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The demographics of resprouting in tree and shrub species of a moist tropical forest

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Summary

1 Individuals of many woody plant species have the ability to respond to damage which causes removal of the crown by producing new branches (sprouts) along the remaining stem. Resprouting by woody plants has received little attention in relatively undisturbed tropical forest.

2 To assess the importance of resprouting for forest dynamics, we estimated resprouting rates and mortality rates of resprouted individuals for the forest as a whole and for individual species in a 50-ha permanent plot in tropical moist forest on Barro Colorado Island, Panama. We tested for differences between species and asked whether the differences were related to phylogeny, growth form or shade tolerance.

3 Among individuals not known to have resprouted previously, we estimate that the annual rate of resprouting is 1.7% for individuals in both small and large size classes (1–9.9 cm d.b.h. and $\geq$ 10 cm d.b.h.). For small and large individuals, respectively, annual mortality of previously undamaged individuals is 2.2% and 1.5%, while that of resprouted individuals is 9.6% and 10.3%. This resulted in survival of 62% of resprouted individuals over 5 years, compared to 90% survival among individuals not known to have resprouted recently.

4 Resprouting rates varied by species and family, but little between growth forms. Species in the families Lauraceae and Piperaceae had high rates of resprouting. Resprouting was common across the spectrum of shade tolerance.

5 Damage to woody forest plants on Barro Colorado Island is frequent, and many species are able to respond by resprouting. Resprouting ability may be an important life history characteristic of woody species on BCI, with individuals experiencing both increases and decreases in size.

Key-words: demography, forest dynamics, mortality, sprouting, vegetative regeneration

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Introduction

Even in the absence of large-scale disturbance, woody plants in tropical forests suffer frequent physical damage (Aide 1987; Clark & Clark 1989; Clark & Clark 1991), after which many species can resprout, producing a new stem and crown (Putz *et al.* 1983; Putz & Brokaw 1989; Guariguata 1998). Resprouting of woody plants after snapping or uprooting is well documented for forests affected by catastrophes such as hurricanes (Walker 1991; Yih *et al.* 1991; Bellingham *et al.* 1994), tornados (Glitzenstein & Harcombe 1988; Peterson &

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Rebertus 1997), logging (Gorchov *et al.* 1993; Pinard & Putz 1996), fire (Williamson *et al.* 1986; Kauffman 1991) or slash-and-burn cultivation (Sampaio *et al.* 1993; Miller & Kauffman 1998), but few studies have examined resprouting in forests without such large-scale disturbance (Putz & Brokaw 1989; Negrelle 1995).

The importance of resprouting for population and community dynamics depends on several demographic parameters: first, the rate of physical damage or dieback (including stem breakage, bending, uprooting, and crown dieback from disease or herbivory); second, the rate of resprouting by damaged individuals; and third, the subsequent performance (growth, mortality, and ultimately reproduction) of these individuals. The ability to resprout may allow advanced regeneration to persist in the understorey, survive damage during gap creation and exploit the resulting gap. Canopy individuals that break or uproot and then resprout may be able to reoccupy part of the gap (Putz & Brokaw 1989; Negrelle 1995). Resprouting ability may also be important for species whose individuals spend their entire lives in the understorey (Greig 1993).

Our understanding of the dynamics of tropical forests will be advanced by documentation of the complex patterns of growth, damage, recovery and death among individuals. Where resprouting is common and individuals that have resprouted survive and grow, models of forest dynamics that omit resprouting will underestimate individual time to maturity because they incorporate unrealistic growth patterns that do not include reductions in size. Resprouting ability can vary between species (Bellingham *et al.* 1994; Zimmerman *et al.* 1994) and may therefore be an important determinant of competitive ability, and thus a key component of plant life history. It has been largely ignored in studies of tropical forest dynamics, and those previous studies that have considered resprouting have been limited to small sample sizes, few species or short periods of time (Putz & Brokaw 1989; Clark & Clark 1991; Guariguata 1998; Rijks *et al.* 1998).

We use data from a 50 hectare permanent plot on Barro Colorado Island, Panama, to investigate the large-scale demography of resprouting. Multiple censuses have provided repeated measurements of individuals larger than 1 cm d.b.h., representing more than 300 species. We estimate rates of resprouting and rates of mortality of resprouted individuals for the entire forest and then for individual species. We conduct simulations to test whether the observed differences between species could result from random variation about a species-independent rate and, finding significant differences, we investigate associations between resprouting ability and species phylogeny, growth form, and shade tolerance.

Methods

STUDY SITE AND CENSUS DATA

All analyses are based on data from the permanent 50 ha forest dynamics plot on Barro Colorado Island (BCI), Panama. BCI is a 1500-ha former hilltop which became isolated when Gatun Lake formed during construction of the Panama Canal. It receives 2500 mm of precipitation annually, which falls mostly during an 8-month wet season. While the whole island is subject to stresses such as drought, notably during strong El Niño Southern Oscillation events (Wright *et al.* 1999), it is free of large-scale disturbances such as hurricanes and fire (Leigh 1999). The permanent plot is on the central plateau of the island and is described in Hubbell & Foster (1983, 1986). An initial census of the plot was conducted between 1981 and 1983 (referred to as the 1982 census hereafter), with identification, tagging and mapping of all individuals whose diameter at breast height (1.3 m) (d.b.h.) was greater than 1 cm. This census found *c.* 235 000 individuals of 305 species of woody plants (see Condit *et al.* 1996a; for a species list). Subsequent censuses were conducted in 1985, 1990, 1995, and a 2000 census is underway, with new recruits to the 1 cm d.b.h. size class added to the data set. On each occasion, all individuals were examined to determine the number of stems $\geq$ 1 cm d.b.h. and d.b.h. of the largest stem. Codes were used to indicate whether the largest-diameter stem had broken, and if so, whether the break was above or below breast height. Further details are given in Condit (1998). We treat the individuals in the plot as a sample of individuals from a larger area of forest and use standard statistical techniques designed to analyse samples of populations. This ensures that we do not draw conclusions from populations too small to give robust results, such as when analysing rare species.

DEFINITION OF TERMS

A *resprouted individual* is one whose largest-d.b.h. stem has broken or suffered crown dieback, and which has produced a new stem growing from below the point of damage. Although a portion of the main stem of such an individual dies, the organism remains alive, retaining some live root and stem material. They are categorized according the first census in which they were recorded as having resprouted, so that a *resprouted-1990 individual* is one that resprouted in the interval between the 1985 and 1990 censuses. *Undamaged individuals* include all those with no history of resprouting in past censuses, including any that resprouted before 1982 or were damaged in ways that did not result in resprouting. Individuals that produced new vertical stems after leaning or falling were not considered to have resprouted unless the original crown died.

When individuals with multiple stems lose their largest stem they may retain a substantial portion of their foliage, and responses may therefore differ from those of a plant that loses its only stem and thus its crown. The resprouting rate of multi-stemmed plants was approximately 50% higher than the resprouting rate of single-stemmed plants, but only 10% of resprouted individuals had multiple stems before resprouting. Therefore, the analyses excluded individuals with more than one stem in the census before resprouting occurred. Since 8% of species were composed mainly of multi-stemmed individuals, this exclusion might bias the results of our species-level analyses. However when we reanalysed the data using both single- and multi-stemmed individuals, we found no important differences from the analyses presented here.

BASIC DEMOGRAPHIC RATES

We calculated forest-wide resprouting rates over two 5-year intervals (1985–90 and 1990–95) as the fraction of undamaged individuals in a census that were recorded in the next census as having resprouted. We calculated 5-year mortality rates of resprouted individuals for the second interval as the fraction of resprouted-1990 individuals that were dead by the 1995 census. We split individuals into two size classes: 1–9.9 cm d.b.h. and ≥ 10 cm d.b.h., based on size in the census prior to resprouting. We also calculated the proportion of recruits (individuals reaching 1 cm d.b.h.) during the period 1990–95 that were caused by resprouting. Recruits caused by resprouting were defined as: (i) individuals that had been larger than 1 cm d.b.h. in the 1982 or 1985 census, resprouted but were below 1 cm d.b.h. in 1990, but grew to at least 1 cm d.b.h. by the 1995 census, or (ii) individuals that had resprouted between 1990 and 1995 and grown back to at least 1 cm d.b.h. in the 1995 census.

The census methodology causes us to underestimate the actual rate of resprouting in two important ways. First, because census workers could not distinguish between 'old' and 'new' resprouted individuals, many individuals that were marked in two different censuses as having resprouted may have only resprouted before the first of these censuses, leaving us unable to assess the rate of resprouting for individuals that already had a history of resprouting. We assumed the second resprouting event referred to the initial event and not a new event of resprouting. Second, individuals that were 1–9.9 cm d.b.h. that broke above breast height and then resprouted were not defined as resprouted individuals during the censuses, causing underestimation of the resprouting rate in the small size class. This issue caused us to use two size classes divided at 10 cm d.b.h. rather than finer-scale divisions.

CALCULATION OF ANNUAL RATES

We do not know the rate at which individuals are damaged but do not resprout, information that would allow us to partition a resprouting rate into the probability of severe damage (stem breakage or dieback) and the conditional probability of resprouting given that damage occurred. Also, individuals may resprout and then die before the next census occurs, with the individuals never recorded as having resprouted. Therefore, the 5-year resprouting rates encompass severe damage, resprouting and survival until the next census. A low rate of resprouting may indicate a low rate of damage, an inability to resprout if damaged, or a very high mortality rate of resprouted individuals soon after resprouting.

To adjust for those individuals that resprout and die within one census interval, we calculated annual rates for the 1990–95 census interval by solving the following set of coupled differential equations:

$$\frac{dU_t}{dt} = (-m_u - r) \cdot U_t$$

$$\frac{dR_t}{dt} = r \cdot U_t - m_r \cdot R_t \qquad \text{eqn 1}$$

$$\frac{dP_t}{dt} = -m_r \cdot P_t$$

where t is the time in years, U_t is the number of undamaged individuals at time t, R_t is the number of newly resprouted individuals, P_t is the number of resprouted individuals recorded in the first of the two censuses (1990 in this case), r is the annual probability of resprouting, m_u is the annual probability of mortality for undamaged individuals, and m_r is the annual probability of mortality for resprouted individuals. By solving the coupled equations in eqn 1 using data from 1990 to 1995, we obtain the following equations for the rates, r, m_u, and m_r:

$$m_r = \frac{\log_e(P_{1990}) - \log_e(P_{1995})}{\Delta t}$$

$$m_u + r = \frac{\log_e(U_{1990}) - \log_e(U_{1995})}{\Delta t} \qquad \text{eqn 2}$$

$$r = \frac{R_{1995}\,(m_r - (m_u + r))}{U_{1990}\,(e^{-(m_u+r)\cdot \Delta t} - e^{-m_r \cdot \Delta t})}$$

where P_{1990} is the number of resprouted individuals in 1990 and P_{1995} the number of those individuals still alive in 1995, U_{1990} is the number of undamaged individuals in 1990 and U_{1995} the number of those individuals that had not died or resprouted as of

1995, and R_{1995} the number of U_{1990} individuals that had resprouted as of 1995. Since census intervals for individuals varied and were not exactly five years, the value Δt is the mean time interval in years between the two censuses for the group of individuals being analysed (Condit *et al.* 1995, 1999). This approach accounts for resprouted individuals that die before being counted in a census by assuming that mortality (m_r) is constant with respect to time since resprouting and can be estimated from the mortality of individuals that resprouted in the previous census interval. While the mortality rate of resprouted individuals is not likely to be constant with time since resprouting, we feel this partial adjustment for mortality is preferable to no adjustment. Annual rates were calculated both forest-wide and at the species level.

We used a bootstrap procedure to calculate 95% confidence intervals for the annual rates. Using the number of undamaged individuals counted in 1990 and the empirical probability of resprouting and surviving until 1995, we resampled the number of resprouted individuals as of 1995 using a series of Bernoulli trials (i.e. a binomial process). Similarly, using the empirical probability of mortality over 1990–95, we resampled the number of previously undamaged individuals that died by 1995. Finally, we resampled the number of resprouted individuals dying over 5 years based on the number of resprouted individuals counted in 1990 and the empirical probability that those individuals died over 1990–95. The resampled numbers of individuals in these three categories were used to calculate the three annual rates (resprouting rate, mortality rate of resprouted individuals, and mortality rate of undamaged individuals) using eqn 2. We repeated these steps 1000 times to obtain 1000 values for each of the three annual rates and estimated 95% confidence intervals using the 25th and 975th ordered values.

VARIABILITY IN ANNUAL RESPROUTING AND MORTALITY RATES AMONG SPECIES

We simulated the three annual rates for each species under a null model of equal annual rates for all species and tested whether the observed variability between species could be accounted for by the null model. For each species for 1990–95, we simulated counts of resprouted individuals, previously undamaged individuals that died, and resprouted-1990 individuals that died. We used a series of Bernoulli trials with the number of individuals equal to the appropriate observed count for each species in 1990 and the 5-year probability calculated by pooling the data across species. With the three simulated counts for each species, we calculated the annual rates using eqn 2. Repeating this 100 times, we obtained 100 simulated values for each species for each of the three annual rates. We constructed 100 cumulative distribution functions of each rate using a single simulated value from each species for each distribution function. The empirical distribution of each rate was then compared visually to the cumulative distributions simulated under the null model.

In all species-level analyses, we excluded species that did not have at least 20 undamaged individuals and five resprouted individuals in the 1990 census. While this was an arbitrary cut-off, there was no indication that the results were affected by one cut-off as opposed to another; reanalysis using species with at least 80 undamaged and 20 resprouted individuals gave the same results. We also performed the analyses using the 5-year rates in place of the annual rates and found no important differences from the results presented here.

ASSOCIATIONS BETWEEN SPECIES-LEVEL CHARACTERISTICS AND ANNUAL DEMOGRAPHIC RATES

To assess possible causes of the species-level variability, we analysed associations of the annual rates with phylogeny, growth form, and shade tolerance. Each species counted as a single data point in these analyses, so abundant species did not dominate results. For the analysis of variance (ANOVA) models, rates were arcsine square-root transformed.

Phylogeny. We tested for differences in rates between families using ANOVA. Since there were a large number of families and few species per family, we then focused on well-represented families (those with at least four species) and visually compared resprouting ability between families using boxplots of the annual resprouting rates and the mortality rates of resprouted individuals.

Growth form. To test for differences in rates between growth forms, we also used ANOVA. Each species was classified into one of four growth forms based on height at maturity: shrub (1–4 m height at maturity), understorey treelet (4–10 m), midstorey tree (10–20 m) or canopy tree (greater than 20 m) (Condit *et al.* 1996a).

Shade tolerance. We plotted the annual resprouting rate against an index of shade tolerance for each species. We used an index based on principle components analysis (PCA) to characterize the relative shade tolerance of 142 species (Condit *et al.* 1996b). This index was based on mortality rate, growth rate and a colonizing index calculated as the fraction of recruits of a species found in light gaps (Welden *et al.* 1991). The PCA index ranged from −2.5 to 7 with shade-intolerant species having the highest values.

Table 1 Demographic status (undamaged, resprouted or dead) of previously undamaged single stem individuals in two size classes at the end of two periods: 1985–90 and 1990–95. Size class and number of stems were determined at the beginning of the time period. Parentheses indicate 95% confidence intervals

Size Class	Total number of stems	Time period	Demographic status at end of time period		
			Undamaged (%)	Resprouted (%)	Dead (%)
1–9.9 cm d.b.h.	187 407	1985–90	83.8 (83.6–84.0)	5.9 (5.8–6.0)	10.3 (10.2–10.4)
	182 624	1990–95	83.1 (82.9–83.3)	5.7 (5.6–5.8)	11.2 (11.0–11.3)
> 10 cm d.b.h.	18 801	1985–90	87.5 (87.0–87.9)	2.7 (2.4–2.9)	9.9 (9.4–10.3)
	18 432	1990–95	85.8 (85.3–86.3)	5.9 (5.6–6.3)	8.2 (7.8–8.6)

Results

BASIC DEMOGRAPHIC RATES

Approximately 6% of previously undamaged individuals resprouted and survived during a 5-year census interval, somewhat less than the proportion of previously undamaged individuals that suffered mortality over 5 years (Table 1). The resprouting rate was 71% of the annual rate of mortality for undamaged small individuals and 115% for undamaged large individuals (Table 2). Resprouting was less common among larger individuals than smaller individuals during 1985–90 but equally likely during 1990–95 (Table 1). The limitations of the census data caused us to underestimate the actual resprouting rates. Five-year mortality rates were higher for resprouted individuals than for undamaged individuals (3.3 and 4.7 times for small and large individuals, respectively, Table 3; 4.3 and 7 times when calculated on an annual basis, Table 2). Resprouted-1990 and resprouted-1995 individuals represented 17% of the recruits into the 1 cm d.b.h. size class between 1990 and 1995. Among resprouted-1990 individuals, 45% were at least 1 cm d.b.h. in 1995, compared to 29% of resprouted-1995 individuals.

The mortality data suggest that a minority of resprouted individuals survive for extended periods of time. Of individuals that were 1–9.9 cm d.b.h. in 1982 and were recorded as having resprouted in 1985, 51% were dead by 1995, compared to 21% of undamaged individuals over 1985–95. The equivalent values for individuals that were ≥ 10 cm d.b.h. are 39% and 19%. The survival of a significant number of resprouted individuals to reproductive stage will depend on whether the mortality rate of resprouted individuals declines to the undamaged level or remains elevated.

Mortality rates for resprouted individuals do decline with time since resprouting. For individuals ≥ 10 cm d.b.h., the 5-year mortality rate of resprouted-1985 individuals fell from 28% over 1985–90 to 15% over 1990–95, although this is still

Table 2 Annual rates (%) for two size classes calculated from 1990 to 1995 data using eqn 2. Simulated 95% confidence intervals are given in parentheses

Annual rate (%)	Small individuals (1–9.9 cm d.b.h.)	Large individuals (> 10 cm d.b.h.)
r (resprouting rate)	1.65 (1.61–1.68)	1.71 (1.59–1.82)
m_u (mortality of undamaged indiv.)	2.23 (2.19–2.27)	1.49 (1.38–1.61)

Table 3 Five-year mortality rates of both undamaged and resprouted individuals in two size classes for the period 1990–95. Size class of resprouted individuals indicates size in 1985 before damage and resprouting occurred. Parentheses indicate 95% confidence intervals

Size class	Total number of stems	Status in 1990	Dead in 1995 (%)
1–9.9 cm d.b.h.	182 624	Undamaged	11.2 (11.0–11.3)
	11 042	Resprouted	36.8 (35.9–37.7)
> 10 cm d.b.h.	18 432	Undamaged	8.2 (7.8–8.6)
	500	Resprouted	38.8 (34.5–43.2)

Small individuals Large individuals

higher than the 8% mortality of undamaged individuals over each 5-year period. Resprouted-1985 individuals in the 1–9.9 cm d.b.h. size class were not recensused in 1990 because of an error during the census, but were recensused in 1995. The annual mortality rate for these individuals over 1985–95 was 7.2%, compared to 9.6% for resprouted-1990 individuals over 1990–95, again consistent with a declining mortality rate. If we assume that the 1985–90 5-year mortality rate of these smaller resprouted-1985 individuals was the same as the 1990–95 5-year mortality rate of smaller resprouted-1990 individuals (37%), then the mortality rate of resprouted-1985 individuals over 1990–95 would have been 23%. This is less than the assumed initial mortality rate of 37%, but higher than the 10–11% 5-year mortality rate of undamaged individuals. The evidence from both size classes suggests that the mortality rate of resprouted individuals declines with time, but continues to be elevated above the mortality rate of undamaged individuals up to 10 years after resprouting.

VARIABILITY IN RATES AMONG SPECIES

Most species had annual resprouting rates and mortality rates for undamaged individuals of $< 5\%$, whereas annual mortality rates of resprouted individuals varied widely, with most species falling between 0% and 25% (Fig. 1a, c & e). In 55% of species, the annual resprouting rate was higher than the annual mortality rate for undamaged individuals. The mortality rate of resprouted individuals was higher than the mortality rate of undamaged individuals in 98% of species. The empirical distribution functions of the three annual demographic rates differ from simulated null model distribution functions (Fig. 1b, d & f), suggesting species-level variability in demography.

Estimated annual rates by species for individuals 1–9.9 cm d.b.h. and ≥ 10 cm d.b.h. are given in Appendices 1 and 2 (in the *Journal of Ecology* archive on the World Wide Web; see the cover of a recent issue of the journal for the WWW address). Of the most common species in the plot, *Hybanthus prunifolius* (shrub, Violaceae), *Mouriri myrtilloides* (shrub, Melastomataceae), *Trichilia tuberculata* (canopy tree, Meliaceae) and *Alseis blackiana* (canopy tree, Rubiaceae), had annual resprouting rates that were in the middle of the distribution, while two understorey species, *Faramea occidentalis* (Rubiaceae) and *Desmopsis panamensis* (Annonaceae), had relatively low resprouting rates. The species with the highest annual resprouting rates in the small size class included *Acalypha diversifolia* (shrub, Euphorbiaceae), *Miconia nervosa* (shrub, Melastomataceae), *Piper cordulatum* (shrub, Piperaceae), *Siparuna pauciflora* (understorey, Monimiaceae), two species of *Nectandra* (midstorey and canopy species, Lauraceae) and three species of *Ocotea* (midstorey and canopy species, Lauraceae). In the large size class, the midstorey species *Casearia sylvestris* (Flacourtiaceae), *Cordia lasiocalyx* (Boraginaceae), *Maquira costaricana* (Moraceae), *Protium costaricense* (Burseraceae), and two species of *Inga* (Fabaceae), and the canopy species *Pterocarpus rohrii* (Fabaceae) had high resprouting rates.

A. diversifolia, *M. nervosa*, *Olmedia aspera* (understorey, Moraceae) and *P. cordulatum* had high mortality rates among resprouted individuals. These species also had high resprouting rates, and there was indeed a positive correlation between resprouting rate and the rate of mortality among resprouted individuals (Spearman rank correlation, r_s, of 0.35; $P = 0.0002$). There was a weak indication of positive correlation between resprouting rate and mortality rate among undamaged individuals ($r_s = 0.15$; $P = 0.08$).

ASSOCIATIONS BETWEEN SPECIES-LEVEL CHARACTERISTICS AND ANNUAL RATES

Phylogeny

Both resprouting rates and mortality rates of resprouted individuals differed significantly between families ($F_{27,99} = 3.33$, $P = 7.0 \times 10^{-6}$; $F_{27,99} = 1.77$, $P = 0.022$. The difference in mortality rates of undamaged individuals between families was only marginally significant ($F_{27,99} = 1.56$, $P = 0.059$). Species in the families Lauraceae, Melastomataceae, Piperaceae and Sapindaceae had high annual resprouting rates, with species in the Melastomataceae and Piperaceae showing the most variability as well (Fig. 2a). Species in the Euphorbiaceae, Melastomataceae and Piperaceae had high annual mortality rates for resprouted individuals, while species in the Annonaceae, Burseraceae, Myrtaceae and Sapindaceae had relatively low mortality rates among resprouted individuals (Fig. 2b). Clonal palms, such as *Bactris* spp. and *Oenocarpus mapoura*, had relatively high resprouting rates, while non-clonal palms, such as *Socratea exorrhiza* and *Astrocaryum standleyanum*, did not resprout.

Growth form

Annual resprouting rates differed significantly between growth forms, with shrubs having slightly higher rates of resprouting, but growth form explained little of the variation in resprouting rates ($F_{3,138} = 6.69$, $P = 0.0003$, $r^2 = 0.13$; Fig. 3a). Mortality rates of resprouted individuals differed significantly between growth forms, with shrubs having higher mortality, but again, growth form

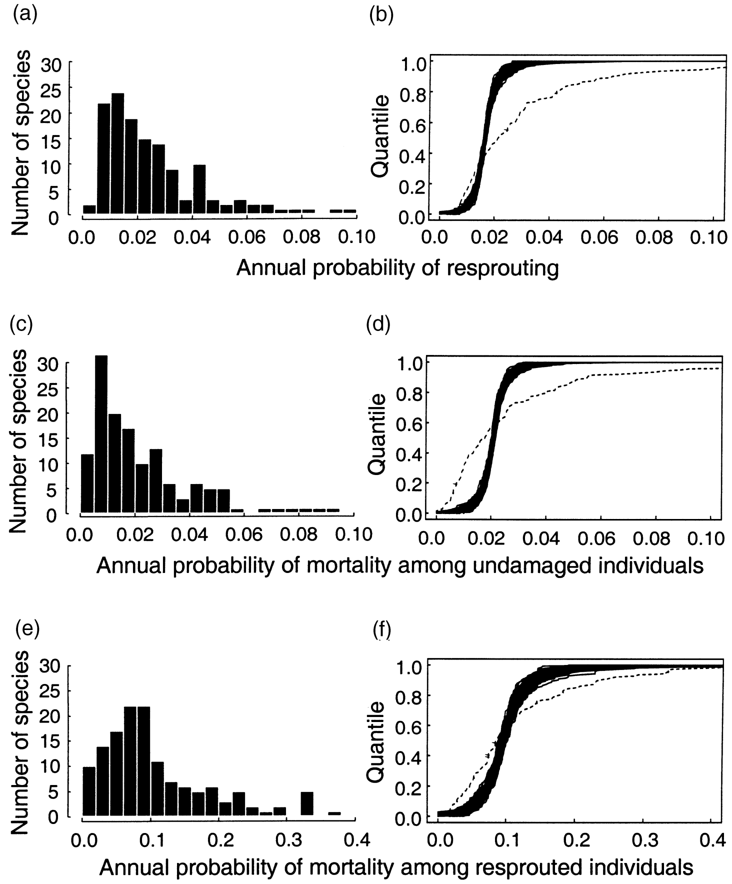

Fig. 1 Variability in annual rates among species. (a, c, e) Histograms of annual rates of species based on the 1990–95 census interval; outlying values are not plotted in the histograms (seven species omitted from a, six from c, and three from e, from a total of 142 species, each with at least 20 undamaged individuals and five resprouted individuals in 1990). (b, d, f) Corresponding cumulative distribution functions. Dashed lines are empirical distribution functions corresponding to the histogram, and collections of solid lines are 100 distribution functions simulated under a null model in which all species have equal rates. Note the change in scale on the *x*-axis (e, f).

explained little of the variation ($F_{3,138} = 3.55$, $P = 0.016$, $r^2 = 0.072$; Fig. 3b).

Shade tolerance

There was no simple relationship between a species' relative shade tolerance and its annual resprouting rate (Fig. 4). The three extremely shade-intolerant species (high PCA values) had low rates of resprouting. Resprouting rates were highly variable for species of intermediate shade tolerance, while the most shade-tolerant species were less variable and had somewhat lower resprouting rates on average than species of intermediate tolerance.

Discussion

The probability that an individual will resprout and survive over a 5-year interval is approximately half the probability that the individual will die. This estimate of the forest-wide resprouting rate is an underestimate, due to census difficulties in recognizing and recording resprouted plants. Resprouted individuals were much less likely to survive than undamaged individuals, but mortality rates decreased with time since resprouting. Resprouting rates and mortality rates varied among species and families, although all families and most species showed resprouting ability. Moreover, species of all stature (small shrubs to large trees) and across life history guilds resprouted. These results suggest that resprouting ability may be an important component of a species life history, affecting mortality and growth rates, and is likely to be important in forest community dynamics.

THE DEMOGRAPHICS OF RESPROUTING

The importance of resprouting for forest dynamics depends on the frequency of severe damage, the probability of resprouting given damage, and survival and growth rates following resprouting. These

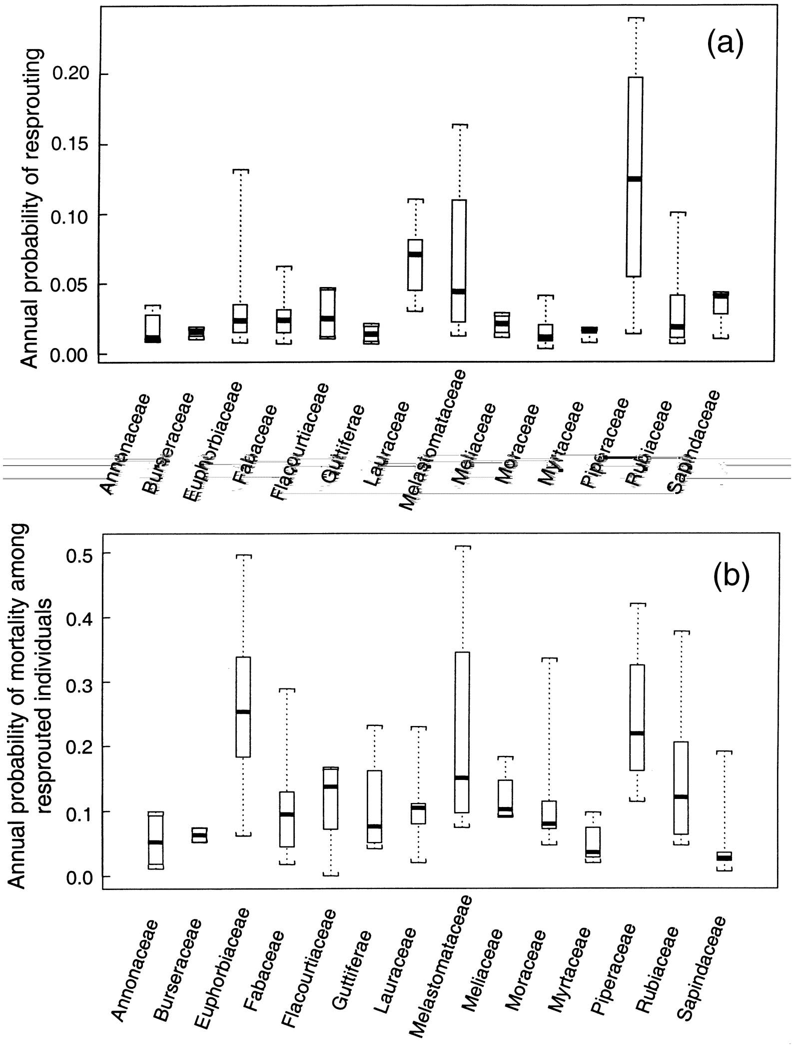

Fig. 2 Boxplots of (a) species annual resprouting rates and (b) species mortality rates for resprouted individuals by family based on the 1990–95 census interval. Only families with at least four species satisfying the criterion in Fig. 1 are included. Blocks indicate middle 50% of species values with horizontal bars indicating the median values. Brackets indicate minimum and maximum rates within a family.

demographic parameters determine whether resprouted individuals reach reproductive age and are likely to vary depending on the forest, including the scale of disturbance affecting the forest.

Damage followed by resprouting was common on BCI during both 1985–90 and 1990–95. Both periods were free of severe drought (such as occurred during the 1983 El Niño), so resprouting is not simply a response to drought. Although census methods prevent accurate comparison of resprouting based on fine-scale size classes, individuals of all sizes resprout, including individuals large enough to be in the canopy. Sampling 1–2.5 m tall saplings of four shade-tolerant species on BCI, Guariguata (1998) found that 3% of saplings experienced severe damage from bending or breakage each year, and all survived until the end of the 2-year study, presumably via resprouting. Putz & Brokaw (1989) estimated that at least 27% of trees ≥ 10 cm d.b.h. showed signs of having broken and resprouted at some point in time. With our data, we could not separate the probability of damage from the probability of resprouting following damage, but Putz & Brokaw (1989) found that 51% of snapped trees ≥ 10 cm d.b.h. and 6% of uprooted trees on BCI resprouted. A majority of both snapped and uprooted saplings and trees resprout in tropical forests damaged by hurricanes (Whigham *et al.* 1991; Yih *et al.* 1991; Basnet 1993; Bellingham *et al.* 1994; Walker 1995).

Resprouted individuals had much higher mortality rates than undamaged individuals, which supports the results of Clark & Clark (1991) and Guariguata (1998). High mortality rates after resprouting imply that few resprouted individuals survive for extended periods of time, unless mortal-

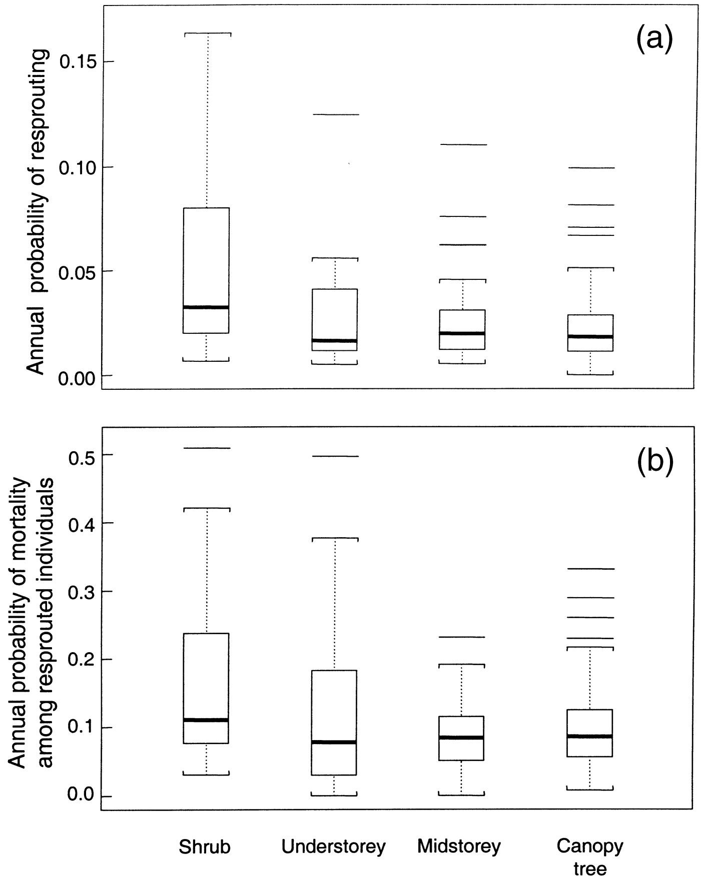

Fig. 3 Boxplots of (a) species annual resprouting rates and (b) species mortality rates for resprouted individuals by growth form based on 1990–95 census interval. Blocks indicate middle 50% of species values, the thick horizontal line in the block is the median, brackets indicate 1.5 times the interquartile range, and thin horizontal lines are outlying values. Species selection as in Fig. 1. One outlying shrub (*Piper cordulatum*) with a resprouting rate of 0.24 is not plotted.

ity rates decline with time. Our data suggest that such a decline does occur, which may allow resprouted individuals to survive and reproduce. Putz & Brokaw (1989) followed a set of BCI trees $\geq$ 10 cm d.b.h. whose trunks snapped between 1976 and 1980 and found 41% survival as of 1987. Guariguata (1998) found that 79% of experimentally bent individuals and 87% of experimentally snapped individuals of four BCI species survived for 4 years. Long-term survival of resprouted individuals has been documented in temperate forests as well (Harcombe & Marks 1983; Peterson & Pickett 1991). Trees derived from stumps that coppice after logging can survive for decades (Johnson 1975; Zahner *et al.* 1985; Murphy & Lugo 1986).

Growth rates also determine the success of resprouted individuals in achieving maturity, but we could not fully investigate growth because the diameter of most resprouted individuals remained < 1 cm d.b.h. and therefore was not measured. The growth of individuals $\geq$ 100 cm d.b.h. that broke above breast height and then resprouted was near zero, significantly less than undamaged individuals of similar size (Paciorek *et al.*, unpublished data). The low growth of these resprouted individuals is unsurprising since individuals must rebuild their crowns and support a large root system, leaving them unable to allocate resources to diameter growth. Experimentally damaged saplings were able to recover 20–50% of their height, on average, over 4 years (Guariguata 1998). Individuals that have resprouted may be particularly likely to suffer damage again, perhaps because of structural weakness (Putz & Sharitz 1991).

Ideally, we would estimate the proportion of mature individuals that have resprouted during their lifetimes and their relative reproductive success. The frequency of resprouting in all size classes suggests a high probability of resprouting before maturity, but the high mortality rates of resprouted individuals suggest that a disproportionate fraction of canopy trees are individuals that avoided damage as juveniles. One approach to quantifying these effects is to estimate the proportion of canopy individuals with a history of resprouting by simulating a population of individuals through time using census data on

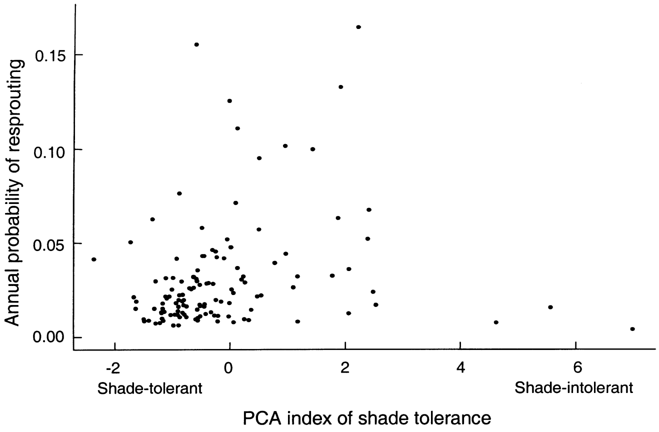

Fig. 4 Species annual resprouting rates based on the 1990–95 census interval plotted against the PCA index of shade tolerance for the species (Condit *et al.* 1996a). Increasing PCA values indicate decreasing shade-tolerance. Species selection as in Fig. 1. *Piper cordulatum*, with an annual resprouting rate of 0.24 and PCA index of −0.35, is not plotted.

resprouting, mortality and growth. Long-term mortality and growth rate data for resprouted individuals are missing, but will become available as future censuses are conducted.

VARIABILITY IN RESPROUTING ABILITY AMONG SPECIES

We found significant differences in both annual resprouting rates and mortality rates of resprouted individuals between species. These differences can be related in part to family, although all families showed an ability to resprout. Growth form appears to explain little of the variability, suggesting a role for resprouting in the dynamics of shrub, understorey, midstorey and canopy tree species. Previous work has also found interspecific variability in resprouting rates, with evidence for differential survival following experimental damage of saplings of four BCI species (Guariguata 1998), high *Piper* resprouting in Costa Rica (Gartner 1989; Greig 1993) and low pine resprouting in Nicaragua (Boucher *et al.* 1990). Bellingham *et al.* (1994) and Zimmerman *et al.* (1994) found interspecific variability in resprouting rates in response to hurricane damage in Jamaica and Puerto Rico. In this study, annual resprouting rates were highly variable across the spectrum of shade tolerance. The three most shade-intolerant species were less likely to be damaged and resprout than many more tolerant species, perhaps because individuals of light-demanding species are in more open areas on which less debris falls. Species of intermediate shade tolerance were more variable in their resprouting ability than more shade-tolerant species and possibly more likely to resprout. A review by Everham & Brokaw (1996) suggested that shade-tolerant species resprout at higher frequencies than pioneer species, while Greig (1993) reported that shade-tolerant *Piper* species were more able to regenerate vegetatively than shade-intolerant species.

A high rate of resprouting could be caused by a high rate of damage, high ability to resprout given damage, or low mortality of individuals after resprouting not properly accounted for by our annualization procedure. Clark & Clark (1991) found that the rate of damage to individuals < 1 cm d.b.h. did not vary among nine species with contrasting life histories, but that shade-intolerant species suffered lower rates of physical damage in larger size classes, which may partially explain the low resprouting rates of the three most shade-intolerant species in this study. If pathogens or herbivory cause crown dieback that leads to resprouting, differences in resprouting rate could be related to differences in susceptibility to these threats. Studies of seedlings have found resprouting related to insect attack (Ibrahim 1991) and fungal infection (Santamour *et al.* 1989). Many saplings on BCI that have recently resprouted show little evidence that they experienced breakage or bending due to falling vegetation (C.J. Paciorek, personal observation). While discussion of sapling resprouting caused by herbivory or disease is speculative, we cannot assume that all resprouting is a result of physical damage from falling vegetation.

If differences in resprouting rates are caused by differences in rates of damage, resprouting rate is likely to be positively correlated with the mortality rate for undamaged individuals because a high mortality rate for a species might be indicative of high levels of damage that cause either mortality or resprouting. The correlation between the resprouting rate and the mortality rate of undamaged individuals was positive, but small. Species in the Lauraceae and Sapindaceae had high annual resprouting rates, but are primarily midstorey and canopy tree species with low mortality rates for undamaged individuals. While differences in rates of damage may play some role, differences in inherent resprouting ability are likely to be the major cause of the variability in resprouting rates.

Inherent resprouting ability is constrained by the anatomy and physiology of buds in the plant stem. Resprouted stems could arise from either dormant axillary buds laid down by the apical meristem or associated tissues (preventitious buds) or from buds forming after injury from largely differentiated tissue (adventitious buds). Species differences in preventitious bud density, activation of preventitious buds, or the ability to form adventitious buds may be partly responsible for differences in resprouting rates. Palms are an excellent example. Lacking dormant vegetative axillary buds, they have little or no ability to sprout from the trunk (Tomlinson 1990; Zimmerman *et al.* 1994). However, clonal palm species, which are common, can produce shoots from basal buds, resulting in individuals with multiple stems (DeSteven 1986). We found that the clonal species were able to resprout.

Species that do not resprout may be at a competitive disadvantage, as severe damage to an individual would cause mortality. Simulations can explore the degree of disadvantage experienced by a species if none of its severely damaged individuals survive via resprouting. However, there may be trade-offs between resprouting ability and other life history traits, such as growth rate or resistance to damage (Bellingham *et al.* 1995). Resprouting ability may be an important life-history trait that differentiates species, provided that resprouted individuals survive and reproduce.

IS BCI UNIQUE?

These results and those of Putz *et al.* (1983), Putz & Brokaw (1989) and Guariguata (1998) suggest that resprouting is common on BCI, a forest that is not affected by large-scale disturbance. While Clark & Clark (1991) focus on rates of damage rather than rates of resprouting, their data suggest that resprouting is common at La Selva, Costa Rica. High rates of resprouting have also been observed in tropical montane forest at Monteverde, Costa Rica (Kinsman 1990; Matelson *et al.* 1995). Numerous studies have documented high rates of resprouting in tropical and temperate forests affected by hurricanes, tornadoes, fire, logging and slash-and-burn cultivation. Information on resprouting is not available for other lowland tropical rain forests that are not affected by large-scale disturbance, but these results raise the possibility that resprouting is common in such forests.

Conclusions

If resprouting rates are high, then resprouting is an important demographic process through which individuals decrease in size and delay mortality. If resprouted individuals continue to die at the high initial rates found in this study, then ignoring these living, but doomed, individuals is reasonable. However, if many resprouted individuals do survive and reproduce, researchers who focus either field work or modelling efforts on undamaged individuals will overestimate individual growth rates, underestimate time to maturity, and fail to understand the complicated demographic processes that determine the success of individuals and species. Simulations based on long-term mortality and growth data from future censuses can address the importance of resprouting for species population dynamics by estimating the proportion of individuals that reach reproductive size despite damage and resprouting.

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References

Aide, T.M. (1987) Limbfalls: a major cause of sapling mortality for tropical forest plants. *Biotropica*, **19**, 284–285.

Basnet, K. (1993) Recovery of a tropical rain forest after hurricane damage. *Vegetatio*, **109**, 1–4.

Bellingham, P.J., Tanner, E.V.J. & Healey, J.R. (1994) Sprouting of trees in Jamaican montane forests after a hurricane. *Journal of Ecology*, **82**, 747–758.

Bellingham, P.J., Tanner, E.V.J. & Healey, J.R. (1995) Damage and responsiveness of Jamaican montane tree species after disturbance by a hurricane. *Ecology*, **76**, 2562–2580.

Boucher, D.H., Vandermeer, J.H., Yih, K. & Zamora, N. (1990) Contrasting hurricane damage in tropical rain forest and pine forest. *Ecology*, **71**, 2022–2024.

Clark, D.B. & Clark, D.A. (1989) The role of physical damage in the seedling mortality regime of a neotropical rain forest. *Oikos*, **55**, 225–230.

Clark, D.B. & Clark, D.A. (1991) The impact of physical damage on canopy tree regeneration in tropical rain forest. *Journal of Ecology*, **79**, 447–457.

Condit, R. (1998) *Tropical forest census plots*. Springer-Verlag, Berlin, and R.G. Landes Co., Georgetown, TX.

Condit, R., Ashton, P.S., Manokaran, N., LaFrankie, J.V., Hubbell, S.P. & Foster, R.B. (1999) Dynamics of the forest communities at Pasoh and Barro Colorado: comparing two 50 ha plots. *Philosophical Transactions of the Royal Society of London B*, **354**, 1739–1748.

Condit, R., Hubbell, S.P. & Foster, R.B. (1995) Mortality rates of 205 neotropical tree and shrub species and the impact of a severe drought. *Ecological Monographs*, **65**, 419–439.

Condit, R., Hubbell, S.P. & Foster, R.B. (1996a) Changes in a tropical forest with a shifting climate: results from a 50 hectare permanent census plot at Barro Colorado Island in Panama. *Journal of Tropical Ecology*, **12**, 231–256.

Condit, R., Hubbell, S.P. & Foster, R.B. (1996b) Assessing the response of plant functional types to climatic change in tropical forests. *Journal of Vegetation Science*, **7**, 405–416.

DeSteven, D. (1986) Comparative demography of a clonal palm (*Oenocarpus mapora* subsp. *mapora*) in Panama. *Principes*, **30**, 100–104.

Everham, E.M. III & Brokaw, N.V.L. (1996) Forest damage and recovery from catastrophic wind. *Botanical Review*, **62**, 113–185.

Gartner, B.L. (1989) Breakage and regrowth of *Piper* species in rain forest understory. *Biotropica*, **21**, 303–307.

Glitzenstein, J.S. & Harcombe, P.A. (1988) Effects of the December 1983 tornado on forest vegetation of the Big Thicket, southeast Texas, U.S.A. *Forest Ecology and Management*, **25**, 269–290.

Gorchov, D.L., Cornejo, F., Ascorra, C. & Jaramillo, M. (1993) The role of seed dispersal in the natural regeneration of rain forest after strip-cutting in the Peruvian Amazon. *Vegetatio*, **107/108**, 339–349.

Greig, N. (1993) Regeneration mode in neotropical *Piper*: habitat and species comparisons. *Ecology*, **74**, 2125–2135.

Guariguata, M.R. (1998) Response of forest tree saplings to experimental mechanical damage in lowland Panama. *Forest Ecology and Management*, **102**, 103–111.

Harcombe, P.A. & Marks, P.L. (1983) Five years of tree death in a *Fagus-Magnolia* forest, southeast Texas (USA). *Oecologia*, **57**, 49–54.

Hubbell, S.P. & Foster, R.B. (1983) Diversity of canopy trees in a neotropical forest and implications for the conservation of tropical forests. *Tropical rain forest: ecology and management* (eds S.J. Sutton, T.C. Whitmore & A.C. Chadwick), pp. 25–41. Blackwell Scientific, Oxford, England.

Hubbell, S.P. & Foster, R.B. (1986) Commonness and rarity in a neotropical forest: implications for tropical tree conservation. *Conservation biology: the science of scarcity and diversity* (ed. M.E. Soulé), pp. 205–231. Sinauer, Sunderland, Massachusetts, USA.

Ibrahim, S. (1991) A note on the coppicing ability of *Shorea* species in peat swamp forests in peninsular Malaysia. *Journal of Tropical Forest Science*, **3**, 301–303.

Johnson, P.S. (1975) Growth and structural development of red oak sprout clumps. *Forest Science*, **21**, 413–418.

Kauffman, J.B. (1991) Survival by sprouting following fire in tropical forests of the eastern Amazon. *Biotropica*, **23**, 219–224.

Kinsman, S. (1990) Regeneration by fragmentation in tropical montane forest shrubs. *American Journal of Botany*, **77**, 1626–1633.

Leigh, E.G. Jr (1999) *Tropical forest ecology: a view from Barro Colorado Island*. Oxford University Press, New York.

Matelson, T.J., Nadkarni, N.M. & Solano, R. (1995) Tree damage and annual mortality in a montane forest in Monteverde, Costa Rica. *Biotropica*, **27**, 441–447.

Miller, P.M. & Kauffman, J.B. (1998) Seedling and sprout response to slash-and-burn agriculture in a tropical deciduous forest. *Biotropica*, **30**, 538–546.

Murphy, P.G. & Lugo, A.E. (1986) Structure and biomass of a subtropical dry forest in Puerto Rico. *Biotropica*, **18**, 89–96.

Negrelle, R.R.B. (1995) Sprouting after uprooting of canopy trees in the Atlantic rain forest of Brazil. *Biotropica*, **27**, 448–454.

Peterson, C.J. & Pickett, S.T.A. (1991) Treefall and resprouting following catastrophic windthrow in an old-growth hemlock-hardwoods forest. *Forest Ecology and Management*, **42**, 205–217.

Peterson, C.J. & Rebertus, A.J. (1997) Tornado damage and initial recovery in three adjacent, lowland temperate forests in Missouri. *Journal of Vegetation Science*, **8**, 559–564.

Pinard, M.A. & Putz, F.E. (1996) Retaining forest biomass by reducing logging damage. *Biotropica*, **28**, 278–295.

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

Putz, F.E., Coley, P.D., Lu, K., Montalvo, A. & Aiello, A. (1983) Uprooting and snapping of trees: structural determinants and ecological consequences. *Canadian Journal of Forest Research*, **13**, 1011–1020.

Putz, F.E. & Sharitz, R.R. (1991) Hurricane damage to old-growth forest in Congaree Swamp National Monument, South Carolina, U.S.A. *Canadian Journal of Forest Research*, **21**, 1765–1770.

Rijks, M.H., Malta, E.-J. & Zagt, R.J. (1998) Regeneration through sprout formation in *Chlorocardium rodiei* (Lauraceae) in Guyana. *Journal of Tropical Ecology*, **14**, 463–475.

Sampaio, E.V.S.B., Salcedo, I.H. & Kauffman, J.B. (1993) Effect of different fire severities on coppicing of caatinga vegetation in Serra Talhada, PE, Brazil. *Biotropica*, **25**, 452–460.

Santamour, F.S. Jr, McArdle, A.J. & Strider, P.V. (1989) Susceptibility of flowering dogwood of various provenances to dogwood anthracnose. *Plant Disease*, **73**, 590–591.

Tomlinson, P.B. (1990) *The structural biology of palms*. Clarendon Press, Oxford, UK.

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

Walker, L.R. (1995) Timing of post-hurricane tree mortality in Puerto Rico. *Journal of Tropical Ecology*, **11**, 315–320.

Welden, C.W., Hewett, S.W., Hubbell, S.P. & Foster, R.B. (1991) Sapling survival, growth, and recruitment: relationship to canopy height in a neotropical forest. *Ecology*, **72**, 35–50.

Whigham, D.F., Olmsted, I., Cabrera Cano, E. & Harmon, M.E. (1991) The impact of Hurricane Gilbert on trees, litterfall, and woody debris in a dry tropical forest in the northeastern Yucatan peninsula. *Biotropica*, **23**, 434–441.

Williamson, G.B., Schatz, G.E., Avlarado, A., Redhead, C.S., Stam, A.C. & Sterner, R.W. (1986) Effects of repeated fires on tropical paramo vegetation. *Tropical Ecology*, **27**, 62–69.

Wright, S.J., Carrasco, C., Calderon, O. & Paton, S. (1999) The El Niño Southern Oscillation, variable fruit production, and famine in a tropical forest. *Ecology*, **80**, 1632–1647.

Yih, K., Boucher, D.H., Vandermeer, J.H. & Zamora, N. (1991) Recovery of the rain forest of southeastern Nicaragua after destruction by Hurricane Joan. *Biotropica*, **23**, 106–113.

Zahner, R., Myers, R.K. & Hutto, C.J. (1985) Crop tree quality in young Piedmont oak stands of sprout origin. *Southern Journal of Applied Forestry*, **9**, 15–20.

Zimmerman, J.K., Everham, E.M. III, Waide, R.B., Lodge, D.J., Taylor, C.M. & Brokaw, N.V.L. (1994) Responses of tree species to hurricane winds in subtropical wet forest in Puerto Rico: implications for tropical tree life histories. *Journal of Ecology*, **82**, 911–922.

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