica Forest.

After the hurricane winds spurred the sprout response we expected other resources to mediate its progression. Despite indications in previous studies (Lugo & Murphy, 1986) that tree growth in Guánica Forest may be P-limited (leaf N : P = 25; phosphorus use efficiency > 6000), soil nutrient pools had little overall influence on sprout initiation, growth or survival. The lack of a nutrient effect was probably the result of nutrient requirements being met by retranslocation in mature trees, which is quite high in Guánica Forest, accounting for 65% of annual P demand and 30% of N (Lugo & Murphy, 1986). However, it is noteworthy that when soil nutrients did influence sprout dynamics, phosphorus was typically involved. The pulse of nutrients that was provided by litter fall returned 100% of annual, non-hurricane year N and 170% of P to the forest floor (Van Bloem, 2004). This pulse of nutrients was short-lived, as concentrations returned to levels measured in non-hurricane years by the following summer (Van Bloem, 2004). The nutrient pulse may have helped support sprouts, but it would also have been used for the rapid refoliation that took place after Hurricane Georges and in regeneration of lost root mass. Long term study of the sprout cohort will determine if growth and survival become more reliant on soil nutrient pools. The lack of association between sprout development and defoliation suggests that light did not play a major role. More likely, the mature trees were able to draw upon a store of nutrients within stems and roots to sustain sprouting.

CONCLUSIONS

The short, shrubby physiognomy of Caribbean dry forests is due in part to the influence of hurricane winds. These winds preferentially remove larger stems, reducing forest basal area and average stem size, but with minimal mortality. Moreover, hurricanes spur a sprouting response – even on undamaged trees – that leads to the generation and maintenance of multi-stemmed trees and forests with high stem density. In the absence of cutting or grazing, this physiognomy is found in much lower proportions in dry forests outside of hurricane-prone regions.

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