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Subtropical dry forest trees with no apparent damage sprout following a hurricane

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Abstract: Hurricane Georges passed over mature dry forest near Guánica, Puerto Rico in September, 1998. The trees of the dense, short-statured Guánica Forest have a multi-stemmed structure unique to the West Indies in the neo-tropics, a characteristic that has been difficult to explain. Following the hurricane, we measured sprout development below breast height on 1407 stems to assess how response to hurricane disturbance may influence dry forest structure. Basal sprouting increased 8-14 fold after Hurricane Georges. Basal sprouting was found on almost 68% of damaged stems and, notably, on about 32% of undamaged stems. Basal sprouting was found in all common species surveyed. The rate of defoliation was not related to sprout production. After two years, sprout mortality was only about 13%. We conclude that continued growth of basal sprouts will contribute to high stem densities and multi-stemmed growth forms commonly found in Guánica Forest and in the hurricane-prone West Indies.

Resumen: El huracán Georges pasó sobre el bosque maduro cerca de Guánica, Puerto Rico, en septiembre de 1998. Los árboles del Bosque Guánica, que es denso y de baja estatura, poseen numerosos tallos, característica que es única de las Indias Occidentales en el Neotrópico y que ha sido difícil de explicar. Después del huracán, nosotros medimos el desarrollo de rebrotes por debajo de la altura del pecho en 1407 tallos con el fin de evaluar de qué manera la respuesta al disturbio del huracán puede influir sobre la estructura del bosque seco. El rebrote basal incrementó entre 8 y 14 veces después del huracán Georges. Se encontró rebrote basal en casi 68% de los tallos dañados y, de manera notable, en cerca de 32% de los tallos no dañados. El rebrote basal fue observado en todas las especies comunes examinadas. La tasa de defoliación no estuvo relacionada con la producción de rebrotes. Al cabo de dos años, la mortalidad de los rebrotes fue tan sólo de alrededor de 13%. Concluimos que el crecimiento continuo de rebrotes basales contribuye a tener altas densidades de tallos y formas de crecimiento con múltiples troncos, comúnmente encontradas en el Bosque Guánica y en general en las Indias Occidentales, susceptibles a los huracanes.

Resumo: O furacão Georges passou sobre uma floresta seca adulta perto de Guánica, Porto Rico em Setembro, 1998. As árvores da floresta densa de Guánica, de baixo porte têm uma estrutura de troncos múltiplos, única nos neo-trópicos das Índias Ocidentais, característica esta que tem sido difícil de explicar. Depois do furacão, foi medido o desenvolvimento dos rebentos abaixo da altura do peito numa amostra de 1407 troncos para avaliar a resposta às perturbações e à forma como influência a estrutura da floresta seca. A rebentação basal aumentou entre 8 – 14 vezes depois do furacão George. Encontrou-se rebentação basal em quase 68% dos troncos afectados e, normalmente, em cerca de 32% dos troncos não afectados. A rebentação basal ocorreu em todas as espécies comuns

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amostradas. A taxa de desfoliação não estava relacionada com a produção de rebentos. Após dois anos, a mortalidade dos rebentos só atingiu cerca de 13%. Conclui-se que o crescimento continuado dos rebentos basais contribuiu para a elevada densidade de troncos e as formas de crescimento de múltiplos troncos encontrados na floresta de Guánica e na zona das Índias Ocidentais propensa aos furacões.

Key words: Forest structure, Guánica Forest, hurricane disturbance, Hurricane Georges, multiple stems, multiple-stemmed, sprouting, subtropical dry forest.

Introduction

Among the environmental factors that influence the structure of tropical and subtropical dry forests are low annual rainfall and seasonal drought. However, comparisons among dry forests with similar climate regimes show that there are major differences in stem density (Murphy & Lugo 1986b, 1990). Generally, stem densities are higher in coastal or Caribbean forests. High densities can result from a multiple-stemmed growth habit of trees which is prevalent in Guánica Forest, Puerto Rico (at least 42% of trees) (Murphy & Lugo 1986b; Ramjohn 2003) and North Andros Island, Bahmas (Smith & Vankat 1992). Drought may be a factor involved in generating multi-stemed trees, but stem densities in Guánica Forest are at least twice that found in continental dry forests (e.g., Chamela and Ecuador) (Josse & Balslev 1994; Lott *et al.* 1987). Considering the similar climates of dry forests throughout the tropics, it seems that the high stem density found in Guánica Forest must be influenced by some other factor. Multi-stemmed trees have been documented as a response to cutting by humans, grazing or browsing by animals, fire damage, or stem breakage by storms (Gonzalez & Zak 1996; Kelly *et al.* 1988; Molina Colón 1998; Murphy *et al.* 1995). Each of these disturbance types would result in the loss of terminal buds and wounding near the base of tree, leading to internal changes in hormone balances which could affect sprouting. Recent discussions of sprouting response to disturbance suggest that sprouting should occur on trees immediately below the point where biomass has been lost (Bellingham & Sparrow 2000; Bond & Midgley 2001). Thus, defoliated trees should sprout from leaf axils while cut trees should sprout from roots or stumps. Our observations in Guánica Forest after Hurricane Georges suggest that strong winds can elicit basal sprout development without breaking stems – thus providing a new explanation for the multi-stemmed growth habit of Caribbean Forests.

Wind stress results in different responses by forests depending on the severity of the wind. Trees in chronically wind-stressed environments are often shorter with larger diameters than individuals of the same species in sheltered environments (Telewski 1995), develop buttresses (Ennos 1995), or produce reaction wood (reviewed in Timell 1986). Compared to chronic low-level stress from the trade winds, hurricanes impact a forest with extreme, but relatively brief, wind stress. However, the effects of a single acute wind event can drastically change the developmental trajectory of a forest (Brokaw & Grear 1991; Foster & Boose 1995; Steudler *et al.* 1991). Hurricane-force winds can inflict plastic damage (i.e., irreversible, as opposed to elastic, or reversible, damage) on stems including defoliation, snapping, uprooting, and branch loss (Foster & Boose 1995). In such cases, trees frequently respond by sprouting, as seen after Hurricane Joan in Nicaraguan wet forest (Vandermeer *et al.* 1990; Yih *et al.* 1991), after Hurricane Hugo in dry forests of Guadaloupe (Imbert *et al.* 1998) and wet forests of Puerto Rico (Walker 1991; Zimmerman *et al.* 1994) and after Hurricane Gilbert in Yucatan dry forest (Whigham *et al.* 1991) and Jamaican montane wet forest (Bellingham *et al.* 1994).

There is some evidence for sprouting in apparently undamaged trees exposed to wind stress. Sprouting has been noted below 2.5 m height on about 47% of "undamaged or lightly damaged" stems following hurricanes in Jamaica (Bellingham *et al.* 1994). In Puerto Rican rainforest about 57% of "undamaged" stems sprouted after Hurricane Hugo in one study (Zimmerman *et al.* 1994), but the location of sprouts on stems was not noted. Sprouts developing within 40-50 cm of the ground may lead to multi-stemmed trees if the sprouts grow and survive. Walker (1991) reported 6% of "upright" (not snapped or uprooted) stems in subtropical wet forest sprouted below 50 cm on the trunk. Imbert *et al.* (1998) and Vandermeer *et al.* (1995) mention sprouting below 50 cm on trunks, but neither specifically state whether undamaged stems sprouted at that height.

To date, no satisfactory explanation for the high stem density of mature dry forest (>12,000 stems ha^{-1}) nor the prevalence of multi-stemmed trees (42%) in study plots near Guánica, Puerto Rico, has been proposed. Because of the governmentally protected status of Guánica Forest, cutting and grazing in the vicinity of our plots has been light or absent in the last 70 years and fire has never been an influential factor. Where cutting has taken place in Guánica Forest, sprouting is common (Molina Colón 1998; Murphy *et al.* 1995), but sprouting is also common in areas which were not subject to cutting. Dunphy *et al.* (2000) analyzed multi-stemmed trees in Guánica Forest and concluded that for a majority of species the growth form was natural – not the result of cutting. The last few hurricanes that have passed over the forest have broken few stems (<13%) (Van Bloem *et al.* 2001). Sprout development following Hurricane Georges has provided new insight into tropical dry forest structure. Following the hurricane, we expected that: (1) sprouting frequency would be higher on damaged stems, (2) sprouting would be proportional to defoliation because sprouting response might be related to biomass loss, and (3) a majority of sprouts produced after Hurricane Georges would die after the first or second dry season due to thinning of new sprouts as they competed for resources. The objectives of this paper are to evaluate these expectations, to report patterns in post-hurricane sprouting, and to assess the potential role of hurricanes in creating multi-stemmed trees and short-statured, dense forests.

Methods

Guánica Forest is comprised primarily of semi-deciduous dry forest and is located along the southwestern coast of Puerto Rico (17° 58′ N, 65° 30′ W). The forest was originally protected in 1917 and its boundaries expanded in the 1930's to include all the plots within this study. Canopy height is generally 5-7 m, and density of live stems (>2.5 cm dbh) averages 12,000 per hectare (Murphy & Lugo 1986b). About 42% of trees are multiple-stemmed and they include 56% of all stems (Murphy & Lugo 1986b). Annual rainfall averages 860 mm, 45% of which comes between September and November, corresponding to the height of hurricane season (Murphy & Lugo 1986a). Mean annual temperature is 25.1°C and the PET/precipitation ratio averages 1.4 (Murphy & Lugo 1986a). Previous investigations in the forest have determined that the multi-stemmed growth habit of the trees cannot be solely explained by cutting, although this is a likely explanation for a few species (Dunphy *et al.* 2000).

Hurricane Georges crossed over the island of Puerto Rico on September 21-22, 1998. The southern portion of the hurricane's eye passed over Guánica Forest. This category 3 hurricane (Saffir-Simpson Index) had sustained winds of 176-184 km h^{-1} with gusts up to 240 km h^{-1} (Bennett & Mojica 1998). Rainfall measured in the forest was 151 mm during the two days of Georges' passage. Average September rainfall in Guánica forest is 155 mm (Murphy & Lugo 1986b). Hurricane-force winds from Georges impacted Guánica forest for about four hours.

In the last 300 years, hurricanes have passed over the areas containing our research sites at an average return rate of 25 years (Miner-Solá 1996; Salivia 1972). The last hurricane that passed over Guánica Forest and had a strength similar to Hurricane Georges was San Felipe in 1928 (Salivia 1972).

We studied sprouting response in five plots in Guánica Forest ranging from 0.01 to 1.44 ha in size and located in various topographic settings that represent a gradient of wind conditions determined by slope, aspect, and elevation. Low elevation, topographically level plots had the least wind exposure while plots at higher elevation (e.g. 175-200 m) with steeper, south-facing slopes had the greatest exposure. All plots were comprised of semi-deciduous forest (Ewel & Whitmore 1973) and had trees permanently marked and censused for previous studies. Our plots included over 40 species of trees, but have relatively high species evenness (Murphy & Lugo 1986b), as is common in many mature subtropical forests. All plots were on the same type of soil, an alkaline clay mollisol over a limestone base. Within these plots, we had 1407 permanently tagged stems of at least 2.5 cm dbh (measured at 1.4 m).

We determined the type and severity of damage to the 1407 tagged stems in our plots within one week of Hurricane Georges. Snapped trunks, uprooting, loss of large branches, and permanent bending of trees beyond 45° from vertical were considered major structural damage. On stems without major damage, defoliation was estimated visually on a percentage basis. Some trees appeared to escape both major stem damage and defoliation and were considered to have no visible damage. The type and rates of damage and species effects resulting from Hurricane Georges will be reported elsewhere.

Following Hurricane Georges, we measured sprout development on the tagged stems within our plots six times over two years. We considered any woody twig growing from a mature stem below breast height at an angle < 45° from the trunk to be a sprout (Dunphy 1996). To quantify pre-hurricane rates of sprouting, we inventoried all old sprouts on 451 tagged stems along 6 transects totaling 680 m in our largest plot. Subsequently, we were able to distinguish new sprouts by their distinctive bark colors as compared to old sprouts. On all of the 1407 tagged stems, we counted all new sprouts growing at breast height (1.4 m) or lower. Technically, some of these sprouts would be considered branches rather than additional stems; therefore, we noted whether new sprouts arose from trunks or roots and where on the trunk new sprouts emerged from tagged stems. In mature trees, it can be difficult to distinguish between branches and stems when they attain diameters ≥ 2.5 cm, grow at angles < 45° from vertical and emerge from trunks below 40 cm, so we attempted to take this into account with our measurements. The length of the longest sprout on each tagged stem was measured to the nearest cm and its point of origin noted (i.e., ground, or height on trunk).

Results

Pre-hurricane sprouts were present on 16 of 451 stems (3.5%). No new sprouts emerged on the 1407 tagged stems in Guánica Forest within eight days of the hurricane. However, new sprouts were present by mid-November, 1998 (8 weeks post-hurricane), on both damaged and undamaged stems, and by January, 1999 (15 weeks post-hurricane), 481 total stems had new sprouts. In June, 2000 (90 weeks post-hurricane), 493 stems had post-hurricane sprouts (34.2%). The plots with the greatest exposure to hurricane winds had the greatest proportion of sprouting stems (Fig. 1). In each plot, the proportion of sprouting stems was 2–3 times the proportion of stems incurring major structural damage.

The proportion of stems sprouting after Hurricane Georges was 8–14 times higher than before the hurricane. The sprout rate (number of sprouts per stem) was 3–13 times higher than pre-hurricane rates (Table 1). While we expected stems with major structural damage to sprout, we were surprised at the increase in sprouting on defoliated stems and stems without any visible damage. The proportion of stems sprouting and sprout rates did not differ with severity of defoliation (Fig. 2).

New sprouts emerged from both roots and trunks of trees, sometimes in both locations for a single stem (Table 2). Over 73% of sprouting stems had sprouts emerging below 40 cm on a stem.

Tree species in Guánica Forest had different sprouting response patterns after the hurricane.

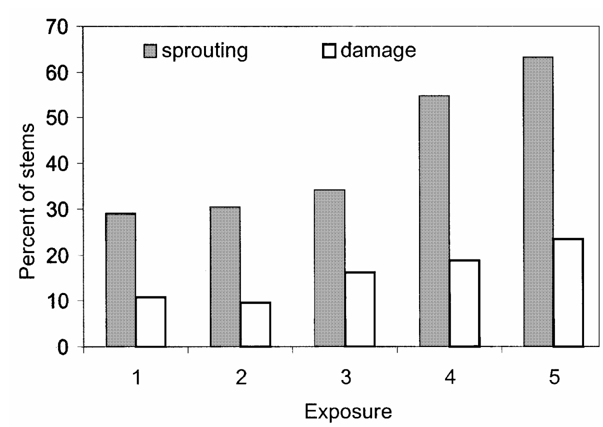

Fig. 1. Percent of stems in Guánica Forest incurring structural damage and with new sprouts relative to wind exposure. Sprouting data are from four months after Hurricane Georges. Structural damage includes snapping, permanent bending, uprooting, or loss of large branches. Exposure is determined by elevation and slope based on wind speeds and directions reported after Hurricane Georges (Bennett 1998), all plots face south. Exposure 1 is most protected at low elevation and a level slope. Exposures 4 & 5 are at the highest elevations, 5 has the steepest slope. Both damage and sprouting are greater at higher exposures (χ^2 tests: $p = 0.016$, $p < 0.00001$ respectively).

Table 1. Sprouting in Guánica Forest, Puerto Rico. Pre-hurricane sprouts were counted on 451 stems. Post-hurricane sprouts were counted on 1407 stems pooled from five plots. Only sprouts developing below breast height (1.4 m) were counted. A sprout was defined as any woody twig with an orientation greater than 45° relative to the ground. Post hurricane sprouts compared against pre-hurricane sprouts using z or t tests as appropriate.

	Total number of stems	% of stems with sprouts	Sprouts per sprouting stem (se)
Pre-Hurricane Sprouts	451	3.5	1.7 (0.3)
Post-Hurricane Sprouts			
Major structural damage	205	48.3***	21.3 (3.3)**
Defoliated stems♀	1153	31.8***	10.1 (1.0)**
No visible stem damage	49	28.6***	5.8 (1.6)*

♀ Stems with defoliation but without major structural damage.
***p < 0.0002; **p < 0.0005; *p < 0.01

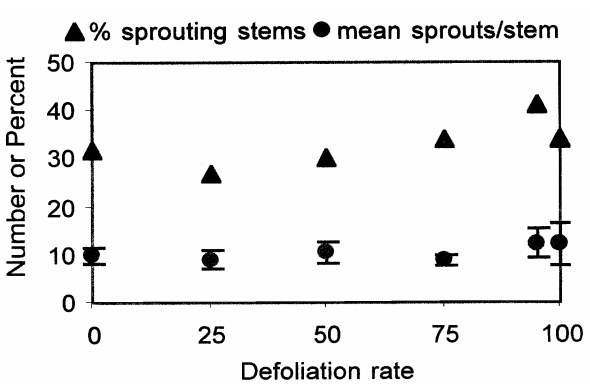

Fig. 2. Trends in proportion of sprouting stems or sprouting rate with defoliation severity in Guánica Forest following Hurricane Georges. Bars are ± 1 SE Pre-hurricane sprouting shown in Table 1. Severity of defoliation is not related to sprouting response. χ^2 tests: p = 0.60 for percent of stems sprouting; p = 0.92 for sprouts per stem.

For species with at least 10 stems in our plots, 4–100% of stems sprouted (Table 3). For our six most common species, each with at least 100 stems, 15–71% sprouted. Sprout rate ranged from 5–34 sprouts per stem for our 6 most common species.

Table 2. Percentage of post-hurricane sprouts arising from trunks or roots. Sample size is number of stems sprouting.

All stems (n = 481)	Percent
Only from roots	21.7
Only from trunk	61.1
From both trunk and roots	17.2
At or below 40 cm on trunk	73.4
Defoliated or no damage stems (n = 382)	
Only from roots	24.3
Only from trunk	58.6
From both trunk and roots	17.0
At or below 40 cm on trunk	75.1

Some produced many short sprouts (e.g. *Exostema caribaeum*) while others produced few long sprouts (e.g. *Coccoloba diversifolia*). For species with at least 20 stems in our plots, the median length of the longest sprouts for each species showed was positively correlated with the number of stems per tree (p = 0.012, Fig. 3) and the percentage of multistemmed trees of a species (p = 0.018).

By January 1999 there were 5898 new sprouts on the 1407 stems in our plots. By June 2000 sprout mortality was 13.6%, leaving 5095 new sprouts. Mortality for sprouts growing from trunks was about 25%, but this was offset by a 20% increase in root sprouts. Mortality of sprouts was 15.8% on stems with major structural damage and 12.4% on defoliated or undamaged stems. By June 2000, 65% of all post-hurricane sprouts were on defoliated or undamaged stems. The longest sprout on each stem averaged 44 cm in January 1999 and doubled to 89 cm in June 2000.

Discussion

Trees responded to Hurricane Georges by producing a large flush of new sprouts, many at or near the base of trees. After two years, survival of sprouts has been surprisingly high. While we expect thinning of the sprout cohort to continue for some time, the proportion of stems producing post-hurricane sprouts suggests that hurricanes can have a long-term impact on forest structure by initiating the production of new stems. We cannot definitively relate the current structure of mature forest to previous hurricanes because we cannot completely quantify past human disturbance in

Table 3. Species effects in proportion of stems sprouting, sprout rates and sprout length for species with at least 10 individuals sampled. All sprouts are post-hurricane. Some individual trees were multi-stemmed, but only one stem per tree was sampled for sprouts.

Species	Number of stems	% sprouting	Sprouts per sprouting stem	Median longest sprout length (cm)	% Multi-stemmed trees	Mean number of stems per tree
Gymnanthes lucida	306	19.9	7.3	24	29.0	1.5
Amyris elemifera	140	10.7	17.3	8	29.2	1.5
Eugenia foetida	113	70.8	12.8	30	24.4	1.4
Exostema caribaeum	107	34.6	33.9	8	8.3	1.2
Coccoloba diversifolia	104	67.3	7.7	92	52.1	3.1
Pictetia aculeata	104	15.4	5.5	16	50.0	2.4
Bursesera simaruba	98	4.1	5.5	24	4.4	1.0
Guettarda krugii	57	22.8	3.0	17	66.7	3.4
Coccoloba microstachya	37	54.1	4.4	81	76.5	6.1
Bourreria succulenta	33	36.4	4.9	76	35.3	1.5
Thouinia portoricensis	33	90.9	18.9	34	68.6	4.2
Krugiodendron ferreum	31	71.0	20.3	17	16.1	1.2
Pisonia albida	29	10.3	14.3	71	34.5	1.6
Tabebouia heterophylla	28	39.3	9.0	61	92.9	6.5
Bucida bucerus	23	30.4	8.9	37	38.1	2.3
Erithroxylon rotundifolium	23	52.2	11.8	51	35.3	2.3
Leucaena leucocephala	14	100.0	19.1	29	23.1	1.4
Crossopetalum rhacoma	12	75.0	8.2	13	53.8	2.5
Eugenia xerophytica	10	100.0	9.1	11	80.0	6.4

the forest, however, the forest after Hurricane Georges is clearly primed to have more stems than before the hurricane. As the sprout cohort thins, we may see patterns begin to develop between the number of stems per tree and the percent of stems sprouting or sprout rate. By 90 weeks post-hurricane, the length of the longest sprout on each tree was positively associated with the mean number of stems per tree and the percent of stems sprouting within a species.

As expected, stems incurring major structural damage had the highest sprouting rates, but sprouting was also common on defoliated and apparently undamaged stems. Sprouting on defoliated stems was notable because allocation of resources to production of new leaves would be less costly than to leaves and woody tissues needed for sprouts. Root biomass is nearly equal to shoot biomass in Guánica Forest (Murphy & Lugo 1986b), so it appears that roots were able to provide enough resources for the production of new leaves and sprouts simultaneously which we ob-

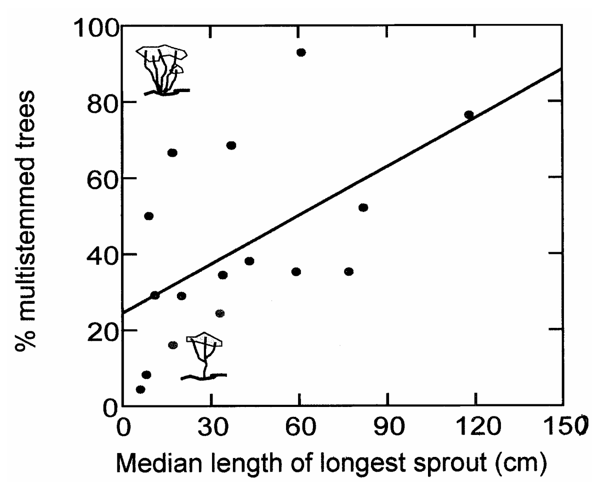

Fig. 3. The median length of the longest sprouts on stems in 16 species of dry forest trees is related to the number of stems of each tree. (p = 0.012) Median sprout length is similarly related to the percent of multi-stemmed trees (p = 0.018). The data are from species with at least 20 trees in our plots. Each point represents a tree species.

served on most stems after Hurricane Georges. The severity of defoliation did not affect sprouting rate, suggesting that defoliation itself was not the mechanism that elicited sprouting.

It is likely that sprout development following the hurricane was influenced by altered hormone balances in trees. High winds and vertical displacement are known to increase ethylene production (Brown & Leopold 1973; Leopold *et al.* 1972; Nelson & Hillis 1978; Telewski & Jaffe 1986). Ethylene production would be highest at the point of greatest bending – below breast height near the root collar (Vogel 1994; Wood 1995). Ethylene has been shown to block auxin transport (e.g. Wood 1985). Because auxin suppresses lateral bud development, blockage of auxin can release these buds (Cline 1991; Kramer & Kozlowski 1979). While we have no direct evidence of altered hormone concentrations following Hurricane Goerges, this model would explain the prevalence of basal sprouting, even on undamaged stems. A mechanism to explain basal sprouting must be applicable across species because basal sprouting occurred on undamaged stems of all species in our plots. Altered hormone balances would be a generalized response to wind stress among all species. Variation in the degree of sprouting response could be the result of unique characteristics of each species in hormone regulation as well as wood density, crown geometry, etc.

Conditions necessary to maintain sprouting as a disturbance recovery mechanism have recently been reviewed by Bellingham & Sparrow (2000). They suggest a tradeoff in recovery strategies between sprouting and seeding. This seems to be the case in Guánica Forest as seedling establishment is generally very low (Molina Colón 1998), while resprouting ability is widespread. Resprouting on mature trees would be supported by well-developed root systems and increasing leaf area to maximize photosynthesis after a disturbance. Resprouting would be a strategy for trees to maximize spatial coverage in order to access more resources (sunlight, water or nutrients) and would, therefore, be a case of reiteration (sensu Halle *et al.* 1978). Bellingham & Sparrow (2000) further suggest that the proportion of biomass lost from a tree following a disturbance will determine whether a tree will resprout and where resprouting will occur on the tree. They suggest that basal sprouting should only become prevalent when a large proportion of above-ground biomass is lost. In this context the amount of sprouting on defoliated stems and stems without any type of visible damage was surprising. Our results suggest that basal sprouting occurs even with the small biomass loss associated with partial defoliation, in contrast to the Bellingham & Sparrow model. Our results likely differ from their predictions because resources following the hurricane (water and nutrients in fresh litter) were high, and thus the reliance on storage organs to support sprouting would be low. Also, our mechanism for eliciting sprout development does not rely on biomass loss, but instead on internal hormone balance altered by exogenous factors.

Conclusions

Hurricane Georges clearly stimulated the development of sprouts above pre-hurricane levels. The production of post-hurricane sprouts was higher in stems with major structural damage than defoliated stems, but not limited to damaged stems nor related to defoliation severity. Sprouts produced on defoliated stems or stems without visible effects of the hurricane accounted for over half of all new sprouts. The amount of production of basal sprouts varied by species, but the phenomenon was not species-specific. After two dry seasons, sprout mortality was low. Our results suggest that hurricane disturbance leaves subtropical dry forest with the potential to greatly increase stem density and the proportion of multiple-stemmed trees, characteristics common to dry forests in the hurricane-prone Caribbean region.

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