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A link between hurricane-induced tree sprouting, high stem density and short canopy in tropical dry forest

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Summary The physiognomy of Caribbean dry forest is shorter, denser and contains a greater proportion of multi-stemmed trees than other neotropical dry forests. Our previous research, conducted after Hurricane Georges in 1998, has shown that dry forest trees sprout near the base following hurricane disturbance, even if the trees have not incurred structural damage. However, for these hurricane-induced sprouts to contribute to the physiognomy of the forest, they must grow and survive. We followed sprout dynamics and stem mortality on 1,407 stems from 1998, after Hurricane Georges, until 2005. The number of surviving sprouts and the proportion of sprouting stems decreased during the 7-year period, but the sprouting rate was still 3-fold higher and the proportion of sprouting stems 5-fold higher than before the hurricane. Mortality of non-sprouting stems (15.4%) was about the same as for sprouting stems (13.9%) after 7 years. The mean length of the dominant sprout surpassed 1.6 m by 2005, with over 13% of the dominant sprouts reaching subcanopy height. Sprout growth and survival varied among species. These results demonstrate that, despite some thinning, hurricane-induced sprouts survive and grow and that the unique physiognomic characteristic of Caribbean dry forests is related to hurricane disturbance.

Keywords: disturbance, forest structure, growth, Guánica Forest, Puerto Rico, regeneration, stem mortality, wind.

Introduction

Research has shown that forest canopy height may be limited by hydraulic conductivity (Koch et al. 2004, Ryan et al. 2006) or physiological constraints caused by air saturation deficit or water availability. However, forest canopies in some locations may never reach their physiological maxima because disturbance factors determine canopy height long before physiological constraints are reached (e.g., Lawton 1982, Smith and Vankat 1992). These forests will be shorter than their counterparts in less disturbed locations (e.g., Murphy and Lugo 1990,

de Gouvenain and Silander 2003), and may also exhibit greater stem density or other structural features that are responses to the local disturbance regime (Bond and Midgley 2001).

For example, the growth form of trees in Caribbean dry forests differs from that in other dry forests, having a much greater frequency of multiple-stemmed individuals than elsewhere. Previous studies have concluded that the growth habit arises naturally, and is not necessarily caused by human activities such as cutting or grazing (Dunphy et al. 2000). Although cutting and grazing will lead to multi-stemmed trees (McLaren and McDonald 2003), mature forests with minimal disturbance have a lower frequency of multi-stemmed trees than dry forests in areas where hurricanes occur (Murphy and Lugo 1986b, Murphy and Lugo 1990, Molina Colón 1998, Dunphy et al. 2000). Located in hurricane prone areas, the multi-stemmed growth form of Caribbean dry forests is likely to be a response to high winds. The low even canopy comprises many stems with small crowns that decrease the force of high winds compared with larger-crowned trees that provide greater wind resistance and whose stems are more likely to snap (Vogel 1994). In addition, a tree with multiple stems is more likely to survive wind disturbance because snapping usually does not affect every stem in a clump (Van Bloem et al. 2005).

On September 21–22, 1998, the eye of Hurricane Georges passed over Guánica Forest, Puerto Rico. Following the hurricane, a substantial flush of new sprouts developed (Van Bloem et al. 2003). While resprouting was expected for broken or uprooted stems, basal sprouts also developed on about 30% of the stems that were only defoliated or that were apparently unaffected by the storm (Van Bloem et al. 2003). However, for these sprouts to contribute to the multiple-stemmed growth form and short canopy characteristic of the forest, they would have to survive and grow to canopy height. The objective of this paper is to report on the growth of sprouts that developed after Hurricane Georges. The evidence indicates that the hurricane-induced sprouts will eventually result in a multi-stemmed growth form of trees and an overall reduced forest stature.

Materials and methods

Guánica Forest comprises primarily semi-deciduous dry forest and is located along the southwestern coast of Puerto Rico (17°58' N, 65°30' W). Mean annual rainfall is 860 mm, with a distinct wet season that peaks from September to November, corresponding to the hurricane season (Murphy and Lugo 1986a). Mean annual temperature is 25.1 °C and the potential evapotranspiration/precipitation ratio averages 1.4 (Murphy and Lugo 1986a). The sections of the forest where our study took place were originally protected in 1919. At the beginning of the study, canopy height was 5–7 m, and density of live stems (> 2.5 cm diameter at breast height, 1.4 m) averaged 12,000 per hectare (Murphy and Lugo 1986b). Leaf area index averaged 3.5 but had a seasonal range from 2.3 to 4.1 (Murphy and Lugo 1986b, Murphy and Lugo 1990). About 42% of trees were multiple-stemmed (Murphy and Lugo 1986b).

Hurricane Georges was a Category 3 storm with sustained winds of 176–184 km h⁻¹ and gusts up to 240 km h⁻¹. In a 24-h span, 151 mm of rain fell (Bennett and Mojica 1998), nearly equal to the September monthly mean (Murphy and Lugo 1986b). The last hurricane of Category 3 strength or greater to impact the forest was in 1928 (Salivia 1972).

Following Hurricane Georges, we measured sprout development and mortality six times over seven years on 1,407 tagged stems in five plots. Each of the plots was located in mature forest dominated by native species. Three of the plots were established before the hurricane for other studies of forest structure (Murphy and Lugo 1986b, Van Bloem et al. 2005). The other two plots were established immediately after Hurricane Georges. Plot size ranged from 0.01 to 1.44 ha and spanned a gradient of hurricane effects and wind exposure (Van Bloem et al. 2005).

Within one week after Hurricane Georges, before any post-hurricane sprouts had developed, we quantified pre-hurricane sprouting rates by inventorying all old sprouts on 451 tagged stems along six transects totaling 680 m in our largest plot. Subsequent sprout censuses on the tagged stems in all five plots were completed in January and June 1999, July 2000, August 2002 and March 2005. In 2000, we tagged the longest sprout on each tree (the dominant sprout) by loosely attaching a cable tie to make subsequent measurements easier. On all of the tagged stems, we counted all new sprouts growing at breast height (1.4 m) or lower. Beginning in 2000, we also noted how many sprouts arose below 40 cm, a height at which they would more clearly be considered stems instead of branches. The length of the dominant sprout on each tagged stem was measured to the nearest cm and its point of origin noted (i.e., root suckers, root crown, or height on stem). We considered any woody twig growing from a mature stem at an angle < 45° from the stem to be a sprout (Dunphy et al. 2000). We distinguished new sprouts by their distinctive bark colors compared with old sprouts. We assumed that all new sprouts that arose by June 1999 were induced by the hurricane, and that new sprouts that arose after June 1999 resulted from other natural causes (e.g., drought, salt deposition, insect damage). Therefore, background sprouting rates were computed based

on new sprouts that arose between each census after June 1999.

Stems were considered dead when they were completely leafless and had dried bark. We computed annual mortality rates, m , as:

$$m = 1 - (1 - (N_0 - N_1)/N_0)^{1/t}$$

where N_0 and N_1 are the number of stems at the start and end of each sampling interval of t years. This equation comes from an exponential model of population decline (Sheil 1995). We used the recruitment rate equation from Burslem et al. (2000):

$$sp = 1 - (1 - n_{sp}/N_t)^{1/t}$$

to model background sprouting rates, sp , where n_{sp} is the number of stems with new post-hurricane sprouts and N_t is the number of living trees at the end of the time interval t (years) that did not sprout following Hurricane Georges.

Results

Fate of sprouts arising following Hurricane Georges

By 2002, only 47% of the original 5,898 hurricane-induced sprouts survived. Mortality rates after this time decreased and 34% of the sprouts were still alive in 2005 (Figure 1). The number of sprouts per stem decreased from 12.3 in January 1999 to 5.8 in March 2005. The length of the dominant sprout on each stem continued to increase over the 7-year study, reaching a mean of 160 cm in 2005 (Figure 1). However, 13.2% of the sprouts reached lengths of at least 3 m and 3.5% grew to over 4 m by March 2005. Of the stems that sprouted following the hurricane and still had sprouts in 2005, 22% had

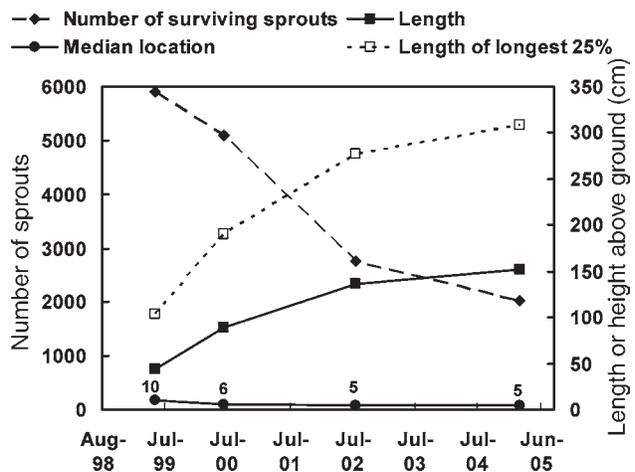


Figure 1. Number of sprouts surviving after Hurricane Georges from September 1998 until March 2005, the median location of emergence of dominant sprouts (height above ground, values above markers), mean length of the dominant sprout on each stem and the mean length of the upper quartile of dominant sprouts. Standard error for sprout lengths is smaller than the symbols.

a dominant sprout that differed from that in June 2000, because either the earlier dominant sprout had died or had been outgrown. In 2005, 83% of all the sprouts were from root suckers, the root crown or the lowermost 40 cm of the stem. These sprouts were substantially longer (166 ± 7 cm; (\pm SE)) than sprouts arising above 40 cm on the stem (112 ± 10 cm). The median location of the dominant hurricane-induced sprouts was 10 cm above the ground in 1999 and declined to 5 cm by 2005 because a greater proportion of the sprouts developing higher on the stem died (Figure 1).

The number of stems with sprouts surviving from Hurricane Georges has gradually decreased over time, dropping from 34% to 18% in seven years (Figure 2). The background sprouting rate (development of new sprouts not associated with hurricane disturbance during each census period after June 1999) helped to maintain the proportion of stems with sprouts at above 30%, nearly ten times greater than the pre-hurricane proportion of 3.5%. Although our observations on periodic sprouting did not begin until 1998, the size distribution of the sprouts we counted to determine the pre-hurricane proportion of sprouting stems suggested that they had been developing for up to 10 years and, therefore, that annual sprouting rates might be about 0.35%. Post-hurricane background sprouting rates were higher than before the hurricane, with 4.8% of the stems developing new sprouts from 1999 to 2000, then dropping to 1.5% from 2002 to 2005 (Figure 2).

Stem mortality since Hurricane Georges

Before Hurricane Georges, annual stem mortality was only 0.3% (Van Bloem et al. 2005). The hurricane-caused mortality rate of stems from mature forest dominated by native species was 2.5% (Figure 3). Since 2000, annual stem mortality has been between 1.4 and 3.3% regardless of whether the stems had sprouts or not. Total mortality for sprouting stems by 2005 was 13.9% compared with 15.4% for non-sprouting stems.

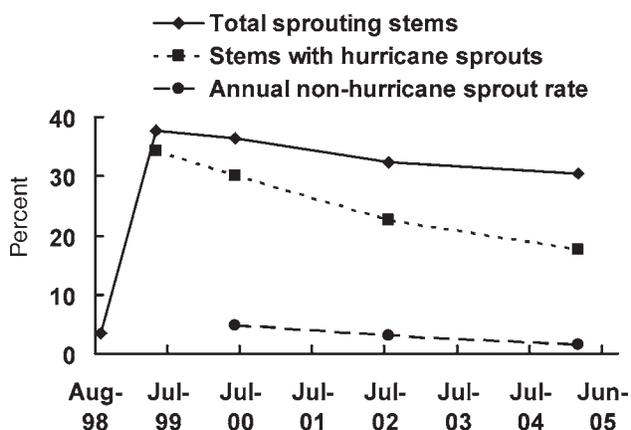


Figure 2. Total percentage of sprouting stems (regardless of cause), the proportion of stems with new sprouts developing after Hurricane Georges from September 1998 until March 2005, and the annual sprouting rate for trees that did not sprout within 9 months after the hurricane. The proportion of trees with sprouts before the hurricane was 3.5%.

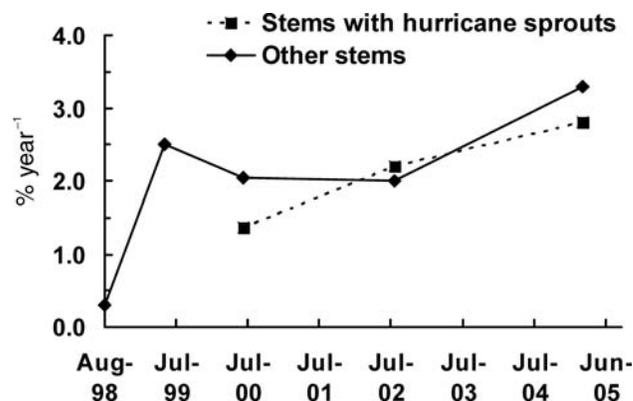


Figure 3. Annual rates of mortality of sprouting stems and non-sprouting stems following Hurricane Georges in September 1998 until March 2005. There was no difference among mortality rates based on sprouting ($\chi^2 = 0.11$ $P = 1.0$). By 2005, total mortality for sprouting stems was 13.9% compared with 15.4% for non-sprouting stems. Mortality for 1998 is background mortality (Van Bloem et al. 2005).

Mortality among the 99 trees in our sample of 1,407 stems that incurred structural damage and sprouted was 31% by 2005, compared with only 8.0% for trees without structural damage.

Species effects

Sprout survival and dynamics differed among species. Four species had mean dominant sprout lengths of >2.0 m (Table 1). Of these, only one species (*Erythroxylon rotundifolium* Lunan) was in the top four species for number of sprouts per stem. Neither sprout growth, survival or percentage of stems sprouting was related to wood density or successional status.

Discussion

To contribute to the multiple-stemmed growth habit of Caribbean dry forest trees, hurricane-induced basal sprouts must survive and grow to canopy height. Although the sprout cohort induced by Hurricane Georges has thinned over the last seven years, the 5.6 sprouts per stem measured in 2005 was much higher than the mean number of stems per tree measured before Hurricane Georges in 1998 and in 1981 (1.8 each time; Murphy and Lugo 1986b, Van Bloem et al. 2003). Only one sprout per stem needs to survive and grow to canopy height to result in a multi-stemmed tree, so this growth form can still be generated by the hurricane even with continued thinning of the sprout cohort. Sprouting patterns differed among species. Only *E. rotundifolium* had both above average sprout growth and above average number of sprouts per stem. For the six species with at least 10 sprouting stems, there was a tendency for the length of their dominant sprouts to be inversely proportional to the number of sprouts per stem ($r^2 = 0.48$; $P = 0.13$), perhaps indicating a trade-off between sprout growth and sprout production.

By 2005, the growth of the dominant sprout on each stem had already generated some multi-stemmed trees, with the mean length of these sprouts exceeding breast height, the min-

Table 1. Species effects on sprouting rate and mean length of dominant sprout. Only species that had at least 10 live stems sampled in 2005 are included. Generally, species with greater growth of the dominant sprout had fewer sprouts per stem. Nomenclature as in Little and Wadsworth (1964) and Little et al. (1974). Successional status (P = pioneer, M = Mature) and wood density from Molina Colón (1998).

Species	Total stems in 2005	Sprouting stems in 2005	Sprouts per stem	Mean length (cm)	Wood density (g cm ⁻³)	Successional status
<i>Pisonia albida</i> (Heimerl) Britton	25	6	3.3	340	0.42	P
<i>Coccoloba diversifolia</i> Jacq.	82	54	3.0	269	0.80	M
<i>Erythroxylon rotundifolium</i> Lunan	10	6	7.5	260	0.97	M
<i>Coccoloba microstachya</i> Willd.	27	20	2.8	230	0.66	M
<i>Bourreria succulenta</i> Jacq.	27	10	1.9	183	1.48	P
<i>Pictetia aculeata</i> (Vahl) Urb.	104	6	2.2	164	0.80	P
<i>Tabebuia heterophylla</i> (DC.) Britton	26	7	5.0	164	0.58	P
<i>Exostema caribaeum</i> Jacq. (Roem & Schult.)	80	8	8.4	134	1.00	P
<i>Thouinia portoricensis</i> Radlk.	23	20	12.1	129	0.86	M
<i>Gymnanthes lucida</i> Sw.	259	74	4.6	112	1.10	M
<i>Eugenia foetida</i> Pers	97	78	10.7	96	0.65	M
<i>Guettarda krugii</i> Urban	49	5	2.6	94	0.79	M
<i>Krugiodendron ferreum</i> (Vahl) Urban	29	9	2.7	85	1.40	M
<i>Bursera simaruba</i> (L.) sarg.	83	2	1.5	84	0.32	P
<i>Amyris elemifera</i> L.	122	2	7.0	72	1.10	M
<i>Bucida buceras</i> L.	23	5	1.4	61	0.93	M

imum height that most foresters use to classify saplings. The 13.2% of dominant sprouts that have already grown at least 3 m have reached the subcanopy in this short-statured forest, thus adding stems to clumps or creating multi-stemmed trees from previously single-stemmed trees. The median location of the dominant sprout (5 cm above ground) also demonstrates that the sprouting response generated multi-stemmed trees, rather than trees with more branches, which would have been our interpretation if the dominant sprouts had tended to be located at 1-m height, for example. The decrease in the median location of the dominant sprout over time resulted from greater mortality of sprouts that developed higher on stems. This phenomenon was already well advanced by July 2000 (Van Bloem et al. 2003).

Since Hurricane Georges, there has been little difference in the mortality of sprouting and non-sprouting trees. Thus, sprouting stems are as likely as non-sprouters to survive and apparently their sprouts will be able to grow enough to reach the canopy. In addition, mortality of sprouting stems that incurred major structural damage as a result of the hurricane (i.e., snapping, uprooting, loss of large branches and leaning beyond 30° from vertical) was only 31% over the 7-year period. Inability to sprout would result in death of snapped stems (Bond and Midgley 2003) and many of these stems might be expected to die due to increased susceptibility to disease, drought, herbivory or decreased competitive ability. Apparently, sprouting mitigates these effects for many trees, resulting in prolonged survival, just as sprouting allows trees to survive coppicing (McLaren and McDonald 2003). Nevertheless, annual mortality rates for all stems (1.4–3.3%) were much greater than before the storm (0.3%) based on a sample of 475 stems followed for 2 to 17 years before Hurricane Georges (Murphy et al. 1995, Van Bloem 2004). In other tropical forests, annual mortality has been shown to remain high for at

least 4 years after hurricane disturbance (Dittus 1985, Lugo and Scatena 1996).

We previously demonstrated that basal sprouting is a prominent response to hurricane winds (Van Bloem et al. 2003). Considering that there was widespread sprouting after the Category-3-strength Hurricane Georges, but not after Hurricane Hortense (Category 1), we conclude that the wind speeds necessary to generate this response must be between 119 and 178 km h⁻¹. The background sprouting rate may be maintained by a suite of other causes (e.g., topkill of some stems from disease or drought or damage from smaller storms or insects).

The mechanism causing the sprouting response to hurricane winds is under study, but does not appear to be related to irradiance because sprouting showed no relationship to defoliation (Van Bloem et al. 2003). The causal factor may be related to a shift in hormone balances. Ethylene may be released near the stem base as a result of the sustained displacement from the vertical (Telewski and Jaffe 1986) by hurricane winds or by root breakage (Ernesto Medina, Instituto Venezolano de Investigaciones Científicas, personal communication). Increased concentrations of ethylene would interfere with downward transport of IAA and limit apical dominance (Erner and Jaffe 1982), resulting in the loss of lateral bud suppression (Eklund and Little 2000). This physiological response to the effects of disturbance by high winds would result in control of canopy height from the base. Thus, the sprouts would occupy empty space and intercept more light while being supported by abundant roots to capture water and nutrients. Basal sprouting following hurricanes is not common to all forest types, however. In subtropical moist and wet forests in Puerto Rico, basal sprouting following hurricanes is rare and these forests regenerate primarily from seed (Walker 1991). Undamaged or partially defoliated stems in these wet-

ter forests may not have enough light to sustain basal sprouts because of the greater leaf area, deeper canopies and taller trees. Sprouting was common in montane rain forests of Jamaica following Hurricane Gilbert in 1988, with about two thirds of the stems having sprouts arising below 2.5 m, but basal sprouting was not assessed. Sprouting tends to be more common in more stressful environments like seasonally dry tropical forests (Bond and Midgley 2001).

Dry forests would be expected to have shorter canopies than moist and wet forests because leaf water potentials are typically lower in arid settings and the closure of stomata by loss of turgor is more common both seasonally and annually. In more mesic forest systems, maximum tree height may be constrained by hydraulic conductance (Koch et al. 2004), where the force of gravity counteracts the pull of transpiration until leaves at the tops of trees lose their turgor and photosynthesis subsequently stops or assimilate is no longer transported out of the leaf (Ryan and Yoder 1997, Ryan et al. 2006). However, gravitational pull only increases leaf water potential by 0.01 MPa m⁻¹ (Woodruff et al. 2004). The 5–10 m height of mature dry forests in the Caribbean (Murphy and Lugo 1986a) is insufficient to impose major gravitational constraints on leaf water potential considering that minimum water potentials for arid zone plants are in the range of –1.3 to –5.0 MPa and that daily fluctuation of leaf water potential can be much greater than 0.1 MPa (Larcher 1995, Brodribb et al. 2003, Diaz and Granadillo 2005). We conclude that the short canopy of Caribbean dry forest is a result of hurricane disturbances that produce a dense forest composed of a large proportion of short, multi-stemmed trees. Our most recent data demonstrate that the longevity and growth characteristics of hurricane-induced tree sprouts have the potential to contribute to long-term forest structure.

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