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Responses of tree species to hurricane winds in subtropical wet forest in Puerto Rico: implications for tropical tree life histories

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Summary

1 The effect of a category 4 hurricane (Hurricane Hugo, 18 September 1989) on subtropical wet forest in Puerto Rico was examined at stand and species levels with respect to the frequency of tree damage, mortality, and resprouting. Data were collected from a 16-ha plot of secondary forest consisting of approximately 13 000 trees > 10 cm DBH representing 88 species.

2 Roughly one-quarter of the trees suffered some type of damage involving the main stem, and mortality due to the hurricane was 9%. Mortality among trees was primarily due to uprooting and broken stems. Many surviving trees sprouted new branches following the hurricane, indicating that this was an important component of stand recovery following hurricane damage.

3 Patterns of species-specific damage and recovery (investigated using 26 common species) appeared to form two distinct groups. One group ('pioneers'), represented by three species, suffered a high frequency of stem breakage and mortality during the hurricane and had a low capacity to sprout new branches after being damaged. The remaining species ('nonpioneers') lost many branches during the hurricane, thereby suffering low to moderate stem damage and mortality, and sprouted many new branches following the hurricane. Stem breakage and related species-specific characteristics were significantly correlated with wood density and shade tolerance.

4 Species exhibited few significant size-specific relationships (using DBH) with respect to hurricane damage, mortality, or resprouting, with the exception of branch damage, which often increased as a function of tree size.

5 The study revealed significant differences among tree species in the degree and type of damage suffered during a hurricane and in the ability to recover from damage and resume a position in the forest canopy. Nonpioneers dominate early in recovery because of the ability to survive a storm and sprout new branches following the storm, while the immediate impact of a hurricane on the abundance of pioneer species is strongly negative.

Keywords: community dynamics, community structure, tropical forest, wind damage

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Introduction

Disturbance is regarded as a critical determinant of community structure in tropical forests (Connell

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1978; Garwood *et al.* 1979; Denslow 1987; Waide & Lugo 1992). The coexistence of large numbers of tree species in tropical forests has often been attributed to the differential response of species to disturbance through its influence on regeneration via seeds (cf. Grubb 1977). Particular attention has been directed at the influence of treefall gaps on the establishment and growth of seedlings and saplings in neotropical forests (Brokaw 1985; Hubbell & Foster 1986; Denslow 1987; Platt & Strong 1989). Despite this

great attention to disturbance and regeneration, relatively little attention has been directed at the response of mature trees to disturbance. The degree to which disturbance (e.g. high winds) damages different species and causes mortality, and the differential ability of tree species to resume growth following damage has rarely been considered (Foster 1988; Clark & Clark 1991).

Other than the ecology of their seeds and seedlings, tree life histories can be distinguished by differences in species' growth rates (Brokaw 1985; Denslow 1987; Clark & Clark 1992). Growth rate is of particular interest to understanding effects of disturbance on forest communities because growth rate is correlated with wood density (Putz *et al.* 1983) such that slow-growing, shade tolerant tree species have more dense wood than faster growing, shade intolerant species (Smith 1970; Lawton 1984). In turn, wood density is a determinant of the frequency and type of damage suffered by trees during windstorms. In Puerto Rico, the frequency with which tree species suffered broken stems during a hurricane was negatively correlated with wood density at one of two study sites (Walker *et al.* 1992). In Panamá, Putz *et al.* (1983) found that uprooted trees had more dense wood than trees with broken trunks, breakage being the most common type of damage in the forest they studied. Thus, it can be expected that during a windstorm, fast-growing tree species would be most susceptible to wind damage.

Putz *et al.* (1983) noted in their study of wind damaged trees in Panamá that many trees with broken trunks resprouted following damage while uprooted trees did not resprout. They suggested that resprouting was one mechanism for weak-wooded species to counter a greater tendency to suffer high stem breakage. This is an important consideration because resprouting may be a significant and overlooked aspect of forest regeneration following disturbance (Putz & Brokaw 1989; Yih *et al.* 1991; Bellingham *et al.* 1994). Putz *et al.* (1983) also showed that broken and uprooted trees in Panamá differed in size; trees with broken stems tended to have a smaller diameter than uprooted trees. To the degree that wind damage or recovery are restricted to trees of a limited size range and size-specific effects differ from species to species, this could lead to significant effects on subsequent forest community structure and dynamics.

In the late 1980s, several strong hurricanes passed through the Caribbean Sea, striking islands and coastal areas of the mainland. These storms generated a variety of studies on the influence of hurricanes on the forests of the region (Boucher 1990; Walker *et al.* 1991; Everham 1994). One of these storms, Hurricane Hugo, passed over the north-east corner of the island of Puerto Rico (Fig. 1) on 18 September 1989 with sustained winds over 166 k.p.h. (Scatena & Larsen 1991; Boose *et al.* 1994). The immediate impact of the hurricane on the Luquillo Experimental Forest (LEF)

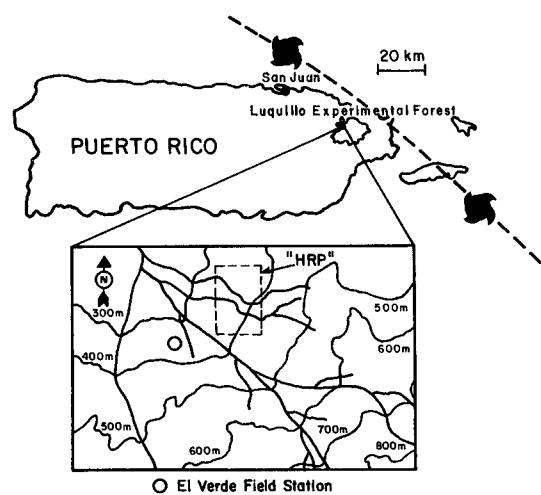


Fig. 1 Location of the Hurricane Recovery Plot (HRP) in the Luquillo Experimental Forest in Puerto Rico and the path of Hurricane Hugo on 18 September, 1989.

was described by Walker *et al.* (1992). In a related study of damage and recovery in a 0.6 ha sample of subtropical wet forest within the LEF, Walker (1991) found no relationship between life history variation among species, amount of damage sustained, or patterns of recovery. However, sample sizes for individual species were often small and trends among species may have been difficult to detect statistically. Acquiring sufficient data to test ecological questions in diverse tropical forests is a common problem, requiring the use of large contiguous plots (Hubbell 1979; Hubbell & Foster 1983). Data from a 16 ha sample of forest in the LEF were utilized to address the following questions:

- 1 What were the stand level characteristics of hurricane damage and recovery of trees in the plot and how does this compare to hurricane damage throughout the LEF and in other Caribbean forests?
- 2 What were the species-specific patterns of damage and response to hurricane damage and how were these associated with wood density and seed and seedling ecology (i.e. shade tolerance)?
- 3 What is the influence of tree size (diameter at breast height) on patterns of tree damage and recovery?
- 4 What are the implications of species- and size-specific patterns of hurricane damage and recovery for posthurricane forest dynamics?

Methods

STUDY AREA

This study was conducted near the El Verde Field Station (EVFS; 18°20'N, 65°49'W) in the north-west section of the LEF (Fig. 1). The area supports tabonuco (*Dacryodes excelsa* Vahl.) forest (subtropical wet forest in the Holdridge System; Ewel & Whitmore 1973), the lowermost (200–600 m a.s.l.) of four vegetation zones occurring along an altitudinal gradient

in the LEF. In addition to tabonuco, the forest in the area is dominated by the palm, *Prestoea montana*, and trees *Manilkara bidentata* and *Sloanea berteriana* (Odum & Pigeon 1970; Brown *et al.* 1983). The general topography is mountainous with north-west- running drainages producing north-east- and south-west-facing slopes (Fig. 1). Soils at the EVFS are mostly Zarzal clay, which are deep oxisols of volcanic origin (Huffaker 1994). Boulders and stones cover 25% of the soil surface (USDA Soil Conservation Service staff, unpublished). Rainfall at the station averages *c.* 350 cm year⁻¹. Although March and April tend to have less rainfall than other months of the year, on average there is no month in which there is < 20 cm of rainfall (Brown *et al.* 1983).

DISTURBANCE HISTORY

Prior to Hurricane Hugo, the most recent destructive hurricanes to strike the LEF occurred in 1928 and 1932 (Scatena & Larsen 1991). Less severe hurricanes struck the forest in 1931 and 1956 (Crow 1980; Wadsworth & Englehardt 1959). Because of human disturbance none of the forest in the 16 ha Hurricane Recovery Plot (Fig. 1) can be considered primary forest. However, the southern portion of the plot (*c.* 6 ha) is similar to virgin stands of tabonuco forest (Odum 1970). A 1936 air photo of the El Verde area indicated that forest cover was > 80% in this part of the plot (M. Fluet, personal communication). The northern portion of the plot was subject to clear cutting or other unidentified agricultural practices (D. Garcia-Montiel, personal communication) prior to 1934 when the El Verde tract was purchased by the USDA Forest Service. The 1936 air photo indicated that much of the northern portion of the plot had forest cover of 20–80% with many large gaps in evidence (Fluet, personal communication). A small area (*c.* 1 ha) appeared degraded and forest cover was < 10%. The northern portion of the plot now supports secondary forest mostly dominated by *Casuarina arborea*. Forests in the El Verde area were subject to stand improvement cutting by the USDA Forest Service in 1937 and 1946, described as 'light thinning' that had the general effect of increasing 'the representation of the species that typify the climax' (F. H. Wadsworth, cited by Odum 1970). The most recent timber harvests, between 1944 and 1953, removed approximately one-half the volume of tabonuco (*D. excelsa*; mostly trees > 50 cm DBH), representing approximately 10% of the stand volume (Odum 1970).

DAMAGE ASSESSMENT

Establishment of the 16-ha Hurricane Recovery Plot (HRP) began eight months after Hurricane Hugo. Following the methods used by Hubbell & Foster (1983) the HRP was surveyed and divided into 400

20-m × 20-m quadrats. All self-supporting woody plants ≥ 10 cm in diameter at a height of 1.3 m (DBH) were identified, measured, tagged, assessed for hurricane damage, and mapped to the nearest meter. To prevent the loss of data due to decomposition of dead trees an initial survey of all quadrats was made between September 1990 and February 1991 to record stems apparently killed by the hurricane. Tagging and mapping of the entire plot was completed in January 1992. Additional dead trees encountered during the survey are not included in the data set, nor was any damage to stems that obviously occurred after the hurricane.

Trees were marked with metal tags on which numbers were pre-stamped. Leaning or prone stems were measured for DBH at 1.3 m along the trunk from the rooting point. If a tree had two or more stems originating below 1.3 m, each stem was measured and tagged separately. Posture was recorded for each stem: standing, leaning (> 45° from the vertical), and prone. Each stem was then assessed for damage due to the hurricane. Five mutually exclusive stem damage categories were used: uprooted stem, stem broken above the ground ('broken'), stem broken at the ground level without uprooting ('root break'), bent (stem bent to > 45° from the vertical), and undamaged. The direction that damaged trees fell and the height and width of uprooted areas were also measured. Trees with undamaged stems were assessed for damage to large branches (> 10 cm). Finally, the presence of any new branches sprouting along the main trunk or at the top of broken stems was recorded. Almost all sprouting was initiated within 19 weeks of the hurricane (Walker 1991).

Trees were identified by sight in the field or from samples collected in the field. The latter were later identified with the assistance of authorities at the University of Puerto Rico and the New York Botanical Garden (NYBG). Voucher specimens are deposited at EVFS and NYBG. Nomenclature follows Little & Wadsworth (1991) and Little *et al.* (1974) unless otherwise noted.

SHADE TOLERANCE OF TREE SPECIES

In order to compare results for hurricane damage in adult trees to seed and seedling ecology, we use a shade tolerance ranking of tree species developed using data collected in two plots located within 200 m of the south-east corner of the HRP by Smith (1970). He assumed that species with large seeds (which he called primary forest species) have a greater capacity to germinate and establish in the shade than those with small seeds (secondary species) and that this would be reflected in higher abundances of seedlings and saplings relative to the abundance of adult trees. The abundance of canopy individuals (trees > 10 cm DBH) were recorded in a total sample of 1.5 ha while abundances of saplings (1.4 m height to 10

cm DBH) and seedlings (to 20 cm height) were recorded in subsamples of 0.28 ha and 64 m², respectively. Seedling abundance was recorded at four times during a single year (Smith 1970). We ranked species' shade tolerance using the average of (1) the rank of seed size, (2) the rank of the frequency of seedlings relative to the abundance of adults and (3) the rank of the relative frequency of saplings. Our ranking differs from the one provided by Smith (1970; Fig. 10) in that he made qualitative adjustments to the combined ranking (which we have not done) and our ranking increases from least to most shade tolerant (not the opposite). Agreement among the three ranked variables was high (Kendall's coefficient of concordance, $W = 0.693$, $P < 0.001$) and, for subsets of species, the ranking exhibited good correlations with data from more detailed studies of species' shade tolerance (Devoe 1989; Guzmán-Grajales 1992). However, this approach suffers the criticisms that increased seed size does not always indicate increased shade tolerance (e.g. Augspurger 1984) and that the relative abundance of seedlings can be influenced by disturbance history, predators, pathogens, mast years, etc., in addition to shade tolerance. Nevertheless, in the absence of more detailed studies, any correlation of aspects of wind damage and recovery and this shade tolerance ranking would suggest that these diverse life history characteristics are related.

Results

STAND-LEVEL DAMAGE AND RECOVERY

At the time of Hurricane Hugo there were 13 078 stems ≥ 10 cm DBH in the HRP (i.e. including trees apparently killed by the hurricane), representing 88 species. Over one-third (34.4%) of the stems were represented by the sierra palm, *Prestoea montana*. Of the total stems alive before the hurricane, 2177 (16.7%) stems were severely damaged: 909 (6.9%) were uprooted, 983 (7.5%) had broken stems, 182 (1.4%) suffered root breaks, and 104 (0.8%) were bent. Damaged stems fell in an average direction of 161.9 degrees, corresponding to peak hurricane winds from the north to north-west (Boose *et al.* 1994). Exposed soil and rock from uprooted trees totalled 0.8 ha. A total of 1178 stems (9.0% of all stems alive at the time of the hurricane) were killed by the hurricane. Almost all mortality resulted from damage involving the main stem (Fig. 2) among undamaged trees in both *P. montana* and in the remaining species, mortality was very low (1% or less). In *P. montana* stem damage almost always resulted in death, whereas dicot trees showed a lower mortality rate (20–60% across all categories of stem damage). Where trees other than palms suffered damage to one or more branches (23% of 8579 stems), mortality was only 2.3%.

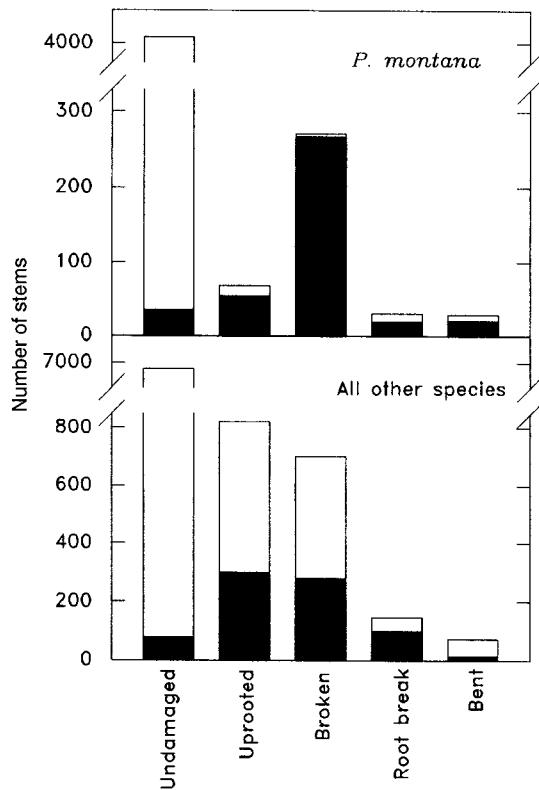


Fig. 2 Frequency of undamaged and damaged main stems in the 16-ha Hurricane Recovery Plot in Puerto Rico. Data are divided into the palm *Prestoea montana* and the remaining dicot tree species. Solid portions of bars indicate tree mortality.

When the surviving stems of nonpalm species were analysed, 64.8% had sprouted new branches 8–28 months after the hurricane. Sprouting was most frequent among trees with broken branches only, but was also high among those with bent and broken stems (Fig. 3).

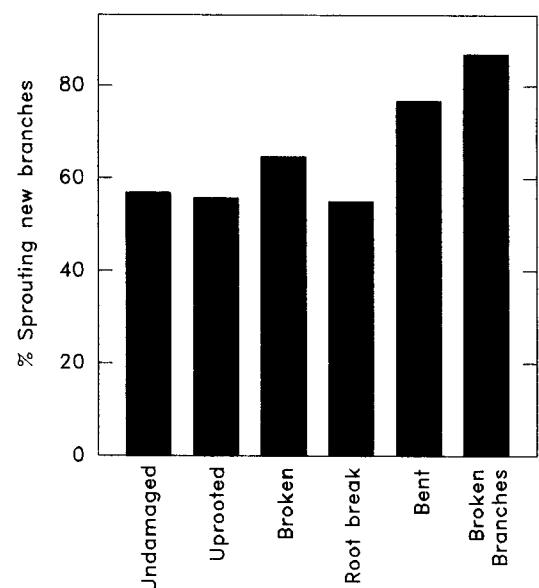


Fig. 3 Percentage of trees (excluding the palm *P. montana*) with new branch sprouts following Hurricane Hugo in various categories of hurricane damage.

SPECIES-SPECIFIC DAMAGE AND RECOVERY

Of 88 species represented in the HRP, 26 species (91.4% of all stems) had a frequency of 100 or more stems. These species were selected for a detailed analysis of the variation in hurricane damage and recovery by individual tree species. Because *P. montana* does not produce branches, it can only be assessed for stem damage, and recovery cannot be assessed by the production of new branches (Table 1). For these reasons, it was excluded from the following analyses.

To summarize the responses of the remaining tree species to Hurricane Hugo, principal components analysis (PCA; SAS 1987) was performed on the following five variables: percentage of trees uprooted, percentage of broken, percentage mortality, percentage of trees with branch damage, and percentage of surviving trees with branch sprouts (Tables 1 and 2). Percentages of root breaks and bent stems were not analysed because these types of damage were uncommon (Fig. 2). Percentages were transformed to arcsine-square roots of proportions prior to analysis.

Two components described 78% of the variation in the five variables. The first principal component (PC I, representing 53.3% of the total variance) was highly significantly correlated with four of five of the original variables. The pattern of loadings (Table 2) indicated species were distinguished by an increasing frequency of stem breakage and positively correlated changes in mortality. PC I also distinguished species by opposite trends in the frequency of branch damage and sprouting. The second principal component (PC II), representing 24.7% of the variation in species' responses, appeared to separate species by the frequency of uprooting (Table 1).

Results of PCA were further assessed by studying correlations of the five variables and their principal components with wood density and shade tolerance (Table 2). Data on wood density were available for 21 of the 25 species (Reyes *et al.* 1992). Wood density was significantly negatively correlated with the frequency of snap-offs among species as well as with PC I (Table 2). In contrast, the proportion of trees with damage to major branches was significantly positively

Table 1 Hurricane damage to main stems and branches, mortality, and resprouting of the 26 common species in the 16-ha Hurricane Recovery Plot in the Luquillo Experimental Forest, Puerto Rico. Nomenclature follows Little & Wadsworth (1991) and Little *et al.* (1974) except *Cecropia schreberiana* Miq. and *Chionanthus domingensis* Lam. Superscript letters refer to plotted locations of species in Fig. 4

| Species | Stems | Uprooted (%) | Broken* (%) | Branch damage† (%) | Mortality (%) | Sprouting‡ (%) |
|--|-------|--------------|-------------|--------------------|---------------|----------------|
| Palms | | | | | | |
| <i>Prestoea montana</i> | 4498 | 1.5 | 6.0 | — | 8.8 | — |
| All other species | | | | | | |
| <i>Alchornea latifolia</i> ^a | 208 | 7.2 | 12.0 | 25.0 | 5.3 | 64.0 |
| <i>Buchenavia capitata</i> ^b | 191 | 13.1 | 4.2 | 51.8 | 0.5 | 74.2 |
| <i>Byrsinima spicata</i> ^c | 158 | 9.5 | 3.8 | 36.1 | 8.2 | 66.9 |
| <i>Casearia arborea</i> ^d | 1094 | 20.8 | 7.9 | 10.1 | 10.6 | 60.2 |
| <i>Casearia sylvestris</i> ^e | 208 | 8.2 | 7.7 | 17.8 | 0.5 | 64.3 |
| <i>Cecropia schreberiana</i> ^f | 136 | 18.4 | 21.3 | 16.9 | 52.9 | 31.3 |
| <i>Chionanthus domingensis</i> ^g | 187 | 35.3 | 9.6 | 29.9 | 32.1 | 63.8 |
| <i>Cordia sulcata</i> ^h | 139 | 0.0 | 10.1 | 22.3 | 2.2 | 33.1 |
| <i>Croton poecilanthus</i> ⁱ | 135 | 9.6 | 6.7 | 36.3 | 16.2 | 83.2 |
| <i>Dacryodes excelsa</i> ^j | 1031 | 1.2 | 3.6 | 29.9 | 1.6 | 80.6 |
| <i>Drypetes glauca</i> ^k | 160 | 8.1 | 3.8 | 23.1 | 5.6 | 79.5 |
| <i>Guarea guidonia</i> ^l | 315 | 7.0 | 6.7 | 34.9 | 1.3 | 68.5 |
| <i>Guettarda valenzuelana</i> ^m | 116 | 6.0 | 9.5 | 26.7 | 4.3 | 73.9 |
| <i>Homalium racemosum</i> ⁿ | 174 | 4.6 | 2.3 | 30.5 | 2.3 | 55.3 |
| <i>Inga laurina</i> ^o | 565 | 9.4 | 14.3 | 23.7 | 15.6 | 68.8 |
| <i>Manilkara bidentata</i> ^p | 667 | 3.4 | 6.4 | 33.9 | 2.1 | 56.4 |
| <i>Matayba domingensis</i> ^q | 256 | 8.6 | 2.7 | 38.7 | 8.2 | 71.5 |
| <i>Miconia tetrandra</i> ^r | 124 | 22.6 | 22.6 | 16.1 | 59.7 | 56.0 |
| <i>Ocotea leucoxylon</i> ^s | 155 | 12.3 | 9.7 | 14.2 | 0.6 | 62.3 |
| <i>Ormosia krugii</i> ^t | 128 | 27.3 | 6.3 | 27.3 | 10.9 | 63.2 |
| <i>Sapium laurocerasus</i> ^u | 157 | 7.6 | 12.1 | 25.5 | 19.1 | 62.2 |
| <i>Schefflera morototoni</i> ^v | 199 | 7.5 | 12.6 | 8.5 | 16.6 | 27.7 |
| <i>Sloanea berteriana</i> ^w | 501 | 3.8 | 9.6 | 27.7 | 3.4 | 66.3 |
| <i>Tabebuia heterophylla</i> ^x | 334 | 2.1 | 6.9 | 26.9 | 5.1 | 64.0 |
| <i>Tetragastris balsamifera</i> ^y | 124 | 7.3 | 3.2 | 21.8 | 3.2 | 77.5 |
| Total – All other species | 8579 | 9.8 | 8.3 | 24.9 | 9.1 | 64.8 |

*Stems broken above ground level.

†Percentage of trees with no stem damage with at least 1 broken branch ≥ 10 cm in diameter.

‡Percentage of surviving trees.

Table 2 Correlation coefficients for variables describing hurricane responses of 25 common tree species in Puerto Rican wet forest. Pearson's correlation coefficients are provided, unless otherwise noted. PC I and PC II are first and second principal components of five variables used to describe hurricane responses (Table 1). Correlations with wood density (g cm^{-3} green volume) are provided from Reyes *et al.* 1992 ($N = 21$ species). The shade tolerance ranking ($N = 21$ species) was derived from Smith (1970; see Methods) and ranks species from least to most shade tolerant

| | Broken | Branch damage | Mortality | Resprout | PC I | PC II | Wood density | Shade tolerance ranking† |
|---------------|--------|------------------|-----------|----------|-----------|----------|-----------------|--------------------------------|
| Uprooted | 0.290 | -0.141 | 0.597** | 0.029 | 0.498* | 0.772*** | -0.107 | -0.205 |
| Broken | | -0.541** | 0.702*** | -0.548** | 0.886*** | -0.066 | -0.534* | -0.489* |
| Branch damage | | | 0.316 | 0.528** | -0.702*** | 0.529* | 0.516* | 0.425 |
| Mortality | | | | -0.346 | 0.826*** | 0.403* | -0.338 | -0.427 |
| Resprouting | | | | | -0.677*** | 0.558** | -0.374 | 0.657** |
| PC I | | | | | | 0.000 | -0.538* | -0.539* |
| PC II | | | | | | | 0.198 | 0.129 |
| Wood density | | | | | | | | 0.525*‡ |

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

†Spearman's rank correlation. ‡ $N = 19$ species.

correlated with wood density (Table 2). The rank of species' shade tolerance ($N = 21$ species) was significantly negatively correlated with the frequency of broken stems and PC I and negatively correlated with the frequency of resprouting. Wood density and the rank of shade tolerance were significantly negatively correlated. Neither wood density nor the rank of shade tolerance were significantly correlated with PC II.

The scatterplot resulting from PC I and PC II (Fig. 4) depicts a group of species with relatively similar hurricane responses surrounded by a halo of five species with distinct responses. These species are, from top to bottom, *Chionanthus domingensis* (g in Fig. 4), *Miconia tetandra* (r), *Cecropia schreberiana* (f), *Schefflera morototoni* (v), and *Cordia sulcata* (h). Three species (*M. tetandra*, *S. morototoni*, and *C. schreberiana*) exhibited the greatest scores on PC I, indicating that they had the highest levels of stem breakage and mortality, and the lowest levels of branch breakage and sprouting. *Cordia sulcata* and *Chion-*

anthus domingensis had, respectively, the lowest (0%) and highest (35%) frequencies of uprooting (Table 1).

DIAMETER RELATIONSHIPS

The relationships of DBH size class to five variables describing species-specific responses to Hurricane Hugo were investigated using contingency tables and G-tests of significance (Table 3). *P. montana* was excluded from these analyses because it has no secondary growth. Contingency tables were constructed to correspond to the ranges of diameters and sample sizes for individual species; diameter classes were either in 5- or 10-cm increments. Because of the variety of ranges in species' DBH and the types of tables constructed, it was difficult to compare patterns among species. Instead, each species was tested against the null hypothesis of no change in the frequency of damage, mortality, or sprouting against diameter class. If the smallest expected value of a particular table was ≤ 1.0 , the data were considered overly sparse (Sokal & Rohlf 1981) and statistical analyses were not conducted. In those tables where statistical analyses initially indicated a significant relationship ($P \leq 0.05$) but where the smallest expected values was ≤ 4 , William's Correction (Sokal & Rohlf 1981) was used to adjust for bias due to the small sample size.

Six of 25 species exhibited significant effect of diameter class on the frequency of uprooting (Table 3), but there were no significant relationships involving stem breakage. Size-specific patterns of damage varied among species. For example, the frequency of uprooting increased with tree size in *Casearia arborea*, while in *Inga laurina* intermediate-sized trees were most likely to be uprooted (Fig. 5a).

Significant associations between branch damage and tree diameter were most common (Table 3). Fourteen species exhibited patterns significantly different

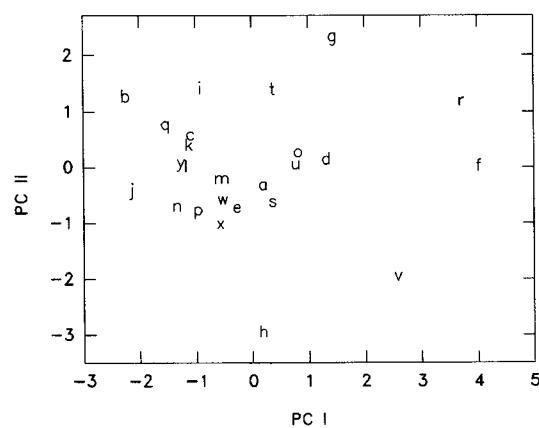


Fig. 4 Scatterplot of first two principal components derived from the analysis of stem damage, mortality, and resprouting of the 25 most common dicot species in the HRP. Individual species are indicated by the letter code allocated in Table 1.

Table 3 Summary of significance tests for relationships of DBH class and frequency of stem damage, mortality, and sprouting of common trees in the Hurricane Recovery Plot. Values are G-tests of significance (Sokal & Rohlf 1981); tests were not conducted on overly sparse data sets (see text)

| Species | d.f. | Uprooted | Broken | Branch damage | Mortality | Sprouting |
|---------------------------------|------|----------|--------|---------------|-----------|-----------|
| <i>Alchornea latifolia</i> | 3 | 3.75 | 3.03 | 13.62** | 5.50 | 3.92 |
| <i>Buchenavia capitata</i> | 5 | 6.75 | — | 13.03* | — | 1.98 |
| <i>Byrsinima spicata</i> | 4 | 3.55 | — | 19.89*** | 5.05 | 17.23** |
| <i>Casearia arborea</i> | 4 | 32.56*** | 1.61 | 33.31*** | 42.59*** | 7.71 |
| <i>Casearia sylvestris</i> | 3 | 0.78 | 6.48 | 8.61* | — | 1.08 |
| <i>Cecropia schreberiana</i> | 3 | 5.75 | 2.56 | 6.54 | 15.80*** | 1.24 |
| <i>Chionanthus domingensis</i> | 2 | 1.34 | 2.54 | 0.73 | 3.36 | 0.34 |
| <i>Cordia sulcata</i> | 2 | — | 0.92 | 3.64 | — | 0.05 |
| <i>Croton poecilanthus</i> | 3 | 0.66 | 7.53 | 8.83* | 1.21 | 1.32 |
| <i>Dacryodes excelsa</i> | 4 | — | 3.31 | 80.25*** | 8.56 | 7.11 |
| <i>Drypetes glauca</i> | 3 | 1.30 | — | 18.33*** | — | 0.74 |
| <i>Guarea guidonia</i> | 4 | 14.58*** | 1.23 | 26.14*** | — | 10.89* |
| <i>Guettarda valenzuelana</i> | 2 | — | — | 4.33 | — | 0.36 |
| <i>Homalium racemosum</i> | 4 | 13.66* | 3.99 | 18.93*** | — | 5.57 |
| <i>Inga laurina</i> | 4 | 18.18** | 6.05 | 14.80** | 42.99*** | 0.92 |
| <i>Manilkara bidentata</i> | 4 | — | 9.34 | 34.74*** | — | 20.21*** |
| <i>Matayba domingensis</i> | 3 | 5.02 | — | 6.11 | 2.98 | 4.03 |
| <i>Miconia tetrandra</i> | 2 | 0.31 | 1.48 | 0.09 | 4.42 | 2.24 |
| <i>Ocotea leucoxyylon</i> | 2 | 1.58 | 0.57 | 2.60 | — | 0.42 |
| <i>Ormosia krugii</i> | 2 | 8.00* | 2.95 | 1.26 | 0.76 | 1.00 |
| <i>Sapium laurocerasus</i> | 2 | 0.87 | 1.28 | 3.55 | 0.51 | 1.97 |
| <i>Schefflera morototoni</i> | 2 | 5.42 | 1.70 | 4.34 | 2.55 | 6.25* |
| <i>Sloanea berteriana</i> | 3 | — | 3.81 | 32.99*** | — | 5.37 |
| <i>Tabebuia heterophylla</i> | 3 | — | 2.52 | 24.53*** | 7.25 | 5.03 |
| <i>Tetragastris balsamifera</i> | 2 | 6.40* | — | 1.51 | — | 2.68 |

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

from expectation. In all but two of these species (*C. schreberiana*, *M. tetrandra*) the percent of trees with damaged branches increased with tree size. This is not surprising since one would expect that as tree size increases the likelihood of having at least one broken branch > 10 cm diameter should increase as well. However, the manner in which the increase occurred varied among species (Fig. 5b).

Few species exhibited significant relationships between diameter class and mortality (Table 3), in part because mortality was very low in some species (Table 1), and statistical analyses could not be conducted. Among those showing significance, percent mortality increased with tree size (Fig. 5c).

Significant relationships between the frequency of trees with newly sprouted branches and DBH class were also infrequent among species. In *Manilkara bidentata* the frequency of sprouting increased with increasing size, while sprouting declined with size in *Byrsinima spicata* (Fig. 5d). These changes, while statistically significant, were not large in any species.

Discussion

Although strong hurricanes remove much of the canopy from tropical forests and cause many stems to uproot or break, they typically result in relatively low levels of tree mortality (7–14%; Brokaw & Walker 1991; Bellingham *et al.* 1992). The stand level damage

in this study follows this generalization; the values of stem breakage, uprooting, and mortality fall within the range of values reported for several recent hurricanes in the Caribbean (Brokaw & Walker 1991). During a hurricane the severity of tree damage is related to the distance of a site from the path of storm and to surrounding topography. Variation in damage due to Hurricane Hugo observed in the LEF provides an example of this (Walker *et al.* 1992; Boose *et al.* 1994). The Bisley Experimental Watersheds were near the storm centre and faced directly into the oncoming winds. As a result, over 60% of trees were downed (Basnet *et al.* 1992; Dallmeier *et al.* 1992; Walker *et al.* 1992). The El Verde area was further from the hurricane and received only 'slight' hurricane damage as classified by Boose *et al.* (1994). However, because this was the most common degree of damage observed throughout the LEF, the results from the HRP should be representative of large areas of the forest.

Mortality among trees in the HRP was closely associated with stem breakage and uprooting, but not with branch damage. Webb (1988) reported a similar pattern among wind-thrown trees in Minnesota but Whigham *et al.* (1991) recorded significant mortality among both trees with severe branch damage and in stem-damaged individuals following Hurricane Gilbert in the Yucatan Peninsula. In the HRP, a large percentage of surviving trees sprouted new branches, a commonly observed response to wind damage in

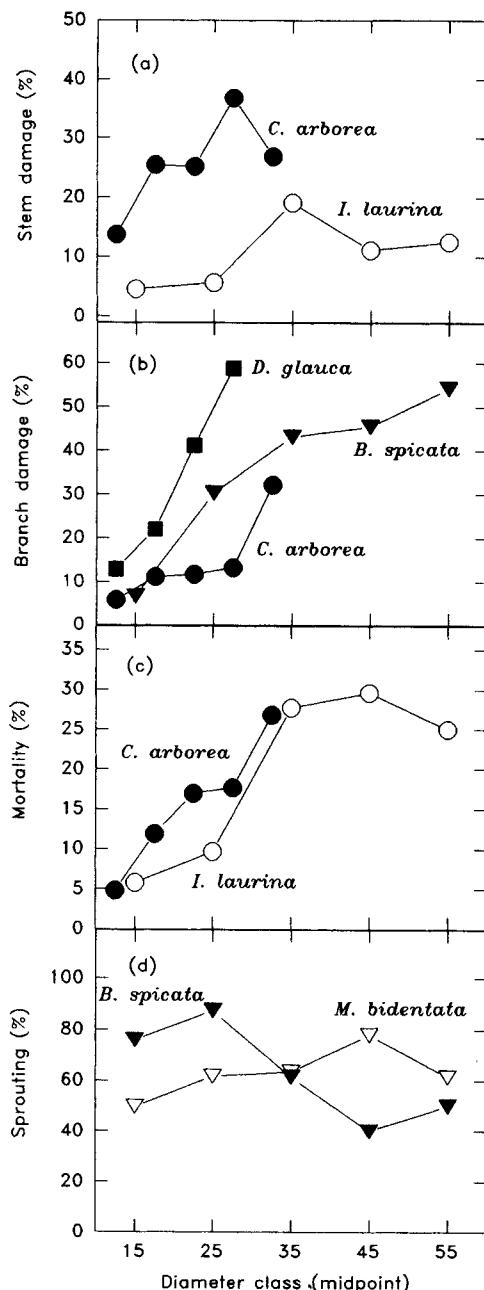


Fig. 5 Examples of species-specific patterns of hurricane damage, mortality, and sprouting plotted as a function of DBH size class. (a) percentage of stems uprooted; (b) percentage of trees with large (> 10 cm in diameter) broken branches; (c) percentage mortality; (d) percentage of surviving trees that sprouted new branches.

wet tropical forests (Brokaw & Walker 1991; Yih *et al.* 1991) but not in temperate forests (Peterson & Pickett 1991). In the HRP, sprouting was most frequent among trees that suffered damage to branches (Walker 1991) without any damage involving the main stem, although more than half of broken and uprooted trees exhibited evidence of sprouting. Walker (1994) has recently shown that although uprooted trees may sprout following a hurricane they will continue to die up to 3.3 years after the storm. This result gives emphasis to the conclusion that sur-

vival and recovery of trees from wind damage is usually highest among trees that limit injury to stems at the expense of large branches.

Most studies of wind damage to temperate and tropical forests have focused on patterns of tree damage at the stand level (summarized by Everham 1994) and have not attempted to decipher species-specific patterns within the stand. Our results indicate that species respond differently to hurricanes both in the amount of damage they receive and, among damaged trees, the type of damage sustained (Foster 1988; Gresham *et al.* 1991; Walker 1991). One potential cause of species-specific differences in damage would be the indirect effects of a topographic bias in species distributions and correlated differences in wind damage. We have conducted preliminary analyses which indicate that there is no strong topographical bias to hurricane damage over the HRP (E. M. Everham *et al.* unpublished data). This is in part due to a strong influence of human disturbance that confounds potential topographic influences on species distributions in the HRP. However, it also reflects of the fact that, while land-forms may control hurricane damage in a predictable manner at relatively large scales (i.e. kilometres; Bellingham 1991; Boose *et al.* 1994), damage may be unpredictable at the scale represented by the HRP, particularly given the modest level of topographic variability represented by the plot (cf. the Bisley Experimental Watersheds, Basnet *et al.* 1992). While we cannot completely eliminate the possibility of an indirect topographic influence on species-specific wind damage on the HRP, we are certain that it is not a dominant effect.

The most common species on the plot is the sierra palm, *Prestoea montana*, but, because of its unique morphology, we have had to exclude *P. montana* from many of our analyses. Elsewhere in the LEF, *P. montana* is commonly found growing in near-monospecific stands in forest flood plains. Here, *P. montana* appears resistant to hurricane damage, suffering only about 1% mortality due to Hurricane Hugo (Frangi & Lugo 1991). Resistance to hurricane mortality in palms is explained by their ability lose their fronds to high winds without losing the sole terminal meristem. The palm mortality observed by Frangi & Lugo (1991) was largely due to the impact of dicot trees falling along the margin of the flood plain and direct wind mortality was observed only among individuals with heavy epiphyte loads. As subcanopy plants in the HRP, palms suffered much higher stem breakage and mortality, and we believe this was probably due to the impacts of surrounding trees which fell on the palms during the hurricane.

Among the 25 other common tree species in the HRP, principle components analysis identified significant trade-offs in the frequency of broken stems, mortality, branch breakage, and branch sprouting (PC I, Table 2). Differences in species-specific damage were correlated with species' wood density. Species

with more dense wood tended to suffer less stem breakage and mortality than those with less dense wood, because denser woods are stronger and less flexible and less likely to break during high winds (Putz *et al.* 1983; Lawton 1984; Walker *et al.* 1992). Species resistant to stem damage were more likely to suffer branch damage, perhaps because trees with higher wood densities permit less torque, increasing the stress on branches. This result may also be a function of tree architecture. Much of the variation in tree architecture is expressed in changes in the relative size of lateral branches to main stems (King 1986; Stevens & Perkins 1992). In a hurricane, such variation in architecture may have strong influence on the relative likelihood of stem vs. branch damage.

There was no support for the suggestion that weak-wooded species were more likely to resprout following stem breakage than species with more dense wood (cf. Putz *et al.* 1983). In fact, the opposite appeared to be true. Low levels of resprouting exhibited by these species may be due to the fact that they possess few resting buds (Swaine & Whitmore 1988) or because of low levels of reserve storage (Chapin *et al.* 1990), or both.

Relationships between aspects of species-specific damage (summarized by PC I, Table 2) and the index of shade tolerance developed from Smith (1970) were also evident. Increasing shade tolerance was negatively correlated with the frequency of broken stems, apparently the result of the positive correlation between shade tolerance and wood density. There was also a strong positive correlation between shade tolerance and the frequency of sprouting, indicating a close correspondence between these distinct life history characteristics.

Patterns of tree damage and recovery associated with stem breakage tend to support Swaine & Whitmore's (1988) view that tropical tree species can be separated into two groups described by 'pioneer' and 'nonpioneer' life history profiles. Swaine & Whitmore (1988) defined these profiles with emphasis given to the importance of a light cue for seed germination (i.e. pioneers) and the ability of seedlings to withstand deep shade (i.e. nonpioneers). Much of the variation in tree damage and recovery in our study was summarized by PC I which, in turn, showed a significant correlation with shade tolerance as well as with species' wood density. Three species, *Cecropia schreberiana*, *Schefflera morototoni*, and *Miconia tetandra*, exhibited extreme scores on this axis and appeared to be separated along this axis from the remaining species. All three are species recognized as typical pioneers or are of genera which include pioneer species elsewhere in the Neotropics (Brokaw 1985; Denslow 1987; Swaine & Whitmore 1988). Recently, Alvarez-Buylla & Martínez-Ramos (1992) have claimed that Swaine & Whitmore's (1988) life-history profiles define the ends of a continuum and do not characterize distinct species groups. While our results do not

support this view, they clearly indicate, whatever the case, that responses of mature trees to wind and other types of disturbance are important characteristics of the life histories of tropical trees.

Principal components analysis also identified significant variation among species in the frequency of uprooting, but the nature of this variation was ambiguous and unrelated to any apparent differences in species' life history. Increased uprooting among species was positively correlated with increased mortality, but relationships to other variables were weak. There was no correlation of uprooting frequency with species' wood density. The causes of uprooting may be complex and may differ from species to species. Variation in rooting architecture, differences in wood composition that are uncorrelated with wood density, and subtle differences in topographic distributions of species (e.g. uprooting may be more common on slopes) are some potential explanations for this variation (Putz *et al.* 1983).

Species were also investigated for differences in size related patterns of hurricane damage and recovery. At sizes above 10 cm DBH, there were few significant patterns of stem damage in any of the tree species on the HRP. Significant patterns were most common for the frequency of branch damage, reflecting the greater frequency of large damaged branches on larger trees. Differences in the way branch damage increased with tree size among species presumably reflects differences in tree architecture. Where patterns were statistically detectable, larger trees were more likely to die from hurricane damage than smaller trees. Tree size had little effect on the probability that surviving trees sprouted new branches, even where patterns were statistically significant. In general, size specific damage and recovery are probably not an important component of species-specific responses to hurricane damage in the HRP, at least among the range of tree sizes investigated (Walker 1991; Yih *et al.* 1991; Wunderle *et al.* 1992).

In summary, consideration of the direct effects of disturbance and immediate responses of forest trees to the causes of disturbance clearly is a valuable addition to the usual attention given to the regeneration of tree species via seeds and seedlings. Our results identified three pioneer species that, as a result of a hurricane, exhibited a combination of (1) higher stem breakage, (2) higher levels of mortality, (3) lower levels of branch breakage, or (4) lower levels of resprouting in contrast to the remaining nonpioneer species. In general, nonpioneers were able to survive the hurricane and sprout new branches, thereby placing them in the situation directly to reclaim a position in the forest canopy. These differing characteristics of pioneer and nonpioneer species were correlated with differences in wood density and an index of species' shade tolerance. To the degree that growth rate places constraints on wood density (Putz *et al.* 1983; Lawton 1984), one would expect to find a cor-

relation between shade tolerance and wood density (Augspurger 1984). As a result of low wood density, fast-growing pioneer species are more susceptible to stem breakage than nonpioneers. As a result of differences in wood density, tree architecture, or both, nonpioneers are more susceptible to branch breakage than pioneers. The infrequency with which pioneers sprout new branches following damage is probably due to both morphological and physiological constraints on resprouting (Swaine & Whitmore 1988; Chapin *et al.* 1990) resulting from the maximization of growth rate.

What are the implications of our findings for post-hurricane forest dynamics? In a modelling study based on the forest at El Verde, Doyle (1980) predicted that hurricanes should contribute to the maintenance of high species diversity in the forest by creating repeated opportunities for the establishment of pioneer species. Our study has shown that the immediate impact of a hurricane on mature pioneer trees is a negative one and that an important component of posthurricane recovery is the sprouting of new branches by non-pioneer species. This result differs from that of Glitzenstein & Harcombe (1988) who showed that tornado damage selects against the dominant canopy species in forests in south-eastern Texas. Noting the ability of tropical nonpioneers to recover from hurricanes, Yih *et al.* (1991) coined the term 'direct regeneration' and discussed its importance to the role of secondary succession in tropical forest dynamics. In general, hurricanes do not extirpate species (Brokaw & Walker 1991), but only modify their relative abundances. Since our study, pioneer species have become very abundant among establishing trees at El Verde (Guzmán-Grajales & Walker 1991; Guzmán-Grajales 1992). The abundance of *C. schreberiana* is particularly greatest in areas of exposed soil caused by tree uprooting (L. R. Walker, unpublished data). With time, pioneers should become more abundant in the forest canopy, but at the expense of many individuals which will become shaded by the redeveloping canopy and die. Beyond this, it is expected that pioneer abundance will decline, as demonstrated by Crow (1980; also see Weaver 1989), until a hurricane disturbs the canopy again.

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