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Running head: Long-term hurricane impacts on tropical forests

Title: Long-term hurricane damage effects on tropical forest tree growth and mortality

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Abstract

Hurricane winds can have large impacts on forest structure and dynamics. To date, most evaluations of hurricane impacts have focused on short-term responses after a hurricane, often lack pre-hurricane measurements, and miss responses occurring over longer time scales. Here we use a long-term dataset (1974–2009, 35 years) of tree stems (> 3 cm in diameter at 1.3 m) in four sites (0.35 ha in total) in montane rain forest (c.1600 m) in Jamaica to investigate the patterns of crown damage in individual stems by Hurricane Gilbert in 1988, and how subsequent growth and mortality were affected by hurricane damage, sprouting, and the incidence of multiple stems.
Topographical position on a mountain ridge was the best predictor of crown damage, followed by crown size and species identity. The average diameter growth rate of stems that survived the hurricane was greater than that pre-hurricane for the whole 21 year post-hurricane period. Growth of stems with damaged crowns increased less than those with undamaged crowns; differences in growth rate between damaged and undamaged trees disappeared after eleven years. Hurricane-damaged stems had 2 to 8 times higher mortality than undamaged stems for 19 years post hurricane. Many stems sprouted shortly after the hurricane, but few sprouts managed to establish (grow to > 3 cm diameter at breast height). However, sprouting and multi-stemming were associated with reduced mortality rate, particularly in damaged trees. From an initial population of 1670 stems in 1974, 54% were still alive in 2009 (21 years after the hurricane). We conclude that despite the high frequency of hurricane damage to tree crowns and the subsequent increased mortality rate in this hurricane-prone tropical montane forest, many stems will be hit and recover from several hurricanes in their lifetime.

Keywords: Bayesian; Caribbean; cyclone; defoliation; demography; disturbance; forest dynamics; forest structure; mortality; multiple-stems; sprouting; tree growth.

INTRODUCTION

Natural disturbances such as fires and hurricanes can have major impacts on forests’ structure and dynamics despite their short duration (from hours to a few days) (Overpeck et al. 1990; Foster et al. 1998). Wind storms can damage large numbers of trees (Coutts and Grace 1995; Vandermeer et al. 2000) affecting subsequent tree demography, forest dynamics and ecosystem
processes (Foster and Boose 1995; Foster et al. 1998). The effects of tropical cyclones are particularly strong (Zimmerman et. al. 1996; Lugo 2008), and their intensity (wind speed and amount of rainfall) is expected to increase in the coming decades due to climate change (Field et al. 2012). Despite the importance of these effects, only a few studies have assessed the long-term (more than a decade) consequences of wind damage on the growth of individual trees (e.g., Merrens and Peart 1992, Busby et al. 2008) and fewer still on tree mortality (e.g., Weaver 1986, Burslem et al. 2000). Most studies are done within a few years of the impact of a cyclone (called hurricanes in the Atlantic), and describe the form of damage and differences between species in damage and mortality (e.g., in Jamaica, Bellingham et al. 1995; in Puerto Rico, Ostertag et al. 2005; see Everham and Brokaw 1996, Lugo 2008, for general reviews). These short-term studies may miss tree and forest responses occurring over longer time scales, and quite often lack pre-hurricane data to serve as a baseline for comparison of post-hurricane dynamics.

The scarcity of long-term studies results in high uncertainties regarding the magnitude and duration of hurricane impacts on tree mortality and growth. In lower montane rain forest in Puerto Rico, mortality rates increased and growth rates were lower in hurricane-damaged stems than in undamaged stems for about four years after a major hurricane (Uriarte et al. 2004, 2012). In Florida, over seven years after Hurricane Kate, growth and mortality rates were higher or lower than pre-hurricane rates depending on the tree species (Batista and Platt 2003). In the Solomon Islands, recruitment and mortality rates were still higher 24–28 year after cyclones struck (Burslem et al. 2000). In New Hampshire, tree growth was higher in a hurricane-damaged stand than in a comparatively undamaged stand, for two of four species for 44–48 years after a hurricane (Merrens and Peart 1992). In South Carolina, previously damaged trees were more likely to be damaged by a subsequent hurricane (Putz and Sharitz 1991). These studies establish
that hurricane effects on tree mortality and growth can be long-lasting, but also highly variable. The factors driving the apparent variation in the magnitude, species-specificity, and duration of hurricane impacts remain unclear.

In Jamaica, our studies of forest dynamics in permanent plots in the Blue Mountains have already shown that mortality and growth increased shortly after a hurricane impact (Bellingham et al. 1995) and that species composition changed over the twenty year period 1984–2004 (with Hurricane Gilbert in 1988), with an increase in rarer species and recruitment of light-demanding species formerly absent from the plots (Tanner and Bellingham 2006). In the current paper we exploit this long-term (14 years pre-hurricane and 21 years post-hurricane) tropical forest dataset to address the following questions: 1. What factors were associated with hurricane damage to tree crowns? 2. What was the magnitude and duration of hurricane-caused damage on stem growth and mortality? 3. Was tree sprouting after the hurricane and possession of multiple stems associated with long-term survival of trees post-hurricane?

**METHODS**

We report analyses of data from before and after Hurricane Gilbert, the eye of which passed less than 10 km South of our study sites on 12 September 1988. Hurricane Gilbert had the lowest atmospheric pressure yet recorded for a North Atlantic cyclone: its wind speeds were up to 194 km h\(^{-1}\) as it crossed Jamaica (Lawrence and Gross 1989). In the subsequent 21 years of our study, no hurricane eye passed over (eastern) Jamaica although there were several near misses in the period 2004–2009. These near misses did not have strong effects on the natural forest as judged by the fact that no stems of the very light-demanding but short-lived species
Bocconia frutescens were observed in the forest in the vicinity of the study sites in 2009, whereas for at least five years after Hurricane Gilbert in 1988 stems of this small tree were widespread. In the 37 years between Hurricanes Charlie in 1951 and Gilbert in 1988, no other hurricane eye passed within 50 km from the study sites. We conclude that the effects we are studying are predominantly attributable to Hurricane Gilbert in 1988 and not those of earlier or more recent but more distant hurricanes.

Our study sites are in forests that are on and near the main ridge of the Blue Mountains of Jamaica (18° 05´N; 76° 39´W, 1500–1650 m altitude). We had four sites (named ‘Col’ 0.09 ha, ‘Mor’ 0.06 ha, ‘Mull’ 0.1 ha and ‘Slope’ 0.1 ha); each site was composed of 6–10 contiguous 10 × 10 m plots (Appendix A; further details in Tanner 1977, Tanner and Bellingham 2006). The Mull, Col and Mor sites are on the crest of an undulating steep-sided main ridge that runs approximately SE to NW. The slope to the NE of the Mull site is 42º and to the SW of it 33º. The main ridge rises by 60 m over a horizontal distance of 150 m from the SE to the Mull site and then falls by about 15 m to the NW into a ‘gap’ in the main ridge where the Col site is situated; it then rises by about 30 m to a knoll where the Mor site is situated (Appendix A). The Slope site is 15–50 m down the northern side of the main ridge. The hurricane came in from the SE and the eye passed overland to the south of the main ridge. Thus the Mull site was most exposed, the Mor next most exposed, the Col was relatively protected by the 15 m decrease in altitude from the Mull to the Col (and the 30 m rise in altitude from the Col to the Mor) and its position ~ 150 m back from the top of the slope leading up to the Mull. The Slope site was the least exposed because of its position on the northern slopes, which were relatively protected from the eye of Hurricane Gilbert (Bellingham 1991).
The stems were measured in 1974, 1984, 1989, 1991, 1994, 2004 and 2009. At each census, all stems with diameter at breast height (dbh, 1.3 m) > 3 cm were scored as live or dead, identified to species, and measured on a painted band (see Appendix B for descriptive statistics of the number of stems, species and stem size for each site). Stems part of multi-stemmed individuals were recorded as separate stems and their connection recorded. In the first re-enumeration after Hurricane Gilbert (1989) crowns of living trees were scored for damage using a four-point qualitative scale: 1) crown-detached (crowns broken off but with epicormic sprouts developing), 2) crown bare (no leaves, i.e., completely defoliated), 3) crown sparse (few leaves), or 4) crown undamaged; herein we amalgamated the three categories 1, 2, and 3 into a category of ‘damaged’ to be compared with ‘undamaged’. For 703 stems with smaller diameter crowns (mean stem dbh 7.2 cm, SE 0.1 cm) the crowns were scored as a whole; for 622 stems with larger diameter crowns (mean stem dbh 15.6 cm, SE 0.3 cm) the crowns were divided into upper and lower portions, which were scored separately; we used only data from the upper portion.

Species names follow Adams (1972), updated and with other authorities from http://www.theplantlist.org/ (Appendix C).

We used hierarchical Bayesian modeling to estimate the effects of spatial location (site, plot) and individual characteristics (species, crown size – large or small – and previous diameter growth rate – an indicator of tree vitality) on the probability of crown damage (‘damaged’ cf. ‘undamaged’) by the hurricane (n = 1259 stems from 48 species, excluding dead trees and tree ferns). Specifically, for every individual stem $i$ of species $j$ growing in plot $l$ at site $k$, the probability of being damaged ($\varphi_{ijkl}$) was modeled as

$$\text{logit} \left( \varphi_{ijkl} \right) = \alpha_k + \gamma_l + \delta_j + \beta_1 \ast \text{crown size}_i + \beta_2 \ast \text{growth rate}_i$$
where crown size was a binary variable (either large or small) and growth rate represents the average stem growth rate during the period 1974–1984 (pre-hurricane). We used relatively non-informative priors for all parameters. Parameters $\beta_1$ and $\beta_2$ had Normal priors with mean 0 and large standard deviation (1000). In this and all subsequent analyses, site effects ($\alpha_k$, $k = 1, \ldots, 4$) were modelled as fixed effects $\alpha_k \sim \text{Normal}(0, 1000)$, while plot ($\gamma_l$) and species ($\delta_j$) effects were modelled hierarchically as $\gamma_l \sim \text{Normal}(0, \sigma_{\text{plot}})$ and $\delta_j \sim \text{Normal}(0, \sigma_{\text{species}})$. Both standard deviations $\sigma_{\text{plot}}$ and $\sigma_{\text{species}}$ had flat priors $\text{Uniform}(0, 10)$.

Stem diameter growth rates over time were modeled as a function of location (site, plot), species, individual and damage score. For this analysis we only included stems surviving the whole study period ($n = 915$ stems from 41 species). Specifically, the average diameter growth rate $G$ of a stem $i$ of species $j$ growing in plot $l$ at site $k$ during census $t$ ($t = 1, 2, \ldots, 6$) was modeled as

$$G_{ijkl} \sim \text{Normal}(g_{ijkl}, \sigma_G)$$

where $g_{ijkl} = \alpha_k + \gamma_l + \delta_j + \omega_i + \beta_t + \omega_t \cdot \text{Damage}_i$.

Damage is a binary variable separating hurricane-damaged from undamaged trees. $\omega_t$ was given a standard non-informative prior, $\omega_t \sim \text{Normal}(0, 1000)$. Site ($\alpha_k$), plot ($\gamma_l$) and species ($\delta_j$) effects were modeled as above. We accounted for individual variation in growth rates by including random individual effects $\theta_i \sim \text{Normal}(0, \sigma_i)$, with inter-individual standard deviation $\sigma_i$ having flat prior $\text{Uniform}(0, 10)$, as well as the residual standard deviation $\sigma_G$.

We modeled stem mortality as a Bernouilli process, accounting for the different duration of census intervals (Ogle et al. 2006). The probability of mortality of any stem during census $t$ ($\tau_{it}$) was equal to $1 - (1 - M_i)^{\gamma_t}$, where $M_i$ is the annual probability of mortality of stem $i$ during census $t$, and $\gamma_t$ is the number of years spanning the census (Lines et al. 2010). The annual
probability of mortality of any stem was subsequently modeled for each census taking into
account its location, species identity and damage status:

\[
\logit (M_{ijkl}) = \alpha_k + \gamma_l + \delta_j + \beta_D \ast \text{Damage}_i.
\]

We modeled site, plot and species effects (\(\alpha_k + \gamma_l + \delta_j\) respectively) as above, and the effects of
damage on mortality were given a standard non-informative prior: \(\beta_D \sim \text{Normal} (0, 1000)\).

Many stems sprouted in response to hurricane damage. We analyzed the variation in
sprouting frequency among stems, plots and species, and the subsequent effects of sprouting on
post-hurricane mortality. In the 1989 census, one year after the hurricane, we recorded the stems
that had sprouted from the crown base (above 2.5 m high). The probability of sprouting was then
modeled as a function of stem location (site, plot), species, damage score (damaged or not) and
crown size (large or small) using the logit link. Subsequently, we assessed whether crown
sprouting and being multi-stemmed had any influence on overall post-hurricane mortality (1989–
2009) by repeating the mortality analysis above for individual trees (n = 1390), this time
including parameters accounting for sprouting, multi-stemming and their interaction.

As we aim to explain tree responses to hurricane damage in these particular sites rather
than extrapolating to other forests, we report finite-population standard deviations throughout
(Gelman and Hill 2007). All analyses were run in R 3.0 (R Development Core Team 2013) and
JAGS 3.3.0 (Plummer 2003) by means of the R2jags package (Su and Yajima 2012).

RESULTS

Crown damage
Hurricane Gilbert caused extensive crown damage: 5–8 months after the hurricane of the 622
stems with larger crowns scored for damage, 38% were undamaged, 28% sparsely foliated, 18%
bare and 16% crown-detached.; of the 703 stems with smaller crowns 66% were undamaged,
22% sparsely foliated, 5% bare and 7% crown-detached. The best predictor of whether a crown
was damaged was topographical position. Trees in the most affected (Mull) site, on a convex
ridge top, had a 37% greater probability of crown damage on average than trees in the least
affected, north-facing, Slope site (Table 1, Fig. 1). The next most important predictors were
crown size and species; having a large crown increased damage probabilities by 26% (calculated
from values in Table 1); and belonging to the most susceptible species (Solanum punctulatum)
increased the probability of damage by 47% compared with the least susceptible species
(Podocarpus urbanii) (Appendix C). However, we did not detect strong differences in
susceptibility to damage amongst most species: only three species had estimated susceptibility
significantly different from zero and mean effect size lay between + and – 0.5 for 38 out of 48
species, including some that were relatively abundant (Appendix C). Finally, pre-hurricane
growth rates only had a small effect on the likelihood that a stem was damaged, as a 1 mm yr\(^{-1}\)
higher growth rate (a big difference given that the average growth rate of all stems alive
throughout the study period was 0.6 ± 0.02 mm yr\(^{-1}\)) translated into only an 8% decrease in the
overall probability of damage (Table 1, Fig. 1).

**Stem growth and mortality**

The average stem diameter growth rate of surviving stems over the full 21-year post-
hurricane period was greater than that pre-hurricane (Fig. 2, Appendix D). Whereas growth rates
of damaged stems were quite stable over the whole post-hurricane period, undamaged stems
showed a four-fold increase immediately after the hurricane, declining to the same level as
damaged trees by 11 years after the hurricane (Fig. 2). Average diameter growth rates of
damaged and undamaged stems 1–3 years after the hurricane (1989-1991) were 77% and 160%
higher, respectively, than before the hurricane (1974–1984). The diameter growth rate of
damaged stems was significantly lower than that of undamaged stems for up to six years post-
hurricane (1989–1991 and 1991–1994; Fig. 2). There was also substantial variation among
species and individuals within species (Appendix D): although surviving trees of all species
responded positively to the hurricane in terms of subsequent growth rate, the increase was much
greater in some species (e.g., *Alchornea latifolia*) than others (*Lyonia octandra*) (Appendix E).
Overall stem mortality rates (damaged and undamaged stems together) were higher in the six
years after the hurricane and slowly returned to pre-hurricane rates 6–21 years post-hurricane
(Fig. 3). The increase was entirely attributable to the significantly greater mortality rates of stems
with hurricane-damaged crowns (3.4% yr⁻¹, 1989–1994) versus stems with undamaged crowns
(0.45% yr⁻¹, 1989–1994). During the same six-year period, the probability of mortality of stems
with undamaged crowns was less than half that of the pre-hurricane years. Hurricane effects on
mortality were long-lasting: stems with damaged crowns had significantly greater mortality than
undamaged stems for between 16 and 21 years post-hurricane (Fig. 3). At the time of the last
census (2009), mortality rates of stems with damaged and undamaged-crowns had still not fully
converged. Hurricane damage thus had longer term effects on mortality than on growth;
differences in stem diameter growth between damaged and undamaged trees mostly disappeared
between six and 16 years after the hurricane (Fig. 2).

Sprouting
Sprouts above 2.5 m on a stem were present on 38% of stems in 1989, a year after the hurricane. The presence of sprouts was very species-dependent, including frequent sprouters (e.g., Eugenia biflora, Lyonia octandra, Chaetocarpus globosus, and Sideroxylon montanum) and non-sprouters (Clusia havetioides and Schefflera sciodaphyllum). On average, large-crowned undamaged trees showed the highest probability of sprouting (33%; Table 2). Damaged stems showed slightly lower sprouting (~25%) regardless of their crown size. Despite the intense post-hurricane sprouting (both above and below 2.5 m on a stem), the percentage of multiple-stemmed individuals hardly changed throughout the 35 year period, from 13.0% in 1974 to 13.5% in 1989, 14.1% in 1994, 14.6% in 2004 and 13.9% in 2009. Sprouting and having multiple stems (which were correlated) were associated with lower long-term (1989–2009) mortality in damaged trees (average mortality rate around 2.3% per year compared to 3.5% for damaged single-stem, non-sprouted trees). Sprouting and multi-stemming effects on mortality were apparently much weaker for undamaged trees; the significant effect for ‘undamaged sprouted multi-stems’ (Table 3) has a wide credible interval and is based on only 23 stems. There were 365 recruits to the plots in years one to six after the hurricane (1989–1994); 34% of these were part of a multi-stemmed individual, not significantly different from the 30% of 121 stems recruited between 1984 and 1989 (four years before and first year immediately after the hurricane in 1988). Thus, stem recruitment after the hurricane derived mostly from sexual regeneration (i.e., seeds or seedling bank) rather than basal sprouting of older individuals.
Hurricane damage: its correlates and its effects on stem growth and mortality

Crown damage caused by Hurricane Gilbert was related to topographic position, crown size and species identity. Our results show that topographic position and the degree of exposure to strong winds are important predictors of damage in sites along a mountain ridge (see also Boose et al. 1994, 2004) and can override other factors (e.g., tree size, species identity) that are often emphasized in the literature on hurricane impacts (Everham and Brokaw 1996). In highly exposed stands, most trees will experience greater damage regardless of their individual characteristics, and vice versa: protected stands will act as ‘refugia’ where both less susceptible and more susceptible trees will be more likely to escape hurricane damage. Topographical effects, when investigated, have sometimes given apparently contradictory results. For example, after different hurricanes affected forests in the Luquillo Mountains in Puerto Rico, Ostertag et al. (2005) reported that trees growing on ridges and valleys were more affected than those on slopes, whereas Scatena and Lugo (1995) found that trees on slopes were more affected than those on ridges; possibly because the root-grafted Dacryodes excelsa was particularly abundant on ridges in that area (Lugo 2008). Another study in a 16 ha plot in the Luquillo Mountains found that topographical effects were of lesser importance than tree size and species identity in determining crown damage caused by Hurricane Hugo (Canham et al. 2010). Therefore, the probability of hurricane damage seems to be determined by the interplay of landscape position and individual tree characteristics (e.g. large trees were more affected). These interactions between intrinsic (individual) and extrinsic (landscape) factors should be considered more thoroughly in future studies assessing patterns of hurricane damage in forests.
The average stem diameter growth rate (all stems damaged and undamaged) was greater for
the full 21-year post-hurricane period than in the pre-hurricane period. The growth of stems with
hurricane-damaged crowns increased less than those with undamaged crowns; this difference
persisted for eleven years after the hurricane hit. The increased stem growth rate after the
hurricane was probably due to increased light reaching the middle and lower levels of the canopy
(Bellingham et al. 1996, Tanner and Bellingham 2006) and reduced below-ground competition,
caused by the severe damage to many large crowns; similar patterns have been found elsewhere
(Lugo 2008). In Puerto Rican rain forests affected by Hurricane Hugo, the diameter growth of
undamaged stems exceeded that of damaged for six of twelve dominant tree species for four
years post-hurricane (Uriarte et al. 2004), in a general context of increased forest growth rates
(e.g., net primary productivity in nearby forests tripled after two hurricanes, Lugo 2008). Other
studies found longer-lasting increases of tree growth post-hurricane, e.g. at least 7 years in
Florida (Batista and Platt 2003), a decade in the Dominican Republic (Sherman et al. 2012) and
>40 years in New Hampshire (Merrens and Peart 1992). Hence, even though increased growth
of surviving trees after a hurricane – especially those less damaged- seems to be a general
phenomenon, there is considerable variation in the duration and magnitude of growth stimulation
among species and forest types. These could be explained by differences in forest structure,
damage intensity, species resilience and post-disturbance recovery strategies, and speed of
canopy closure after the hurricane (Lugo 2008). Our results confirm that, even within the same
forest, post-hurricane growth rates will vary substantially between species and trees within
species depending on the amount of damage (Fig. 2, Appendices D and E). Hence studies based
on short-term time series (e.g. lacking evaluation of damage immediately after the hurricane, or
pre-hurricane growth data) and focused on stand rather than individual scales (e.g. analyzing
changes in total basal area rather than individual stems’ demography) may miss more subtle yet important long-term consequences of hurricane disturbances on forest dynamics.

Higher tree mortality rates after hurricanes have often been documented (Everham and Brokaw 1996), though the duration of that increase is rarely reported. In the Jamaican forest in this study, mortality of damaged stems was higher for about 19 years after a severe hurricane. In forests of the Luquillo Mountains in Puerto Rico, Hurricane Hugo caused increased tree mortality over about four years (Uriarte et al. 2004) but this effect was not evident by a third census 11–12 years after the hurricane (Uriarte et al. 2012). Despite the increased mortality post-hurricane, many trees are likely to survive several hurricanes; in Jamaica, 54% of the initial population of 1670 stems in 1974, 71% of all stems present in 1984 (before Hurricane Gilbert), and 59% of those damaged by the hurricane were still alive by 2009. Average annual mortality rates in the 21 years post-hurricane were 0.5% higher (1.6%) than pre-hurricane baselines (1.1%). Thus, although return times of hurricanes to the Jamaican Blue Mountains are very irregular, given that the average is ~ 25 years (five hurricanes eyes passed within 20 km of the Blue Mountains between 1870 and 2010), most stems will experience more than one hurricane in their lifetime. This seems to be true in other forests, too; in Puerto Rico, 26% of stems >4.1 cm dbh survived from 1946 to 2000 (Weaver 2002), a period that included hurricanes in 1956, 1989 and 1998.

Role of sprouting in post-hurricane recovery

After a hurricane, epicormic sprouting on tree trunks is obvious (Yih et al. 1991 in Nicaragua; Bellingham et al. 1994 in Jamaica; Zimmermann et al. 1994 in Puerto Rico). Sprouting is an efficient means of mobilizing stored reserves to regain lost biomass and leaf area.
Hurricanes often cause widespread defoliation and sprouts may help maintain photosynthesis in the years immediately after the hurricane while the stems regrow their main canopy. In Puerto Rican rain forests affected by Hurricane Hugo, Walker (1991) asserted that widespread sprouting and minimal breakage of large branches would result in tree recovery despite that fact that 56% of trees were defoliated, and Boucher (1990) made similar predictions about Nicaraguan rain forests affected by Hurricane Joan. In our study sprouting was positively related to survivorship: stems with hurricane-damaged crowns that sprouted above 2.5 m height had much lower mortality (2.3% per year over the 21-year post-hurricane period) than non-sprouted stems (3.5%). Some sprouts from below 1.3 m survived and grew large enough to be included in stem censuses (≥3.0 cm dbh), but two-thirds of the newly recruited stems five years after the hurricane originated from seedlings, not sprouts from existing tree stems. The importance of sprouting for post-disturbance recovery is however strongly species-specific (Table 2; Dietze and Clark 2008; Uriarte et al. 2012). Beyond new stem recruitment, basal sprouts contribute to multi-stemmed individuals having a greater chance of survival than single-stemmed individuals, in Jamaica (Bellingham & Sparrow 2009) Samoa (Webb et al 2014) and probably Puerto Rico (Uriarte et al. 2012). However, experimental removal of basal sprouts will be necessary to establish if sprouting causes increased survival or if it is simply that more vigorous individuals have both more sprouts and higher survival.

**Long-term effects of hurricanes at the stand level**

In Jamaica, stems with 32% of the total basal area present in 1974 had died by 2004 (Tanner and Bellingham 2006). However, total basal area per plot remained very similar due to the increased growth of survivors (Fig. 2) and the increased post-hurricane recruitment (Tanner
and Bellingham 2006) that compensated for the basal area mortality. Results from several other countries also show that the total stand basal area can remain quite stable or recover quickly after major wind damage (Lugo 2008), though there are often other changes such as shifts in species composition (Bellingham et al. 1995) or stand structure including shifts to more, smaller, stems (Bellingham et al. 1995; Merrens and Peart 1992). Such changes can happen slowly, even in the course of several centuries (Foster et al. 1998; Lugo 2008). The disturbance regime is likely to govern responses. We have shown that in Jamaica, where the average return interval for hurricanes is 25 years, a single hurricane increased overall growth for the whole 21 year post-hurricane period and hurricane damaged stems had reduced growth for eleven years and increased mortality for 19 years. However, some forests are subject to several powerful cyclonic storms within a decade; for example, in northeastern Australia (Webb 1958), Taiwan (Lin et al. 2011), and the northeastern USA (Papaik and Canham 2006). The consequences of damage to individual stems in these “hyper-disturbed” forests have not been determined. The species composition of forests and the traits of individual species, including their susceptibility to pathogens, are likely to determine responses to repeated disturbances. In species-rich forests, differential damage among species (Canham et al. 2010) can result in long-term differences in growth among species (Appendix E). This in turn can lead to compositional shifts along a continuum of resilient to resistant species (Bellingham et al. 1995, Batista and Platt 2003; see also Wonkka et al. 2013), which is likely to be related to time since disturbance (Holling 1973). Finally the high variability in frequency of hurricane impacts at any location (Healey 1990, Sherman et al. 2012) will further complicate these effects. Thus, the interaction of disturbance regimes and species differential responses generate complex and varied patterns of forest dynamics (Papaik & Canham 2006).
Conclusion

Long-term monitoring of forest plots can provide important insights on the effects of hurricanes and other natural disturbances on tree demography and forest stand dynamics. The availability of pre-hurricane data enabled us, for instance, to detect a significant overall increase of stem growth rates following the hurricane. In the absence of pre-hurricane baseline data, hurricane-induced changes in tree demography would remain undetected or, even worse, misinterpreted. Furthermore, the demographic impacts of hurricane damage can be long-lasting – in Jamaica, 19 years for mortality and 11 for growth. In forests where there is a lot of topographic diversity (as in Jamaica), position in the landscape is a strong determinant of hurricane damage; after which crown size and tree species are the next most important correlates. Recovery from damage was higher in multiple stemmed trees and stems with sprouts above 2.5 m. Some basic aspects of forest structure are often not greatly affected by hurricanes – for example, total basal area. Other aspects of structure, like canopy height and crown diameters, are likely to be more affected by hurricanes but are rarely recorded before hurricanes (a notable exception is the study of Wunderle et al. 1992).

Despite the high frequency of damage to tree crowns and associated increased mortality rate, most stems survived long after the hurricane. Given the high frequency of hurricanes and windstorms in many tropical areas, it is likely that many canopy trees will be damaged and recover from several severe disturbances in their lifetime.

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LITERATURE CITED


Supplemental material

Appendix A. Map of the location of the four study sites.

Appendix B. Forest site characteristics in 1984.

Appendix C. Species’ relative susceptibility to hurricane damage as recorded in 1989.

Appendix D. Hurricane damage effects on stem growth rates over time.

Appendix E. Hurricane damage effects on tree growth rates for the most abundant species.
Table 1. Estimated effects of location (site and plot), species identity, crown size and pre-hurricane growth rate (1974-1984) on the probability of damage by the hurricane (recorded in 1989), for 1259 stems of 48 species (tree ferns were excluded) that were alive in 1974, 1984 and 1989. Mean effect size, standard error and 2.5% and 97.5% credible intervals are shown (logit scale); positive mean values indicate higher probability of damage compared to small-crowned stems with zero net growth pre-hurricane, which were used as the baseline.

<table>
<thead>
<tr>
<th></th>
<th>mean</th>
<th>se</th>
<th>2.5%</th>
<th>97.5%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site Col</td>
<td>-1.10</td>
<td>0.30</td>
<td>-1.70</td>
<td>-0.52</td>
</tr>
<tr>
<td>Site Mor</td>
<td>-0.25</td>
<td>0.30</td>
<td>-0.83</td>
<td>0.37</td>
</tr>
<tr>
<td>Site Mull</td>
<td>0.45</td>
<td>0.26</td>
<td>-0.06</td>
<td>0.95</td>
</tr>
<tr>
<td>Site Slope</td>
<td>-1.43</td>
<td>0.27</td>
<td>-1.99</td>
<td>-0.91</td>
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<tr>
<td>Large crown</td>
<td>1.28</td>
<td>0.15</td>
<td>1.00</td>
<td>1.57</td>
</tr>
<tr>
<td>Pre-hurricane growth rate (cm yr⁻¹)</td>
<td>-4.12</td>
<td>0.97</td>
<td>-6.02</td>
<td>-2.26</td>
</tr>
</tbody>
</table>

Random effects (standard deviations)

<table>
<thead>
<tr>
<th></th>
<th>mean</th>
<th>se</th>
<th>2.5%</th>
<th>97.5%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td>0.68</td>
<td>0.12</td>
<td>0.47</td>
<td>0.93</td>
</tr>
<tr>
<td>Plot</td>
<td>0.46</td>
<td>0.09</td>
<td>0.29</td>
<td>0.65</td>
</tr>
</tbody>
</table>
Table 2. Effects of stem location (site and plot), species, crown size and damage status on the probability of sprouting after the hurricane (n = 1670 stems from 63 species). Mean effect size, standard error and 2.5% and 97.5% credible intervals are shown (logit scale); positive mean values indicate more sprouting compared to undamaged, small-crowned stems used as baseline.

<table>
<thead>
<tr>
<th></th>
<th>mean</th>
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<th>2.5%</th>
<th>97.5%</th>
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</thead>
<tbody>
<tr>
<td>Site Col</td>
<td>-1.99</td>
<td>0.39</td>
<td>-2.77</td>
<td>-1.25</td>
</tr>
<tr>
<td>Site Mor</td>
<td>-0.64</td>
<td>0.40</td>
<td>-1.43</td>
<td>0.14</td>
</tr>
<tr>
<td>Site Mull</td>
<td>-1.47</td>
<td>0.35</td>
<td>-2.16</td>
<td>-0.81</td>
</tr>
<tr>
<td>Site Slope</td>
<td>-1.89</td>
<td>0.36</td>
<td>-2.60</td>
<td>-1.19</td>
</tr>
<tr>
<td>Undamaged and large crown</td>
<td>0.78</td>
<td>0.20</td>
<td>0.39</td>
<td>1.17</td>
</tr>
<tr>
<td>Damaged and small crown</td>
<td>0.43</td>
<td>0.18</td>
<td>0.07</td>
<td>0.79</td>
</tr>
<tr>
<td>Damaged and large crown</td>
<td>0.40</td>
<td>0.18</td>
<td>0.05</td>
<td>0.74</td>
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</tbody>
</table>

Random effects (standard deviations)

<table>
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<tr>
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<th>2.5%</th>
<th>97.5%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td>1.48</td>
<td>0.23</td>
<td>1.11</td>
<td>2.00</td>
</tr>
<tr>
<td>Plot</td>
<td>0.62</td>
<td>0.11</td>
<td>0.43</td>
<td>0.85</td>
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</table>
Table 3. Effects of tree location (site and plot), species, hurricane damage, sprouting and multi-stemming on the long-term probability of mortality of individual trees (1989-2009; n = 1390).

Mean effect size, standard error and 2.5% and 97.5% credible intervals are shown (logit scale); positive mean values indicate higher probability of mortality compared to undamaged, single, non-sprouted stems used as baseline.

<table>
<thead>
<tr>
<th></th>
<th>mean</th>
<th>se</th>
<th>2.5%</th>
<th>97.5%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site Col</td>
<td>-4.28</td>
<td>0.22</td>
<td>-4.72</td>
<td>-3.84</td>
</tr>
<tr>
<td>Site Mor</td>
<td>-4.52</td>
<td>0.27</td>
<td>-5.05</td>
<td>-4.00</td>
</tr>
<tr>
<td>Site Mull</td>
<td>-4.32</td>
<td>0.22</td>
<td>-4.74</td>
<td>-3.89</td>
</tr>
<tr>
<td>Site Slope</td>
<td>-4.83</td>
<td>0.22</td>
<td>-5.27</td>
<td>-4.39</td>
</tr>
<tr>
<td>Undamaged sprouted (single stem)</td>
<td>-0.32</td>
<td>0.23</td>
<td>-0.78</td>
<td>0.13</td>
</tr>
<tr>
<td>Undamaged multistem (not sprouted)</td>
<td>-0.20</td>
<td>0.46</td>
<td>-1.17</td>
<td>0.60</td>
</tr>
<tr>
<td>Undamaged sprouted multistem</td>
<td>-2.14</td>
<td>1.29</td>
<td>-5.29</td>
<td>-0.24</td>
</tr>
<tr>
<td>Damaged (single stem, not sprouted)</td>
<td>1.17</td>
<td>0.15</td>
<td>0.87</td>
<td>1.47</td>
</tr>
<tr>
<td>Damaged sprouted (single stem)</td>
<td>0.72</td>
<td>0.20</td>
<td>0.34</td>
<td>1.11</td>
</tr>
<tr>
<td>Damaged multistem (not sprouted)</td>
<td>0.74</td>
<td>0.28</td>
<td>0.16</td>
<td>1.28</td>
</tr>
<tr>
<td>Damaged sprouted multistem</td>
<td>0.10</td>
<td>0.29</td>
<td>-0.49</td>
<td>0.62</td>
</tr>
</tbody>
</table>

Random effects (standard deviations)

<table>
<thead>
<tr>
<th></th>
<th>mean</th>
<th>se</th>
<th>2.5%</th>
<th>97.5%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td>0.90</td>
<td>0.12</td>
<td>0.67</td>
<td>1.15</td>
</tr>
<tr>
<td>Plot</td>
<td>0.17</td>
<td>0.09</td>
<td>0.01</td>
<td>0.34</td>
</tr>
</tbody>
</table>
Figure legends

Figure 1. Probability of hurricane damage according to stem location (four sites: Col, Mor, Mull and Slope), crown size and pre-hurricane (1974–1984) diameter growth rate (n = 1259 stems). Shaded areas represent 95% credible intervals. Dots represent observed growth rates for damaged and undamaged trees.

Figure 2. Stem diameter growth rates (mean ± SE) prior to and following Hurricane Gilbert for crown-damaged and crown-undamaged stems. The dashed line marks the year of the hurricane (1988), data are plotted in the middle of the census period and staggered for clarity. Only stems surviving the whole period (1974–2009) were included in this analysis (n = 915 stems).

Figure 3. Effects of hurricane damage on stem mortality (mean ± SE) across the whole study period. The dashed line marks the year of the hurricane (1988), data are plotted in the middle of the census period.