DAMAGE AND RESPONSIVENESS OF JAMAICAN MONTANE TREE SPECIES AFTER DISTURBANCE BY A HURRICANE[1]

P. J. Bellingham[2] and E. V. J. Tanner[3]
Department of Plant Sciences, University of Cambridge, Downing Street, Cambridge, CB2 3EA, United Kingdom

J. R. Healey
School of Agricultural and Forest Sciences, University of Wales, Bangor, Gwynedd, LL57 2UW, United Kingdom

Abstract. A severe hurricane affected Jamaican montane rain forests in 1988. We made local and widespread measurements of tree condition in three periods: prehurricane 1974–1984 (preh.); hurricane 1984–1989 (h.); and post-hurricane 1989–1992 (post-h.). In the h. period, 7.22% of stems and 4.72% of the total basal area died; crown loss was the most frequent cause of mortality. Among individual tree species, the hurricane caused a large range in mortality (0–26%) and non-fatal damage. Post-h. mortality was greater than mortality in the h. period, and varied among species. Post-h. stem growth rates (all species combined) were more than double the prehurricane rates, but species showed a considerable range from no significant increase to eight times greater.

We classified 20 common tree species using damage scores (normalized h. mortality, plus normalized change in mortality from preh. to post-h., plus normalized complete crown loss in h.) and response scores (normalized change, preh. to post-h., in recruitment to the ≥3 cm dbh size class, plus normalized change in growth rate from preh. to post-h., plus normalized frequency of sprouts). Species were assigned to one of four groups: resistant (11 species), with low damage and low response; susceptible (5 species), with high damage and low response; resilient (1 species), with high damage and high response; and usurpers (3 species), with low damage and high responsiveness. The grouping of species was broadly related to their regeneration requirements. Most species with seedlings usually found under closed canopy were resistant; three of the four species with seedlings usually found on landslides were also resistant. Species with seedlings most frequently found in gaps included resilient, susceptible, and usurper species, but were not usually resistant.

It is likely that the three species classified as usurpers will increase their relative abundance in the forest in the next decades and that *Cyathea pubescens*, which was very susceptible, will decrease in relative abundance of adults. Most of the other species are likely to have small changes in their relative abundances. Thus, at present, hurricanes have few long-term effects on the forests, although a change in the disturbance regime may alter this.

Key words: disturbance regime; growth rates; hurricane; Jamaica; montane trees; mortality; recruitment; tropical forests.

INTRODUCTION

In long-lived plant communities, many studies of the effects of disturbance on community stability have focussed on two aspects: resistance (the extent to which communities resist change by disturbance) and resilience (the extent to which communities recover to their original condition after disturbance) (Leps et al. 1982, Halpern 1988). Disturbance caused by severe storms and hurricanes usually results in differential resistance of species (e.g., Wadsworth and Englerth 1959, Whitmore 1974, Foster 1988a, Webb 1988, Walker 1991) and differential resilience of species (e.g., Merrens and Peart 1992). We used permanently labelled trees in the

mountains of Jamaica to measure the damage and response of all the commoner tree species in order to discover whether or not damage and response were correlated with species characteristics. Such correlations would allow us to predict the effects of hurricanes. We also used the results to predict the likely changes in community composition and structure over the next few decades.

Previous studies of Hurricane Gilbert, which passed over Jamaica on 12 September 1988, showed that levels of mortality and damage caused to the montane rain forests during the hurricane were low compared with other forests affected by hurricanes (summarized in Brokaw and Walker 1991). These earlier studies (Bellingham 1991, Bellingham et al. 1992) examined patterns of mortality and damage caused by the hurricane and subsequent recovery (sprouting) at a community level; in this paper, we explore variation in damage and response within the community. For all tree species in

the community, we assessed damage by measuring mortality, crown loss, defoliation, uprooting, and partial breakage. We looked for correlations between mortality and stem size, wood density, and leaf characteristics. Response to the hurricane was assessed by recruitment of each species to tree size class (≥ 3 cm dbh), growth rates of each species, and sprouting. We used measures of damage and response to produce a two-dimensional depiction of species, which can then be loosely classified into resistant, susceptible, resilient, and usurper. This classification is probably applicable to a wide range of plant communities.

METHODS

Study site

The study area was the crest and the area 250 m south and north of the crest (1300–1920 m above sea level) along the 5 km of ridge between John Crow Peak and High Peak in the western Blue Mountains of Jamaica (18°05′ N, 76°38′ to 76°40′ W). Here, upper montane rain forests vary in composition according to exposure to the prevailing northeast trade winds, to physiography, and to differences in soils (Shreve 1914, Grubb and Tanner 1976, Tanner 1977). The geology of the study area is highly complex, with at least eight ·rock types in highly faulted strata, and includes metamorphic blue schists, green schists, and amphibolites, marine shales and reef limestones, and igneous rocks. Soils of most of the study area are immature lithosols on the steep slopes of the range. On less steep areas of the slopes and on ridge tops, soils are more stable, less stony and more mature, yellow brown or pale brown loams (Grubb and Tanner 1976).

Jamaica is at the edge of the western Caribbean zone of frequent hurricanes (Alaka 1976). Between 1903 and 1988, nine hurricanes passed within 60 km of eastern Jamaica (including the Blue Mountains), five between 1903 and 1916, and one each in 1944, 1951, 1980, and 1988 (Neumann et al. 1978, Thompson 1983, Lawrence and Gross 1989). Hurricane Allen, in 1980, caused substantial damage to plantations of *Pinus caribaea* but relatively little damage to the montane rain forests in the Blue Mountains (Thompson 1983). Hurricane Gilbert was the strongest hurricane yet recorded in the Caribbean (Lawrence and Gross 1989); it caused substantial damage to forests throughout Jamaica, including the Blue Mountains (Bellingham et al. 1992).

We collected data from three sample areas totalling 1.10 ha:

1) The Tanner and Healey (T/H) plots recorded February–April 1989 (5–7 mo after the hurricane), four sites in close proximity on or near the Grand Ridge of the Blue Mountains, with contiguous permanent 10 × 10 m plots sampling 0.46 ha in total, (0.35 ha set up in 1974; Tanner 1977, Tanner et al. 1990), and three discrete 10 × 10 m plots nearby (control plots of Healey 1990, set up in 1986), for a combined total of 0.49

ha. The T/H plots were enumerated in January–February 1974 and May–August 1984 (i.e., a 10.4-yr prehurricane period), and February–May 1989 (i.e., a 4.6-yr hurricane period). A 0.35-ha subset of these plots was recorded after the hurricane in January–May 1991 (i.e., a 2-yr post-hurricane period).

2) The Mabess River transect (MRT), recorded May 1989, 26 nonbounded plots at 40-m intervals along a transect parallel to the Grand Ridge of the Blue Mountains in the Mabess River Valley, containing 20 individuals per plot (after the method of Hall 1991), and sampling a total area of 0.29 ha.

3) The Bellingham plots (PJB), mostly shown in Bellingham (1991), recorded May–August 1990 (20–23 mo after the hurricane), 16 permanent 200 m² permanent plots sampling 0.32 ha within an area of 2.5 km².

Nomenclature for the time periods is as follows. There was a prehurricane period 1974–1984 (during which the forest was unaffected by hurricanes, except slightly by Hurricane Allen in 1980) for 35 of the T/H plots. There was a hurricane "period" for all plots: 1984–1989 for the T/H plots, the first (1989) enumeration of the MRT plots, and the 1990 enumeration of the PJB plots (MRT and PJB plots had no prehurricane enumerations). There was a post-hurricane period 1989–1991 for 35 of the T/H plots.

Assessments of mortality and damage caused by the hurricane

We used the first post-hurricane records taken between February 1989 and August 1990, i.e., between 5 and 23 mo after Hurricane Gilbert, to estimate mortality and damage to stems caused by the hurricane. In total, 5334 stems ≥ 3.0 cm dbh were sampled and identified to species. Multiple stems were noted and the number of individuals was assessed.

After the hurricane, stems were deemed dead if they lacked epicormic sprouts and/or had rot above break height. Angiosperm and gymnosperm stems that lacked bark were considered to have died before the hurricane and were not recorded. These criteria were devised following the earliest post-hurricane assessments of mortality in these forests (Bellingham et al. 1992). Some mortality could have been caused by storms since Hurricane Gilbert; in other instances, stems killed by the hurricane may have been mistaken as prehurricane fatalities. Mortality of individuals was assumed only when all constituent stems were dead.

We assessed hurricane damage to stems, both living and dead, in three categories (cf. Bellingham 1991):

1) Broken stems, divided into two groups: those with complete crown loss, where only a standing trunk remained; and those with partial breakage, in which a major part of the crown was either snapped off or snapped over, but some of the crown remained intact.

2) Uprooted stems ($\geq 40°$ angle from their prehur-

ricane position and with freshly exposed soil about the root plate).

3) Stems that had been completely defoliated (excluding stems that lost crowns, but including stems that were either partially broken or uprooted). We included stems that remained bare and those in which the only new leaves were on epicormic sprouts from main stems, while twigs remained bare or were dead.

Among stems killed by the hurricane, we investigated whether some forms of damage had been fatal more often than others. We determined whether or not stems of different size were damaged in different ways, examining both killed and surviving stems, for all species and for individual species where ≥50 stems were damaged. Among stems that survived the hurricane, we investigated differences in levels of damage between species with densities of ≥20 stems in the plots. We examined whether or not the percentages of individuals killed were related to taxonomic group, testing among families and orders with four or more species.

Wood density

Wood density (oven dry mass and dry volume) was measured in small blocks of wood taken from trunk samples (0 or 1.3 m above the soil surface) collected for biomass estimation (Tanner 1980).

Comparisons of prehurricane, hurricane, and post-hurricane periods

In 35 of the T/H plots in the prehurricane, hurricane, and post-hurricane periods, we calculated for all species and for the nine commonest species (where $n \geq$ 50 throughout the census period): annual mortality; annual recruitment; and relative basal area increment (RBAI), where

$$\text{RBAI} = \frac{\ln \text{BA}_{t_1} - \ln \text{BA}_{t_0}}{t_1 - t_0}.$$

Here, BA is basal area in square meters, and t is time in years. These data were collected for each stem that survived between 1974 and 1991, and also for all stems at each inventory (i.e., including stems that did not survive to the next inventory).

Evaluation of damage and responsiveness

For each of 20 common species, we derived indices of damage caused by the hurricane and response following the hurricane. Damage indices were the sum of three variables: (1) hurricane mortality (T/H, MRT, and PJB plots); (2) short-term change in mortality (annual percentage mortality in the post-hurricane period minus annual percentage mortality in the prehurricane period) (T/H plots); and (3) percentage of stems that lost crowns during the hurricane (T/H, MRT, and PJB plots). For each variable, the range among the 20 species was normalized between 0 and 1.0; the sum of the three variables for each species was also normalized.

The responsiveness indices for each species were the sum of three variables: (1) change in recruitment rate (annual percentage recruitment in the post-hurricane period minus that in the prehurricane period) (T/H plots); (2) change in growth rate (RBAI in the post-hurricane period minus that in the prehurricane period) (T/H plots); and (3) frequency of sprouting (T/H, MRT, and PJB plots, Bellingham et al. 1994). We normalized each of these variables between 0 and 1.0 and normalized the total scores.

Statistical analyses and nomenclature

Values for individual species were compared with the overall value for all species using G tests (employing Williams' correction where appropriate) and χ^2 tests. We carried out several hundred such tests in total, so we expect that some of the 'significant' differences, especially those at $P < 0.05$, were a result of random variation. However, we seldom attached great importance to individual comparisons where $P > 0.01$. Other tests of trends among species were made using ANOVA and correlations. Following ANOVA, individual species were compared using Scheffé F-tests (fuller details can be found in Bellingham 1993). Throughout the text, variations around the mean are plus or minus one SE.

Nomenclature follows Proctor (1985) for ferns and Adams (1972) for flowering plants, except for the gymnosperm *Podocarpus urbanii* Pilger, and *Gordonia haematoxylon* Swartz, *Guarea glabra* Vahl., *Ocotea patens* (Swartz) Nees, *Sideroxylon montanum* (Swartz) Pennington, and *Urbananthus critoniformis* (Urban) R. King and H. Robinson.

RESULTS

Initial effects of the hurricane

Mortality.—Levels of mortality within 23 mo after the hurricane for all species combined were 7.22% of 5334 stems, 4.72% of the total basal area (54.2 m²), and 6.34% of 4414 individuals. These three percentage assessments of mortality (by stems, basal area, or individuals) did not differ significantly (ANOVA of arcsine square-root transformed data, $F_{2, 138} = 0.373$, $P = 0.69$, using the 47 most common species). Three species (*Cyathea furfuracea*, *Hedyosmum arborescens*, and *Mecranium purpurascens*) had significantly greater mortality, and four abundant species (*Chaetocarpus globosus*, *Eugenia virgultosa*, *Guarea glabra*, and *Maytenus jamaicensis*) had significantly lower mortality of stems, basal area, and individuals than the average (Table 1).

Not surprisingly, the mortality of species assessed by stems was strongly correlated with mortality of species assessed by basal area ($r_{47} = 0.90$, $P < 0.001$). Over all species, there was no correlation between mortality and stem size. However, in some species a greater than expected percentage of basal area was killed, i.e., the hurricane tended to kill larger rather than smaller

Species	n		m^2		n	
Cyathea furfuracea	146	***	0.49	***	143	***
Mecranium purpurascens	125	***	0.23	***	83	***
Hedyosmum arborescens	312	***	1.80	***	264	***
Ocotea patens	75	**	0.18	*	41	
Palicourea alpina	50	*	0.09		48	**
Myrsine coriacea	26		0.11		25	
Cyathea pubescens	161	*	1.52	***	159	*
Symplocos octopetala	30		0.12		30	
Cinnamomum montanum	22		0.61		41	
Miconia quadrangularis	33		0.11		27	
Vaccinium meridionale	198		2.41		117	
Meriania purpurea	131		0.52		113	
Ilex macfadyenii	123		0.53		71	
Cleyera theaeoides	26		0.25		17	
All species combined	**5334**		**54.19**		**4414**	
Cinchona officinalis ‡	42		0.11		16	
Lyonia octandra	237		2.90		179	
Alchornea latifolia	165		3.15		111	
Schefflera sciadophyllum	90		0.25		49	
Viburnum alpinum	32		0.26	**	15	
Psychotria corymbosa	149		0.23		123	
Gordonia haematoxylon	38		1.35		35	
Turpinia occidentalis	58		1.41		55	
Clethra occidentalis	446		7.11		406	
Urbananthus critoniformis	63		0.11		52	
Podocarpus urbanii	371	*	4.99	***	365	
Clusia havetioides	88		0.48		73	
Ilex vaccinoides	22		0.16		15	
Miconia rigida	25		0.04		20	
Solanum punctulatum	50		1.38	*	34	
Cyrilla racemiflora	227		6.06	***	138	*
Calyptranthes rigida	27		0.08		21	
Eugenia marchiana	32		0.13		31	
Haenianthus incrassatus	37		1.28	**	34	
Ilex obcordata	40		0.17		23	
Eugenia monticola	43		0.13		43	
Guarea glabra	244	***	2.69	**	241	***
Dendropanax pendulus	167	***	0.62		125	*
Eugenia virgultosa	285	***	1.10	*	271	***
Maytenus jamaicensis	154	***	1.42	**	134	**
Boehmeria caudata	21		0.04		14	
Chaetocarpus globosus	95	**	1.67	***	66	*
Clethra alexandri	32		0.26		26	
Dendropanax arboreus	64	*	0.60		53	*
Ilex harrisii	54	*	0.44		49	
Pittosporum undulatum ‡	53	*	0.18		53	*
Psychotria sloanei	22		0.06		19	
Sideroxylon montanum	55	**	0.98	*	47	

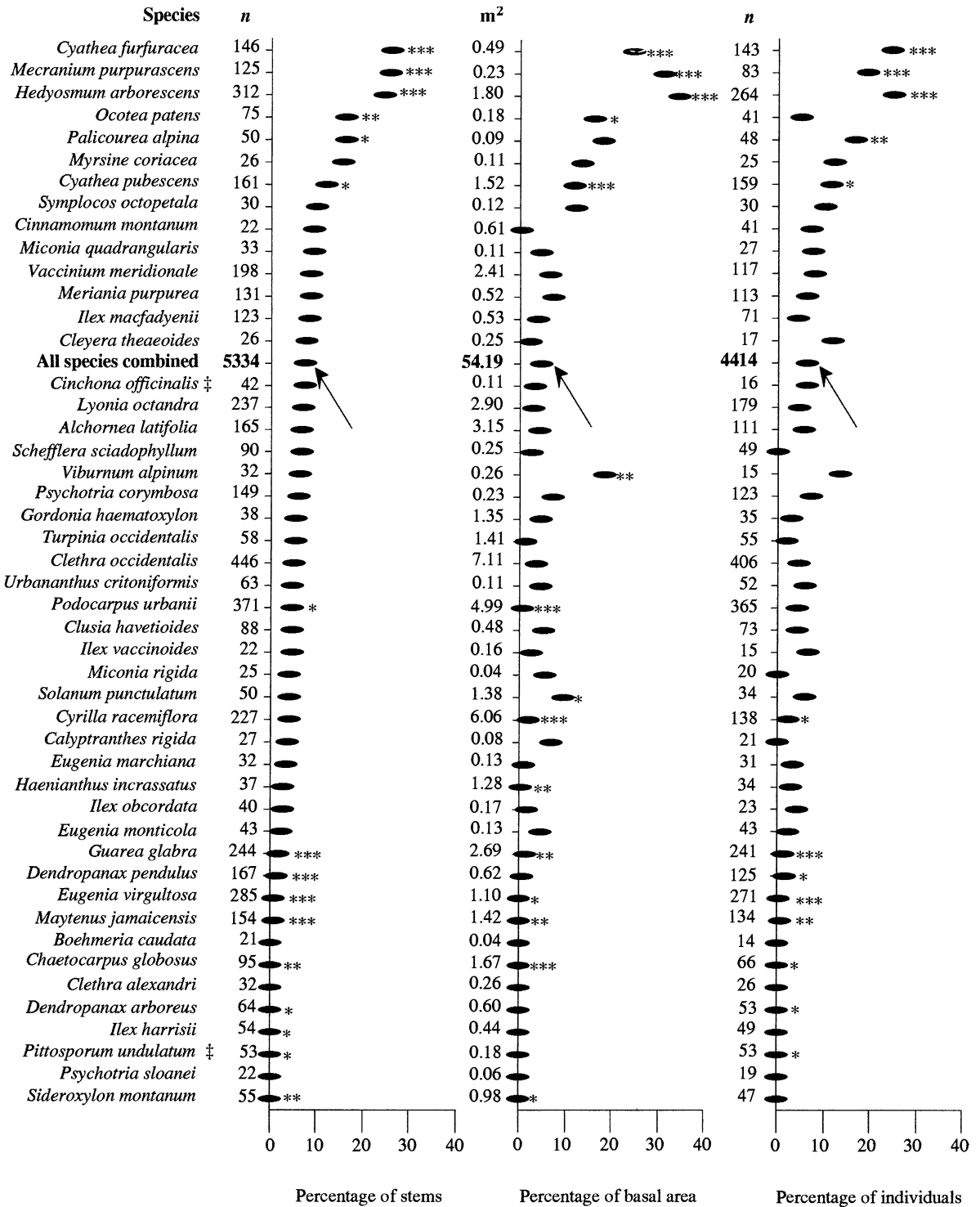| 0 10 20 30 40	0 10 20 30 40	0 10 20 30 40
Percentage of stems	Percentage of basal area	Percentage of individuals

FIG. 1. Mortality caused by Hurricane Gilbert in 47 tree species in montane forests in the Blue Mountains of Jamaica, assessed 5–23 mo after the hurricane, as percentage mortality of stems, basal area, and individuals (n, number of stems or individuals sampled). Differences between individual species and all species combined were compared using adjusted G tests ($*P < 0.05$, $**P < 0.01$, $***P < 0.001$). ‡, introduced species.
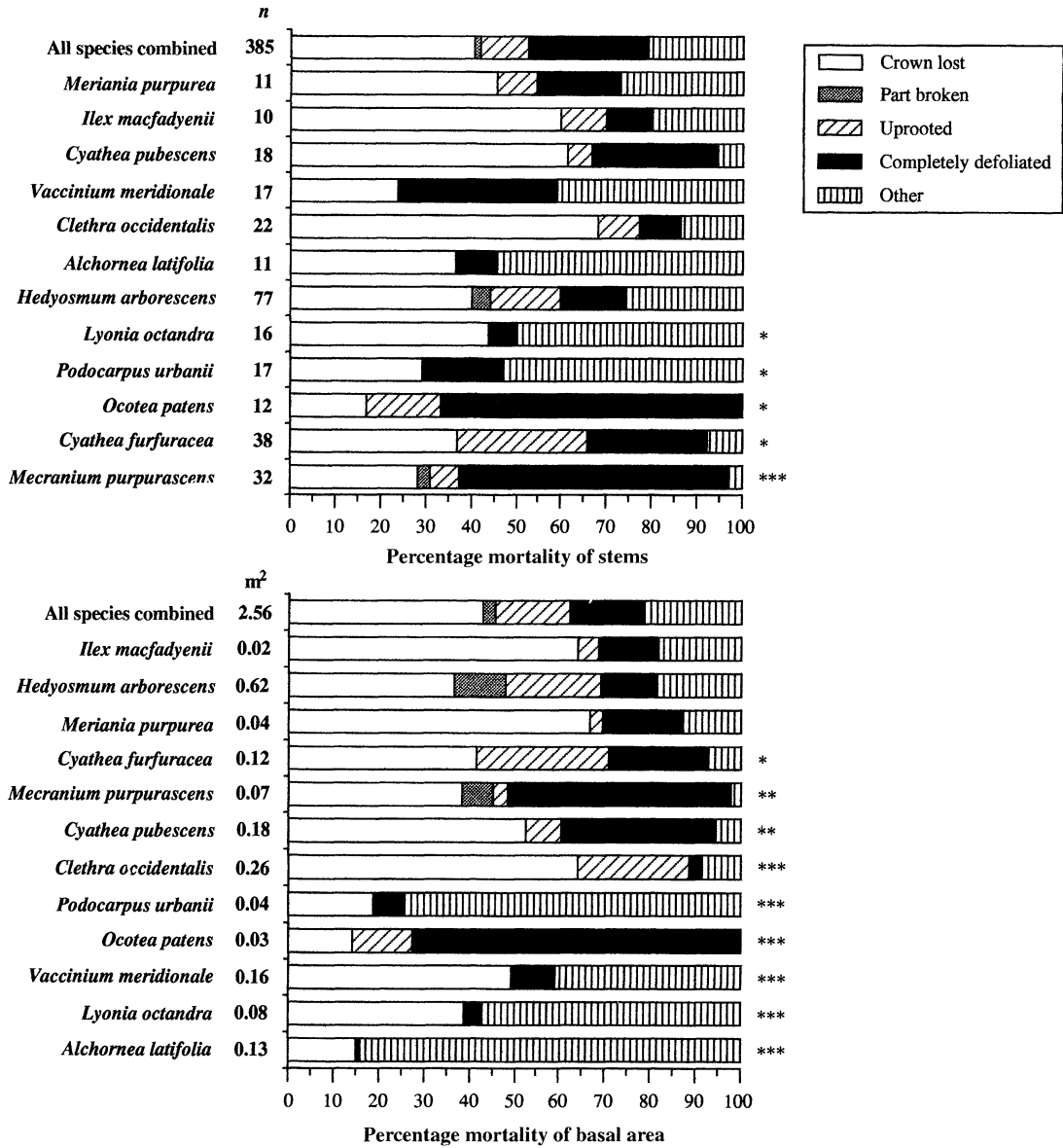
FIG. 2. Causes of mortality among all species combined and among species in which ≥10 stems were killed by Hurricane Gilbert, as percentages of dead stems and dead basal area. Sample sizes (*n*, no. of stems; basal area in m²) are indicated for each species. Causes of mortality shown include: complete loss of crown; partial breakage (i.e., part of the crown was lost but some remained); uprooting ≥40° from perpendicular; complete defoliation; other, including uprooting <40° from perpendicular and stems which 'died on their feet' (Grubb 1977). Significant differences of individual species from all species combined were determined using contingency tables (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$).

stems; these included *Hedyosmum arborescens* and *Viburnum alpinum*. In other species, e.g., *Cinnamomum montanum*, a greater than expected percentage of stems was killed, i.e., the hurricane tended to kill more small than large stems.

Of 4414 individuals sampled, 14.8% had multiple stems, but the range among species was considerable, e.g., no individuals of *Eugenia monticola* or *Pittosporum undulatum* had multiple stems, whereas 48% of *Ocotea patens* individuals, 55% of *Schefflera sciadophyllum* individuals, and 80% of *Viburnum alpinum*

individuals had multiple stems. There was greater mortality among individuals with single stems (7.0% of 3760 individuals) than those with multiple stems (2.8% of 654 individuals) among all species combined ($G = 21.06$, $P < 0.001$). Mortality of individuals was strongly correlated with mortality of stems ($r_{47} = 0.91$, $P < 0.001$).

Causes of mortality.—Complete loss of crowns was the main cause of mortality among all species combined, both as a percentage of stems (40%) and of basal area (43%, Fig. 2). Relatively little mortality resulted

TABLE 1. Diameter at breast height of stems in Jamaican montane rain forests in various categories of damage caused by Hurricane Gilbert. Differences among categories were significant (ANOVA: $F_{4,5329} = 20.80$, $P = 0.0001$). The same superscript letter indicates no significant differences between categories (Scheffé F tests, $P < 0.05$).

Stem category	No. of stems	Stem dbh (cm), mean ± 1 SE
Stems that lost crowns	340	9.3 ± 0.4[ab]
Partially broken stems	226	12.4 ± 0.5[c]
Uprooted stems	280	9.2 ± 0.2[ab]
Completely defoliated stems	1020	9.9 ± 0.2[b]
Comparatively undamaged stems	3468	8.6 ± 0.1[a]

from uprooting. However, some species had significantly different patterns of mortality from the average of all species, e.g., *Mecranium purpurascens* and *Ocotea patens* apparently died mostly as a result of defoliation. Most stems that died from 'other' causes (i.e., not breakage, uprooting, or defoliation) had been partially uprooted (i.e., <40° from perpendicular) or had died 'on their feet' with leaves still present, and, at the time of assessment, had not fallen over or disintegrated.

Among the 340 stems of all species combined that lost crowns during the hurricane, 46.2% were killed. However, mortality among some species that lost crowns was significantly greater than this; crown loss was always fatal among tree ferns, as well as being the main cause of their mortality (Fig. 2), and it was fatal for 78% of the 40 stems of *Hedyosmum arborescens* that lost crowns. By contrast, loss of crown was less often fatal for other species, e.g., *Cyrilla racemiflora* (14% mortality of 42 stems that lost crowns) and *Eugenia virgultosa* (0% mortality of 13 stems); (*G* tests, $P < 0.001$).

Among 280 uprooted stems of all species combined, only 14.6% were killed. As with crown loss, uprooting death was significantly greater (*G* tests, $P < 0.001$) for both *Cyathea furfuracea* (65% mortality, $n = 17$ uprooted stems) and *Hedyosmum arborescens* (67%, $n = 18$). Of 1020 stems completely defoliated during the hurricane, 9.90% were killed. For some species, the proportion of completely defoliated stems that were killed was significantly greater (*G* tests, $P < 0.01$), e.g., *Cyathea furfuracea* (71% mortality, $n = 14$ completely defoliated stems), *Hedyosmum arborescens* (28%, $n = 39$), *Mecranium purpurascens* (45%, $n = 42$), and *Ocotea patens* (67%, $n = 12$). For other species, complete defoliation only rarely resulted in mortality, e.g., *Alchornea latifolia* (0.9%, $n = 110$), *Clethra occidentalis* (1.4%, $n = 142$), and *Eugenia virgultosa* (2%, $n = 59$) (*G* tests, $P < 0.01$).

Size of stems and damage.—Stems that lost crowns, those that were uprooted, and those that were completely defoliated did not differ in size, but stems that were partially broken were larger than other damaged stems (Table 1). Stems that lost crowns or were up-

rooted were not significantly different in size from undamaged stems (Table 1).

Loss of crowns (both fatal and non-fatal) occurred at different heights among species (ANOVA: $F_{14, 272} = 5.55$, $P = 0.0001$, tested among 15 species in which ≥10 stems lost crowns). Tree ferns tended to break off near their bases (height of break was 0.5 ± 0.1 m (mean ± 1 SE) for *Cyathea furfuracea* and 0.5 ± 0.2 m for *Cyathea pubescens*), compared with many trees that broke higher up their stems (e.g., 3.2 ± 0.3 m for *Clethra occidentalis* and 3.3 ± 0.3 m for *Cyrilla racemiflora*, both significantly higher than in tree ferns; Scheffé F tests, $P < 0.05$).

Non-fatal damage.—Among stems that survived the hurricane, the frequency with which a species lost crowns was correlated with its frequency of complete defoliations ($r_{47} = 0.30$, $P < 0.05$: Tables 2A, 2C). By contrast, there was no correlation between crown loss and uprooting ($r_{47} = -0.16$, $P > 0.05$) or between complete defoliation and uprooting ($r_{47} = -0.17$, $P > 0.05$).

Specific characteristics and hurricane damage.—Wood density (Table 3) was not correlated with crown loss, uprooting, or complete defoliation in 19 species ($r_{19} = 0.10$, -0.02, and -0.31, respectively, all $P > 0.05$). Similarly, there were no differences (ANOVA: arcsine square-root transformed data, $F_{3,36} = 0.36$, $P = 0.78$) between the frequencies of defoliation among species with different leaf sizes (from Grubb and Tanner 1976) and there was no correlation ($r_{36} = -0.15$, $P > 0.05$) between lamina thickness of species (from Tanner and Kapos 1982) and defoliation. However, as specific leaf area (from Tanner and Kapos 1982) increased, defoliation decreased ($r_{24} = -0.28$, $P < 0.05$). There were no differences in mean percentage of mortality, crown loss, uprooting, or defoliation among the families Aquifoliaceae, Melastomataceae, Myrtaceae, and Rubiaceae, or the orders Celastrales, Ericales, Myrtales, and Rubiales (ANOVAs, arcsine square-root transformed data, $P > 0.05$).

Comparisons between the prehurricane, hurricane, and post-hurricane periods

Mortality and recruitment.—Among all species combined, mortality in the T/H plots in the hurricane period was nearly double that of the prehurricane period in terms of stems, but was only slightly increased in terms of basal area. For many species, mortality during the hurricane period was not substantially greater, and in a few cases e.g., *Alchornea latifolia* and *Cyrilla racemiflora* was less than in the prehurricane period (Table 4). By contrast, mortality during the hurricane period increased substantially for other species, especially *Hedyosmum arborescens* (Table 4).

In the T/H plots, delayed mortality was apparent (Table 4). In the post-hurricane period, mortality of both stems and basal area among all species combined was more than double that of prehurricane levels (2.59%/yr

TABLE 2. Non-fatal damage to stems of 47 tree species in Jamaican montane forests, assessed 5–23 mo after Hurricane Gilbert, as percentages of stems that (A) lost crowns; (B) were uprooted; and (C) were completely defoliated (*n*, no. stems sampled that survived the hurricane; *n* for defoliated stems excludes stems that lost crowns). Differences between individual

A) Stems that lost crowns			B) Uprooted stems		
Species	*n*	%	Species	*n*	%
Cyrilla racemiflora	218	16.5***	Urbananthus critoniformis	60	22***
Symplocos octopetala	27	11*	Ocotea patens	63	21***
Solanum punctulatum	48	10*	Cinnamomum montanum	20	20**
Cinnamomum montanum	20	10	Psychotria sloanei	22	18**
Mecranium purpurascens	93	10**	Clusia havetioides	84	15***
Meriania purpurea	120	8.3*	Boehmeria caudata	21	14*
Cleyera theaeoides	24	8	Schefflera sciadophyllum	84	13**
Dendropanax pendulus	165	7.3*	Ilex macfadyenii	113	11.5**
Vaccinium meridionale	181	6.1	Chaetocarpus globosus	95	11*
Haenianthus incrassatus	36	6	Ilex harrisii	54	11*
Ilex harrisii	54	6	Pittosporum undulatum†	53	11*
Ilex obcordata	39	5	Mecranium purpurascens	93	10*
Ilex vaccinoides	21	5	Miconia quadrangularis	30	10
Eugenia virgultosa	283	4.6	Calyptranthes rigida	26	8
Clethra occidentalis	424	4.2	Miconia rigida	24	8
Sideroxylon montanum	55	4	Palicourea alpina	42	7
Hedyosmum arborescens	236	3.8	Viburnum alpinum	30	7
All species combined	4949	3.70	Gordonia haematoxylon	36	6
Alchornea latifolia	154	3.2	Haenianthus incrassatus	36	6
Chaetocarpus globosus	95	3	Cyathea furfuracea	108	5.6
Clethra alexandri	32	3	Cyathea pubescens	142	5.6
Miconia quadrangularis	30	3	Ilex vaccinoides	21	5
Urbananthus critoniformis	60	3	All species combined	4949	4.83
Guarea glabra	240	2.9	Psychotria corymbosa	140	4.3
Ilex macfadyenii	113	2.7	Turpinia occidentalis	55	4
Podocarpus urbanii	354	2.3	Guarea glabra	240	3.3
Palicourea alpina	42	2	Cyrilla racemiflora	218	3.2
Turpinia occidentalis	55	2	Lyonia octandra	221	3.2
Psychotria corymbosa	140	1.4	Dendropanax pendulus	165	3.0
Schefflera sciadophyllum	84	1	Eugenia marchiana	31	3
Lyonia octandra	221	0.9*	Ilex obcordata	39	3
Maytenus jamaicensis	153	0.7	Eugenia virgultosa	283	2.8
Boehmeria caudata	21	0	Hedyosmum arborescens	236	2.5
Calyptranthes rigida	26	0	Podocarpus urbanii	354	2.3**
Cinchona officinalis†	39	0	Eugenia monticola	42	2
Clusia havetioides	84	0	Sideroxylon montanum	55	2
Cyathea furfuracea	108	0.0*	Solanum punctulatum	48	2
Cyathea pubescens	142	0.0**	Clethra occidentalis	424	1.9**
Dendropanax arboreus	64	0	Alchornea latifolia	154	1.3*
Eugenia marchiana	31	0	Maytenus jamaicensis	153	1.3*
Eugenia monticola	42	0	Vaccinium meridionale	181	1.1*
Gordonia haematoxylon	36	0	Meriania purpurea	120	0.8*
Miconia rigida	24	0	Cinchona officinalis†	39	0
Myrsine coriacea	22	0	Clethra alexandri	32	0
Ocotea patens	63	0	Cleyera theaeoides	24	0
Pittosporum undulatum†	53	0	Dendropanax arboreus	64	0
Psychotria sloanei	22	0	Myrsine coriacea	22	0
Viburnum alpinum	30	0	Symplocos octopetala	27	0

mortality of stems post-hurricane vs. 1.14%/yr pre-hurricane). Among individual species, this was most evident in the cases of *Clethra occidentalis* and *Hedyosmum arborescens* (Table 4). Delayed mortality mostly affected larger stems in *Hedyosmum arborescens* (Fig. 3).

Recruitment rates during the hurricane and prehurricane periods were more or less equivalent among all species combined (in terms of stems) and for four of the commonest species (Table 4), but increased during the hurricane period for *Alchornea latifolia, Clethra occidentalis, Cyathea pubescens,* and *Hedyosmum arborescens,* and decreased for *Eugenia virgultosa, Po-*

docarpus urbanii, and *Vaccinium meridionale.* There were major increases in recruitment rates (into the ≥3 cm dbh class) during the post-hurricane period compared with the hurricane and prehurricane periods. In terms of numbers of stems, the post-hurricane increase in mortality rate among all species combined was more than offset by a sharp increase in the rate of recruitment (Table 4), although for basal area, not surprisingly, the rate of loss far exceeded the rate of recruitment (Table 4). Although this general pattern was the same for many individual species, e.g., *Alchornea latifolia, Eugenia virgultosa,* and *Hedyosmum arborescens,* one species (*Clethra occidentalis*) showed a pronounced increase

species and all species combined were compared using adjusted G test (* P < 0.05, ** P < 0.01, *** P < 0.001). †, introduced species.

C) Completely defoliated stems		
Species	n	%
Alchornea latifolia	149	73.2***
Solanum puntulatum	43	67***
Turpinia occidentalis	54	57***
Clethra alexandri	31	52***
Ilex harrisii	51	49***
Chaetocarpus globosus	92	45***
Ilex vaccinoides	20	40*
Sideroxylon montanum	53	38**
Lyonia octandra	219	37.0***
Clethra occidentalis	406	34.5***
Palicourea alpina	41	32*
Gordonia haematoxylon	36	31
Ilex obcordata	37	30
Haenianthus incrassatus	34	29
Urbananthus critoniformis	58	28
Mecranium purpurascens	84	27
Myrsine coriacea	22	27
Symplocos octopetala	24	25
Eugenia virgultosa	270	23.7
Cinnamomum montanum	18	22
All species combined	4766	19.28
Miconia quadrangularis	29	17
Ilex macfadyenii	110	15.5
Vaccinium meridionale	170	14.7
Boehmeria caudata	21	14
Eugenia monticola	42	14
Cyrilla racemiflora	182	14.3
Guarea glabra	233	13.3*
Miconia rigida	24	13
Hedyosmum arborescens	227	12.3**
Psychotria corymbosa	138	10.1**
Meriania purpurea	110	10.0*
Viburnum alpinum	30	10
Dendropanax pendulus	153	9.8**
Cleyera theaeoides	22	9
Psychotria sloanei	22	9
Cinchona officinalis†	39	8
Ocotea patens	63	6**
Cyathea furfuracea	108	3.7***
Dendropanax arboreus	64	3***
Cyathea pubescens	142	2.8***
Podocarpus urbanii	346	1.4***
Calyptranthes rigida	26	0**
Clusia havetioides	84	0***
Eugenia marchiana	31	0**
Maytenus jamaicensis	152	0.0***
Pittosporum undulatum†	53	0***
Schefflera sciadophyllum	83	0***

TABLE 3. Wood densities of Jamaican montane rain forest trees (samples from ground level or 1.3 m above the ground). Sample sites: ds, dry slope forest; mor, Mor Ridge forest; mull, Mull Ridge forest; wdm, well-developed Mull Ridge forest (Tanner 1977).

Species	Density (g/mL)	Sample site
Alchornea latifolia	0.51	mor
Brunfelsia jamaicensis	0.86	wdm
Chaetocarpus globosus	0.66	mor
Citharexylum caudatum	0.98	wdm
Clethra occidentalis	0.60	ds
Cyrilla racemiflora	1.02	mor
Dendropanax arboreus	0.55	wdm
Eugenia marchiana	0.91	wdm
Eugenia monticola	1.03	wdm
Eugenia virgultosa	1.04	wdm
Guarea glabra	0.67	wdm
Hedyosmum arborescens	0.64	mull
Ilex macfadyenii	0.73	wdm
Lyonia octandra	0.97	mor
Maytenus jamaicensis	0.87	wdm
Ocotea patens	0.85	wdm
Piper arboreum	0.48	wdm
Podocarpus urbanii	0.62	mull
Psychotria corymbosa	0.53	wdm
Psychotria sloanei	0.65	wdm
Solanum punctulatum	0.62	wdm
Vaccinium meridionale	0.73	mor
Xylosma nitida	0.88	wdm

stems in the smallest size class increased at every inventory (for all species combined).

Clethra occidentalis remained the most abundant species throughout the 17 yr of inventory; its total basal area remained similar (Fig. 4B), although the total number of stems decreased (Fig. 4A). The pattern was similar for *Podocarpus urbanii,* the next most abundant species. *Lyonia octandra* and *Hedyosmum arborescens* reached their lowest abundances immediately after the hurricane in 1989 (Fig. 4A), but large increases in recruitment of these species (Table 4 and Fig. 3) resulted in increased abundances by 1991. By contrast, *Cyathea pubescens* decreased substantially in both abundance and basal area, falling sharply after the hurricane. *Eugenia virgultosa* and *Guarea glabra* were the two species that increased most consistently in abundance throughout the 17-yr period (Fig. 4A). Their increases in abundance during the prehurricane period continued in the hurricane and post-hurricane periods; their increase in basal area over the 17 yr was modest (Fig. 4B).

Growth rates.—Relative basal area increments (RBAIs) decreased significantly from the prehurricane period to the hurricane period, but then increased dramatically in the post-hurricane period (for all species combined and for most of the common species, using all stems that were alive between at least two of the four inventories). Post-hurricane RBAIs for *Alchornea latifolia* were eight times larger than prehurricane RBAIs (Scheffé F-tests, P < 0.05); for *Hedyosmum arborescens,* they were nearly six times larger (Table

in mortality rate but no concurrent increase in recruitment rate. *Chaetocarpus globosus* is notable for having a low level of both mortality and recruitment throughout the 17-yr period.

Comparisons of the size class distributions over the 17-yr period in the T/H plots showed little change in total numbers of the largest stems (>25 cm dbh) for all species combined and for the four most abundant species (Fig. 3); the largest stems apparently were those least affected by the hurricane. The largest decreases concurrent with Hurricane Gilbert occurred in the dbh size classes 5.1–10 and 10.1–15 cm. The number of

TABLE 4. Annual mortality and recruitment of tree species in the T/H plots in three periods over 17 yr (the 1984–1989 period included Hurricane Gilbert) expressed as stem density and basal area.

	Stems (no·ha⁻¹·yr⁻¹)			Basal area (m²·ha⁻¹·yr⁻¹)		
	1974–1984	1984–1989	1989–1991	1974–1984	1984–1989	1989–1991
Mortality						
All species combined	51.9	93.8	152.9	0.432	0.551	1.55
Alchornea latifolia	2.5	1.9	4.3	0.0487	0.0140	0.0452
Chaetocarpus globosus	0.5	0.6	1.4	0.0019	0.0070	0.0112
Clethra occidentalis	3.6	6.2	17.1	0.0166	0.0530	0.222
Cyathea furfuracea	1.1	3.7	5.7	0.0033	0.0174	0.0078
Cyathea pubescens	2.5	1.9	11.4	0.0411	0.0158	0.210
Cyrilla racemiflora	2.7	1.9	7.1	0.0344	0.0409	0.145
Eugenia virgultosa	0.5	1.2	2.9	0.0086	0.0013	0.0086
Hedyosmum arborescens	6.9	25.5	41.4	0.0783	0.190	0.472
Ilex macfadyenii	3.6	5.0	8.6	0.0175	0.0092	0.0424
Lyonia octandra	2.7	8.1	4.3	0.0328	0.0416	0.0691
Podocarpus urbanii	3.0	5.0	7.1	0.0082	0.0070	0.0796
Vaccinium meridionale	3.0	5.0	2.9	0.0219	0.0577	0.0160
Recruitment						
All species combined	72.5	69.6	235.7	0.0098	0.0093	0.0235
Alchornea latifolia	2.5	3.1	11.4	0.0004	0.0003	0.0014
Chaetocarpus globosus	0.8	0.0	1.4	0.0003	0.0000	0.0001
Clethra occidentalis	1.4	1.9	0.0	0.0002	0.0003	0.0000
Cyathea furfuracea	1.1	1.2	2.9	0.0004	0.0003	0.0018
Cyathea pubescens	0.5	1.9	0.0	0.0003	0.0021	0.0000
Cyrilla racemiflora	1.1	1.2	5.7	0.0002	0.0008	0.0005
Eugenia virgultosa	4.7	1.2	21.4	0.0006	0.0001	0.0017
Hedyosmum arborescens	9.6	13.0	54.3	0.0013	0.0012	0.0050
Ilex macfadyenii	2.7	2.5	5.7	0.0003	0.0002	0.0005
Lyonia octandra	3.0	2.5	7.1	0.0004	0.0002	0.0005
Podocarpus urbanii	5.2	0.6	4.3	0.0006	0.0001	0.0003
Vaccinium meridionale	3.0	1.2	4.3	0.0003	0.0001	0.0003

5). There were considerable differences in RBAI among the eight species in each inventory period (ANOVAs: $P = 0.0001$; Table 5), with *Hedyosmum arborescens* having consistently greater RBAI than most other species.

The dramatically higher RBAIs in the post-hurricane period are due both to increased growth of stems present before the hurricane and to smaller stems recruited in the 1989 inventory. For stems present in the earliest (1974) inventory and alive in the most recent (1991) inventory, post-hurricane RBAIs were more than double prehurricane RBAIs (Scheffé F tests, $P < 0.05$). Increases in RBAIs were even greater when the entire standing stock was included (i.e., including new recruits; Table 5).

DISCUSSION

Initial effects of the hurricane

Initial mortality caused by Hurricane Gilbert in Jamaican montane forests was low, and comparable with mortality caused by hurricanes in other Caribbean island forests (e.g., 7.2% mortality of stems in Jamaican forests from 1984 to 1989, cf. 7% in Puerto Rican forests (Walker 1991) and 2% in Dominican forests (Lugo et al. 1983), both of which were instantaneous measures). Many studies of initial hurricane effects (summarized in Brokaw and Walker 1991) indicate that, although initial mortality during hurricanes is

higher than prehurricane levels, the increase is not very great, as was the case in this study (Table 4).

Overall levels of mortality, however, belied the variation among species (Fig. 1). Different levels of mortality among species are important because they have immediate effects on forest composition. For example, up to 25% of the stems, basal area, and individuals of three common species (*Cyathea furfuracea*, *Hedyosmum arborescens*, and *Mecranium purpurascens*) were killed. Other studies have shown a considerable range in mortality among species following disturbance by wind (Dittus 1985, Glitzenstein and Harcombe 1988, Walker 1991, Zimmerman et al. 1994). Several studies have shown that some forest communities are more susceptible to wind damage than others. There is often more extensive mortality in forests dominated by gymnosperms than in those dominated by angiosperms (e.g., Foster 1988a, Boucher et al. 1990), and wind damage to gymnosperms is often fatal (e.g., Thompson 1983, Peterson and Pickett 1991). However, in Jamaican forests the common gymnosperm *Podocarpus urbanii* had low levels of mortality (Fig. 1) and damage (Table 2).

Most Jamaican montane forest tree species (44 of 47 common species) had multiple-stemmed individuals. Some level of stem mortality may have been sustainable for some species (e.g., *Ocotea patens* and *Schefflera sciadophyllum*) in which individual mortality was
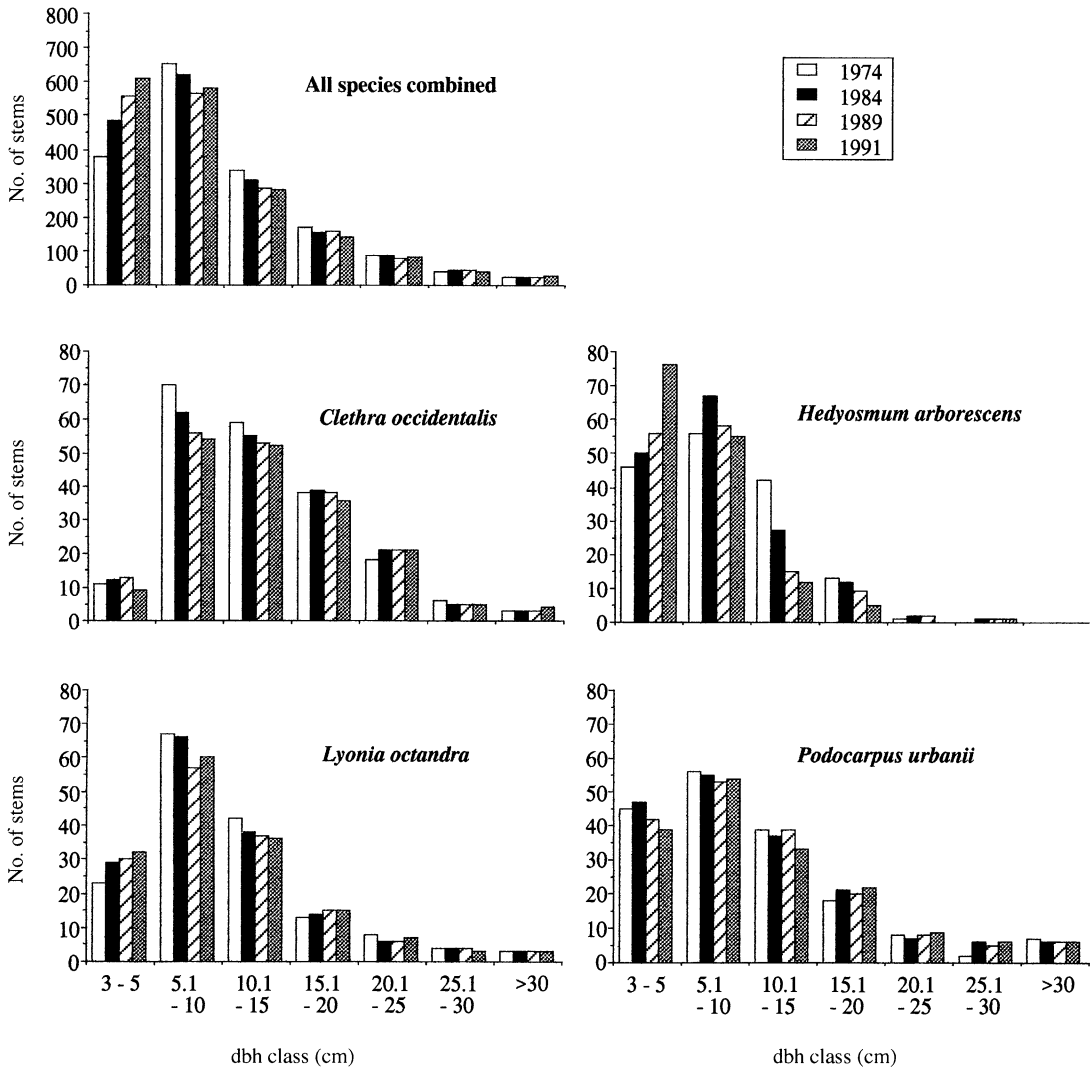
FIG. 3.   Diameter size class distribution of all tree species combined and four species with ≥100 stems in T/H plots at four inventories over 17 yr in the Blue Mountains of Jamaica.

less than that of stems (Fig. 1), but the pattern was not consistent; individual mortality exceeded that of stems for other species (e.g., *Cleyera theaeoides*). In Jamaican forest, factors other than, or in addition to, hurricanes probably influence development of multiple-stemmed individuals, which are a feature of tropical montane forests that are not affected by hurricanes. In some Venezuelan montane forests, for example, 9% of individuals had multiple stems (Kelly et al. 1994), compared with 15% in Jamaican forests.

In Puerto Rican forests, high survivorship and low damage in the common tree *Dacryodes excelsa* was attributed by Basnet et al. (1993) to anchoring by root grafting between individuals. This may also explain the low mortality of some Jamaican montane forest trees, e.g., *Haenianthus incrassatus,* which forms intraspecific root grafts; it may also be true for *Cyrilla racemiflora,* which forms root grafts in other sites (Thomas

1960). Being more firmly anchored by root grafts may mean less flexibility among stems (cf. King 1986) and, consequently, increased likelihood of breakage; but this may not result in increased mortality. For example, crown loss in *Cyrilla racemiflora,* while frequent, was seldom fatal; most mortality in this species was caused by uprooting. Putz and Sharitz (1991) attributed the low frequency of uprooting of *Taxodium distichum* in South Carolina forests during Hurricane Hugo to this species' relatively deep rooting. In Western Samoa, widespread uprooting of trees during a cyclone was attributed to shallow root systems of trees in shallow soils developed over basalt (Wood 1970). Using experimental techniques, Fraser (1962) showed that small increases in rooting depth considerably increased resistance to uprooting. Putz et al. (1983) believed that this would predict a higher proportion of uprooted trees on steeper terrain. However, despite shallow soil on
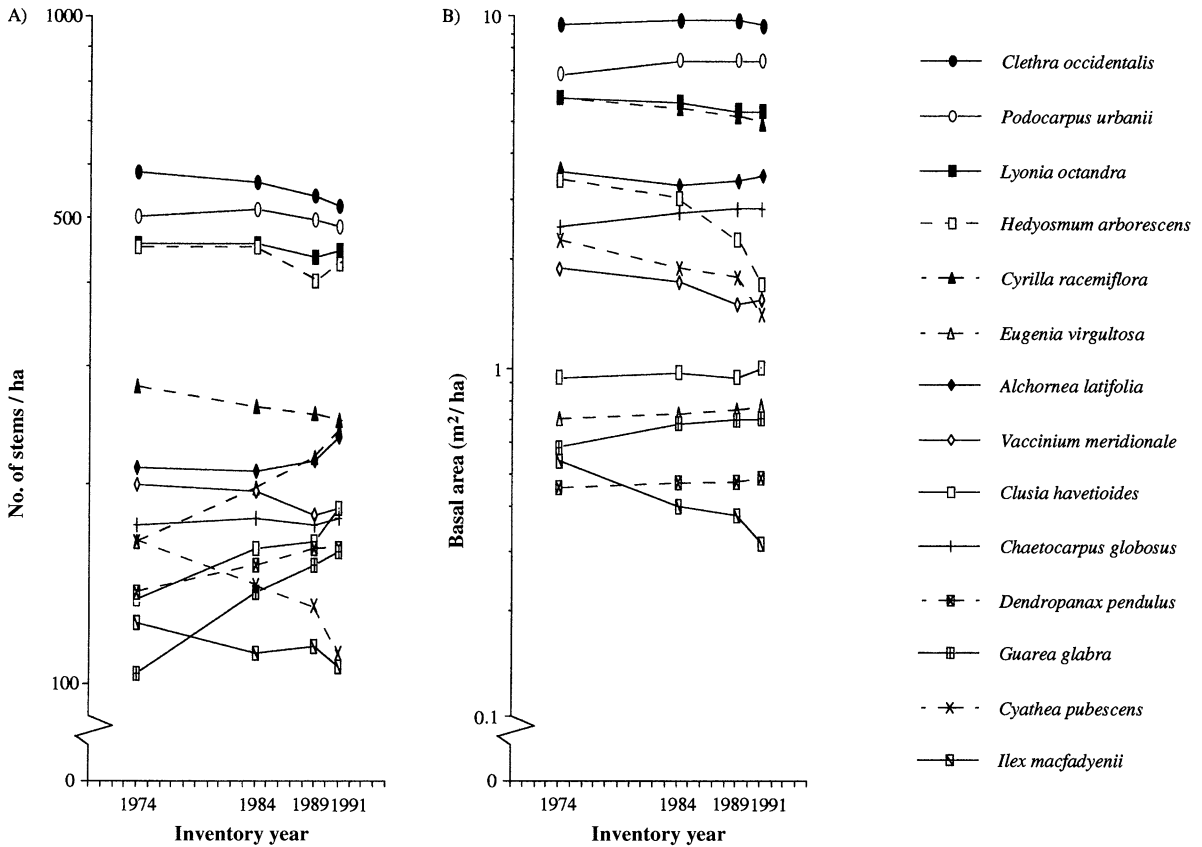
FIG. 4. Changes in (A) abundance (stem density) and (B) basal area of trees in T/H plots at four inventories over 17 yr. Data are shown on a logarithmic scale for 14 species with ≥100 stems/ha throughout the period.

slopes in the Blue Mountains (Grubb and Tanner 1976), uprooting was relatively infrequent in Jamaican montane forest compared with other studies (Brokaw and Walker 1991: Table 1). There are no data on root architecture and root depth for trees in these forests. Most of the uprooting of *Clusia havetioides* and *Chaetocarpus globosus* (Table 2) occurred in forest on deep acid mor humus where these species are common (Grubb and Tanner 1976, Tanner 1977) and where the semi-

prostrate habit of many trees may have resulted from previous wind storms. However, the deep A horizons in these sites were only rarely disrupted by trees being blown over during the hurricane (cf. Sugden et al. 1985).

In Jamaican montane forests, there was no difference in the size of stems that lost crowns, those that were uprooted, and those that were undamaged (see also Bellingham 1991, Bellingham et al. 1992). However, most

TABLE 5. Relative basal area increment, RBAI (in $m^2 \cdot m^{-2} \cdot yr^{-1}$; mean ± 1 SE) of all species combined and nine individual species in the T/H plots in three inventory periods over 17 yr. The 1984–1989 period included Hurricane Gilbert. Data are presented for the standing stock, including stems that died or were recruited between 1974 and 1991. Species are ranked from greatest to least RBAI in the most recent 1989–1991 (post-hurricane) inventory period. Significant differences detected by ANOVA among RBAIs among inventory periods are shown for each species; the same superscript letters indicate no significant differences between inventory periods (Scheffé F tests, $P < 0.05$).

	1974–1984	1984–1989	1989–1991	P (ANOVA)
Hedyosmum arborescens	0.022 ± 0.002[a]	0.015 ± 0.003[a]	0.131 ± 0.010[b]	0.0001
Alchornea latifolia	0.011 ± 0.003[a]	0.010 ± 0.003[a]	0.088 ± 0.017[b]	0.0001
All species combined	0.008 ± 0.000[a]	0.004 ± 0.001[b]	0.040 ± 0.002[c]	0.0001
Eugenia virgultosa	0.012 ± 0.002[a]	−0.001 ± 0.002[b]	0.036 ± 0.005[c]	0.0001
Vaccinium meridionale	0.008 ± 0.001[a]	0.003 ± 0.000[a]	0.033 ± 0.001[b]	0.0001
Podocarpus urbanii	0.009 ± 0.000[a]	0.003 ± 0.000[b]	0.026 ± 0.001[c]	0.0001
Clethra occidentalis	0.005 ± 0.001[a]	0.003 ± 0.001[a]	0.021 ± 0.003[b]	0.0001
Cyrilla racemiflora	0.003 ± 0.001[a]	0.001 ± 0.001[a]	0.013 ± 0.004[b]	0.0005
Lyonia octandra	0.003 ± 0.001[a]	0.001 ± 0.002[a]	0.008 ± 0.002[b]	0.0027
Chaetocarpus globosus	0.007 ± 0.002	0.010 ± 0.002	0.008 ± 0.003	0.7133

other studies of wind damage to trees, including some on the effects of hurricanes, have shown that stems with large diameters were more likely to be broken or uprooted, and those of smaller diameter were least likely to be damaged (e.g., Webb 1989, Gresham et al. 1991). Furthermore, most studies have shown that stems of smaller diameter tend to break and those of larger diameter tend to be uprooted (e.g., Lugo et al. 1983, Putz et al. 1983, Peterson and Pickett 1991, Walker et al. 1992). Brokaw and Walker (1991) attributed the lack of difference in relative sizes of broken, uprooted, and undamaged stems in Jamaican montane forests to the small range of diameters relative to other forests examined after hurricanes. However, trees of larger diameter in Jamaican forests tended to be defoliated more frequently than those of smaller diameter, as was the case in Puerto Rican forests (Walker 1991).

The lack of correlation between wood density and crown loss, uprooting, or complete defoliation in Jamaica was at first surprising, but there is a parallel from Puerto Rico, where trees with denser wood were less damaged at only one of two sites (Walker et al. 1992). Other studies have suggested that species with greater wood density are more resistant to strong winds (Lawton 1984) and hurricanes (Yih et al. 1991). Crown loss has been shown, in other studies, to be least frequent among species with dense wood (Putz et al. 1983, Zimmerman et al. 1994). In Panamanian lowland forests, species with dense wood were uprooted most frequently (Putz et al. 1983).

Tree architecture may be an important determinant of interspecific differences in mortality and damage during hurricanes (Frangi and Lugo 1991). The introduced tree *Pittosporum undulatum* has much deeper crowns than native trees (T. C. R. Goodland, *personal communication*), and its greater crown to stem ratio may be a reason for its greater uprooting (Table 2). Tree ferns that survived the hurricane generally did so by shedding all their leaves, in the way that palms did in Puerto Rican forests (Frangi and Lugo 1991). Greatest wind force may often act on the upper parts of crowns (Petty and Swain 1985), rendering taller species in mixed stands more susceptible to damage (e.g., Foster 1988a, Webb 1989). However, in Jamaican forests, some of the species with greatest mortality seldom reach the canopy. To some extent, greater mortality in these species may have resulted from debris falling from the canopy, e.g., in *Cyathea furfuracea,* but others such as *Mecranium purpurascens* died mostly as a result of defoliation (Fig. 2).

High levels of crown loss in Jamaican forests did not necessarily result in high mortality (Fig. 2, Table 2). This was similar to the situation in lowland rain forests of Panama, where the greatest frequency of crown loss was among weak-wooded, fast-growing species that sprouted readily to regain crown volume (Putz et al. 1983, Putz and Brokaw 1989). In Jamaican montane forests, most trees produced sprouts; stems

that lost crowns sprouted more frequently than intact stems (Bellingham et al. 1994), so their long-term survival may be high. Some of the species with a high incidence of non-fatal crown loss (e.g., *Solanum punctulatum,* Table 2) are weak-wooded, apparently fast-growing species that sprouted readily (Bellingham et al. 1994). Other species that had high frequencies of non-fatal crown loss (e.g., *Cyrilla racemiflora*) also sprouted readily but were slow-growing (Table 4).

Lack of correlation between leaf size or thickness and the frequency with which species were defoliated suggests that the hurricane was indiscriminate as a cause of defoliation. Correlation of lower damage with higher specific leaf area (SLA) suggests that tougher leaves were more brittle and that softer leaves bent with the wind. Some species with high foliar N (e.g., *Solanum punctulatum,* Tanner 1977) were among those most frequently defoliated, but these species were more frequent in sites where nutrient supply is less likely to be limiting (Tanner 1977, 1985), so the relative cost of producing new leaves may be low.

Post-hurricane effects

In the 2–3 yr after the hurricane, mortality rates in Jamaican montane forests were more than double the prehurricane levels. Delayed mortality was much more evident in some species than others. Mortality rates increased substantially between the hurricane and post-hurricane periods in the case of *Hedyosmum arborescens,* but for other species such as *Lyonia octandra,* mortality in the post-hurricane period was less than in the hurricane period (Table 4). Delayed mortality after hurricanes has been observed in other ecosystems (Knowlton et al. 1981).

One of the most likely reasons for delayed mortality was the slow onset of pathogen attack through wounds. Among stems that survived crown loss in a lowland forest in Panama, 60% died during the subsequent 7 yr, which Putz and Brokaw (1989) attributed to pathogen attack. A possible reason for delayed mortality in Jamaica was the effect, on newly produced leaves, of a dry season in 1990 and a prolonged dry season in 1991. Low soil moisture under the forest canopy during post-hurricane droughts has been recorded in Jamaican (Dalling and Tanner 1995) and Puerto Rican forests (Parotta and Lodge 1991). The effect of the droughts could be seen in tree ferns, where many leaves produced soon after the hurricane began to wilt by May 1989. The dry seasons of 1990 and 1991 were much drier than that of 1989. Low soil moisture may also have caused stress to angiosperms that did not have sclerophyllous leaves (Tanner and Kapos 1982), especially among stems that had produced many new leaves following extensive defoliation during the hurricane. This may have been a reason for delayed mortality in these species (e.g., *Turpinia occidentalis,* Table 7).

Increased growth of stems remaining after stands

PLATE 1. Forest interior north of the Grand Ridge of the Blue Mountain. Left: May 1989 (8 mo after the hurricane). Canopy dominated by recently refoliated *Cyathea pubescens* and forest floor covered by woody debris. Right: May 1990 (20 mo after the hurricane). Canopy and subcanopy refoliation well advanced, and substantial growth of seedlings and saplings that germinated after the hurricane (dominated by *Palicourea alpina*).

have been thinned is well-known in silviculture, and increased growth rates in surviving stems have been demonstrated in other forests after hurricanes. Following hurricane damage to a forest in New Hampshire, diameter increment among four common tree species more than doubled throughout the subsequent 49-yr period (Merrens and Peart 1992). In Jamaican montane forests, most species had significantly higher RBAIs in the post-hurricane period, but there was a great range of responses. Some species (e.g., *Chaetocarpus globosus*) showed no change in RBAI.

Tree species: resistant, susceptible, resilient, and usurper

Scores of damages (based on mortality and crown loss) and responsiveness (based on recruitment, growth rates, and sprouting) for 20 common species allowed us to define four types of response to the hurricane: resistant species, susceptible species, resilient species, and usurper species (Fig. 5). Clearly, the axes are continuous and it is the relative positions of the species that are most important. There are no clear breaks in the damage scores for the 20 species; the response scores were also a continuum except for two outliers, *Cyathea pubescens* (low response) and *Hedyosmum arborescens* (high response). The exact positions of the species also depend on which criteria are chosen to calculate the damage and response.

Resistant species (those with low damage scores and low response scores) include 11 of the 20 commonest species. Susceptible species (those with high damage and low response) include one highly susceptible species, *Cyathea pubescens*, and four others that have

moderate to high damage scores and average recovery scores, making them intermediate between susceptible and resilient. *Hedyosmum arborescens* is the only resilient species (with high damage and high response), separate from all other species in the analysis (Fig. 5). The usurpers (with low damage and high response) include *Alchornea latifolia* and *Eugenia virgultosa*, which were little-affected during the hurricane and grew more after the hurricane, presumably because of damage caused to neighboring stems of other species. Another species we classify as a usurper is the introduced invasive tree *Pittosporum undulatum*, which had low levels of damage (Fig. 1 and Table 2) and high responsiveness (0.213 ± 0.020 $m^2 \cdot m^{-2} \cdot yr^{-1}$ RBAI in T/H plots 1991–1994, $n = 6$). It was also readily recruited as seedlings into experimental gaps (Healey 1990). *Ilex macfadyenii*, a species that, by our criteria, is a usurper (Fig. 5), was more damaged and less responsive than other usurpers and is near the boundary between usurper and resilient species.

It is likely that usurpers will increase their abundance in the forest in the next few decades; conversely, susceptible species will decrease in abundance. Both resistant and resilient species may maintain their relative abundances, but by different means (cf. Boucher et al. 1994). In Fig. 5, a diagonal line drawn from the origin would separate those species likely to increase in abundance (above the line) and those likely to decrease (below the line); those near the line (mostly resistant and resilient species) will not change much. We have not included seedling recruitment in this analysis and it is possible that future forest composition will reflect increased seedling recruitment. However, the crowns

PLATE 2. Root pit formed during the hurricane by the uprooting of a large *Juniperus lucayana* Britton in the Wet Slope site of Tanner (1977). Top: December 1988 (3 mo after the hurricane). No seedling regeneration apparent. A 0.5-m scale is present in the foreground. Bottom: January 1992 (40 mo after the hurricane). Regeneration of *Bocconia frutescens* (left) and *Brunellia comocladiifolia* (right), which germinated after the hurricane.

of canopy trees present before the hurricane have largely refoliated, and most of the cohort of seedlings recruited after the hurricane are now strongly shaded and will not reach the canopy in the next few decades.

In a study of Nicaraguan rain forest recovery after a hurricane, Boucher et al. (1994) described *Qualea paraensis* as a resistant species because its adult trees all survived the hurricane, and *Vochysia ferruginea* as resilient because all its adults were killed but its saplings and seedlings had high survivorship and growth. It is likely that our classification of species into resistant, susceptible, resilient, and usurper will continue to be generally useful.

The reactions of individual trees to the hurricane may be related to the sites where seedlings of their species are found long after disturbance by hurricanes. Most species with seedlings that are usually found under closed canopies were resistant. Also, three of the four species known to regenerate on landslides were resis-

tant. Most resistant species (both closed-canopy and landslide regenerators) are relatively slow-growing, although most increased their growth and recruitment after the hurricane (Table 7). The four species known to regenerate on landslides (Table 6; Dalling 1994) are perhaps incapable of rapid growth and would not be expected to have high responsiveness. Their leaf N concentrations are low (0.99% dry mass, $n = 4$ species, Tanner 1977) compared with overall means for the "Mull Ridge" (1.61%) and "Wet Slope" forests (1.27%) of Jamaica.

Species with seedlings that regenerate most frequently in gaps include resilient, usurper, and susceptible species; most had at least average responsiveness (Fig. 5). Potentially, most of these species are relatively fast growers (for this forest) and had high post-hurricane absolute BA increments (Table 7). Some also had high levels of recruitment from an advance regeneration of saplings (*Hedyosmum arborescens*) or sprouts (*Alchornea latifolia*). *Cyathea pubescens* was a susceptible species with low responsiveness, and is thus likely to have a short-term decrease in population.

In this forest, understory seedlings tend to persist when gaps are created (Healey 1990); thus, seedlings of the usurper species *Eugenia virgultosa* had the highest relative abundance under closed canopy before gap creation, and remained the most abundant and fastest growing species after gap creation (Healey 1990). Several other studies have shown that existing stems, recruited under closed canopy, benefit more than gap-demanding species by formation of canopy gaps (at least in the first few years after gap formation). Both seedlings (e.g., Uhl et al. 1988, Brown and Whitmore 1992) and saplings (e.g., Webb 1989) benefit from the gaps. Adult trees of *Eugenia virgultosa* and the resistant species *Guarea glabra* also increased in abundance in Jamaican montane forests between 1974 and 1984, a period not substantially affected by hurricanes; this increase continued in the hurricane and post-hurricane periods (Fig. 4). In other places, it has also been shown or inferred that "shade tolerant" species increased growth after hurricanes. In New Hampshire, USA, growth rates of *Fagus grandifolia*, a species considered shade tolerant, increased in those stands more, rather than less, affected by a hurricane (Merrens and Peart 1992). In Puerto Rico, the palm *Prestoea montana* (considered late successional; Walker 1991) was little damaged and suffered generally low mortality during Hurricane Hugo (Frangi and Lugo 1991, Walker 1991). Before Hurricane Hugo, the age structure of a population of this palm was attributed to growth of an advance regeneration following a 1932 hurricane (Lugo and Rivera Batlle 1987). In lowland Nicaraguan rain forests, Yih et al. (1991) described regrowth of "primary forest species" after a hurricane as "direct regeneration." In Puerto Rican forests, "primary forest species" were less damaged than "pioneer" species (Zimmerman et al. 1994).

TABLE 6. Responses of stems of 20 common species (≥3 cm dbh) in Jamaican montane forests to the effects of Hurricane Gilbert. Initial hurricane effects were assessed among 5334 stems, sampling 1.10 ha in T/H, MRT, and PJB plots. Percentages of surviving stems with sprouts were determined from this sample by Bellingham et al. (1994). The most common sites of seedling regeneration (based on relative abundance) for these species are: CC, seedlings under closed canopy; CC/G, seedlings with approximately equal relative abundances under closed canopy and gaps; G, seedlings under canopy gaps; and L, seedlings on landslides. Regeneration sites were determined by 1, Sugden et al. (1985); 2, Healey (1990) and 3, Dalling (1994).

| | | | Initial effects | | Regeneration | | |
| | | | % stem mortality | % live stems that lost crowns | % stems with sprouts | Seedling sites | |
Responses to hurricanes	Species	Species code	% stem mortality	% live stems that lost crowns	% stems with sprouts	Seedling sites	Sources
Resistant	Chaetocarpus globosus	CG	0.0	3.2	85.3	Unknown	1, 2
	Clethra occidentalis	CO	4.9	4.2	46.9	G, L	1, 2, 3
	Clusia havetioides	CH	4.5	0.0	0.0	CC	1
	Dendropanax pendulus	DP	1.2	7.3	43.6	Unknown	2
	Guarea glabra	GG	1.6	2.9	67.5	CC	2
	Lyonia octandra	LO	6.8	0.9	89.6	L	1, 3
	Maytenus jamaicensis	MJ	0.7	0.7	8.5	CC	2
	Podocarpus urbanii	PU	4.6	2.3	91.5	Unknown	2
	Psychotria corymbosa	PC	6.0	1.4	54.3	CC/G	2
	Sideroxylon montanum	SM	0.0	3.6	83.6	CC/G	2
	Vaccinium meridionale	VM	8.6	6.1	79.0	L	3
Usurpers	Alchornea latifolia	AL	6.7	3.2	76.6	G	1, 2
	Eugenia virgultosa	EV	0.7	4.6	82.7	CC	2
	Ilex macfadyenii	IM	8.1	2.7	78.8	G	2
Resilient	Hedyosmum arborescens	HA	24.4	3.8	68.8	G	1, 2
Susceptible	Cyathea pubescens	CP	11.8	0.0	0.0	G	2
	Cyrilla racemiflora	CR	4.0	16.5	93.1	L	1, 3
	Mecranium purpurascens	MP	25.6	9.7	89.2	Unknown	1, 2
	Meriania purpurea	ME	8.4	8.3	64.2	Unknown	2
	Turpinia occidentalis	TO	5.2	1.8	74.5	CC/G	2

TABLE 7. Comparisons of Jamaican montane forest trees in pre-hurricane (PRE, 1974–1984) and post-hurricane (POST, 1989–1991) periods. Data are derived from a 0.35 ha subsample of T/H plots. RBAI, relative basal area increment, ABAI, absolute basal area increment.

| | | Mortality (% stems/yr) | | Recruitment (% stems/yr) | | Mean RBAI ($m^2 \cdot m^{-2} \cdot yr^{-1}$) | | Mean ABAI ($cm^2$/yr) | |
Responses to hurricanes	Species	PRE	POST	PRE	POST	PRE	POST	PRE	POST
Resistant	Chaetocarpus globosus	0.3	0.8	0.5	0.8	0.007	0.008	1.2	0.6
	Clethra occidentalis	0.6	3.2	0.2	0.0	0.005	0.021	0.7	1.6
	Clusia havetioides	0.2	3.7	1.7	7.6	0.010	0.022	0.0	0.6
	Dendropanax pendulus	0.6	1.0	1.8	1.0	0.000	0.023	0.0	0.6
	Guarea glabra	0.3	1.0	2.9	4.5	0.017	0.042	0.8	1.2
	Lyonia octandra	0.6	1.0	0.6	1.6	0.003	0.008	0.4	0.0
	Maytenus jamaicensis	0.0	0.0	4.1	6.3	0.011	0.051	0.3	0.8
	Podocarpus urbanii	0.6	1.5	1.0	0.9	0.009	0.026	1.3	1.9
	Psychotria corymbosa	3.8	3.3	5.5	6.7	0.006	0.061	0.7	0.7
	Sideroxylon montanum	1.2	0.0	0.8	2.0	0.008	0.031	0.7	1.0
	Vaccinium meridionale	1.6	1.6	1.6	2.4	0.008	0.033	0.1	1.4
Usurpers	Alchornea latifolia	1.2	2.0	1.2	5.0	0.011	0.088	0.8	4.5
	Eugenia virgultosa	0.3	1.4	2.3	9.0	0.012	0.036	0.4	0.8
	Ilex macfadyenii	2.9	8.3	2.4	5.9	0.007	0.043	0.1	0.7
Resilient	Hedyosmum arborescens	1.6	10.4	2.1	12.8	0.022	0.131	1.1	3.1
Susceptible	Cyathea pubescens	1.6	8.7	0.4	0.0	0.001	0.010	0.1	0.5
	Cyrilla racemiflora	1.0	2.9	0.4	2.4	0.003	0.013	0.1	0.9
	Mecranium purpurascens	4.4	5.0	3.8	5.0	0.011	0.032	0.4	0.4
	Meriania purpurea	1.3	2.5	0.9	3.7	0.012	0.051	0.4	1.7
	Turpinia occidentalis	0.0	13.6	1.7	0.0	0.003	0.043	0.4	1.9

FIG. 5. Damage and responsiveness of the 20 most common species in the enumerated plots in montane rain forest in Jamaica (see *Methods* for details of score calculations). AL, *Alchornea latifolia*; CG, *Chaetocarpus globosus*; CH, *Clusia havetioides*; CO, *Clethra occidentalis*; CP, *Cyathea pubescens*; CR, *Cyrilla racemiflora*; DP, *Dendropanax pendulus*; EV, *Eugenia virgultosa*; GG, *Guarea glabra*; HA, *Hedyosmum arborescens*; IM, *Ilex macfadyenii*; LO, *Lyonia octandra*; ME, *Meriania purpurea*; MJ, *Maytenus jamaicensis*; MP, *Mecranium purpurascens*; PC, *Psychotria corymbosa*; PU, *Podocarpus urbanii*; SM, *Sideroxylon montanum*; TO, *Turpinia occidentalis*; VM, *Vaccinium meridionale*.
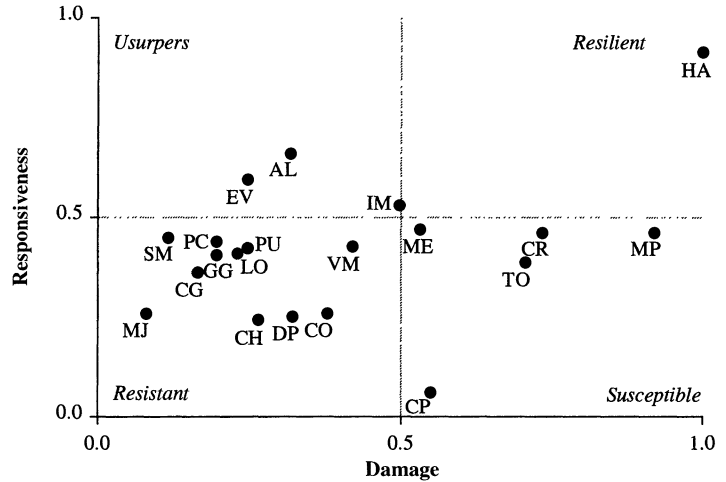
Pioneer species (sensu Swaine and Whitmore 1988) can also increase after hurricanes. In Jamaican montane forests, for example, the pioneer *Brunellia comocladiifolia* germinated and grew after Hurricane Gilbert (Bellingham 1993). In other parts of the tropics, long-term studies of hurricane effects on forests have also shown that pioneer species become first more abundant and then, after a few decades, less abundant in the absence of further disturbance (Whitmore 1974, Crow 1980, Weaver 1986a, 1989). Conditions created by hurricanes may also enable recruitment of species that regenerate rarely by seed. In Puerto Rican montane forests, Weaver (1986b) believed that the size structure of a population of *Cyrilla racemiflora* was due to recruitment of stems following hurricanes in 1867 and 1932. By contrast, seedlings of *Cyrilla racemiflora* were not recorded under canopies defoliated by Hurricane Gilbert in Jamaica (Dalling 1992).

The disturbance regime of hurricanes

We have described the damage and response of species following a single disturbance event. Grubb and Hopkins (1986) stressed that community stability is influenced by the disturbance regime, which they suggested had four basic dimensions: intensity, frequency, extent, and timing of disturbances.

The intensity of hurricanes as disturbance events is probably most important for forests. The intensity of a hurricane is dictated by its minimum sea level pressure, speed of movement, and the distance of its eye from the forests (Boose et al. 1994). Oliver and Stephens (1977) examined the history of a temperate forest in Massachusetts over 149 yr, a period during which the forest was disturbed by people and by hurricanes. They found that only the most intense disturbances resulted in the recruitment of a new cohort of canopy species. It is possible that global warming will affect the frequency and intensity of cyclones. Using a Carnot cycle model, Emanuel (1987) projected that a doubling of the present atmospheric CO_2 concentration could

result in a 40–50% increase in cyclone intensity. Using another model, Ryan et al. (1992) projected that a doubling of the present atmospheric CO_2 concentration could double the likely rate of cyclone formation. If either or both of these predictions are borne out, the change in disturbance regime could have important effects on Jamaican forests.

Hurricane frequency in the Caribbean is variable (Reading 1990). Since 1871, the average frequency of hurricanes with eyes <60 km from eastern Jamaica has been once every 9 yr (Neumann et al. 1978, Lawrence and Gross 1989). There have been prolonged periods (e.g., 1951–1980) when no hurricanes hit Jamaica, but there were four hurricanes between 1874 and 1886, and five between 1903 and 1916 (Neumann et al. 1978). There are records of even shorter intervals between hurricanes, e.g., 40 d between successive hurricanes in Mauritius in 1960 (Sauer 1962). The generally low levels of mortality and damage recorded after Hurricane Gilbert might have been increased had there been another hurricane in quick succession. There is evidence that trees weakened during strong winds are more susceptible to damage in subsequent strong winds (Coutts 1983).

In extent, Hurricane Gilbert affected all of Jamaica to some degree, but caused patchy damage to Jamaican montane forests (Bellingham et al. 1992). In general, hurricanes affect swathes up to 120 km wide, with sites closer to the eye more affected. Hurricane Allen, which was intense (Woodley et al. 1981) passed 60 km from the forests of the Blue Mountains and caused much less severe damage than Hurricane Gilbert, which passed within 10–15 km (cf. Thompson 1983, Bellingham et al. 1992). Forests in New Hampshire suffered much more extensive hurricane damage than those in Jamaica, probably a result of the selection pressure of more frequent hurricanes in Jamaica; New Hampshire had only two severe hurricanes in 484 yr (Bormann and Likens 1979). The New Hampshire forests were resilient because the relative abundances of species

were approaching prehurricane conditions 46 yr after a hurricane (Foster 1988a); the Jamaican forests were relatively resistant.

The timing of hurricanes relative to the timing of seed production might affect seedling recruitment after a hurricane. Among a range of common species in Jamaican montane forests, there is a peak of production of propagules in July and August (Tanner 1982), immediately before the period of maximum likelihood of hurricanes (Naughton 1982). When hurricanes strike as early as June (Naughton 1982), species that produced seed earlier in the year may be at a competitive advantage. However, we do not know the relative importance of seeds produced before and after hurricanes, nor the relative importance of regeneration from seed vs. reformation of the canopy by sprouting of damaged canopy trees.

Are Jamaican montane forests stable when disturbed by hurricanes?

Despite the fact that Hurricane Gilbert was the most intense hurricane recorded in the Caribbean in this century, and despite the fact that the eye passed within 10–15 km of the study area (Lawrence and Gross 1989), we believe that only one of 20 common species was strongly susceptible to its effects (Fig. 5). Thus, in the short term, Jamaican montane forests could be considered stable. Walker (1991) and Yih et al. (1991) believed that there would be little change in the relative abundance of species after hurricanes affected Puerto Rican and Nicaraguan forests, respectively. However, Connell and Sousa (1983) warned that persistence of long-lived individuals did not give evidence of community stability. They believed that long-term studies of forests affected by disturbance (e.g., Oliver and Stephens 1977) showed no evidence of stable states.

Harper (1977) distinguished a "disaster" from a "catastrophe" using the criterion that disasters affect successive generations of species and thus have selective consequences, whereas catastrophes occur too rarely to have selective consequences. On average, hurricanes hit Jamaica once every 15 yr. Notwithstanding that return times of hurricanes to particular areas of forest may be less frequent (Bellingham 1991), hurricanes are disasters because they will probably affect any given generation of most forest trees. The selective pressures of hurricanes may operate at different stages of a species' life history and may be quite different for long-lived than for short-lived species. A single individual of a long-lived species may be affected by hurricanes several times. For example, some individuals of *Cyrilla racemiflora* in Puerto Rico may be >1000 yr old and have survived several hurricanes (Weaver 1986b). By contrast, the short-lived *Bocconia frutescens,* a "pioneer" species (sensu Swaine and Whitmore 1988), was very rare in Jamaican montane forests before Hurricane Gilbert, and confined to large gaps and forest margins. After the hurricane, it germinated under

defoliated canopies and in gaps throughout the forest (Bellingham et al. 1992). Many of these plants were short-lived; some reached 5 m in height, flowered and fruited prolifically, and died within 3.5 yr of the hurricane. Thus, except when there is an unusually short period between them, hurricanes do not affect most adults of *Bocconia frutescens.* Direct selective pressures of hurricanes are few on such short-lived species and rare on adults; selection pressure is likely to be strongest in the immediate aftermath of the hurricane.

Over the longer term, hurricanes maintain a cycle of disturbance and recovery (cf. Woodley et al. 1981), including secondary succession involving recruitment of species that regenerate most frequently in gaps (cf. Whitmore 1974, Foster 1988b). Continued monitoring of our permanent plots (and of permanent seedling plots, not reported in this paper) will reveal whether or not seedlings established after the hurricane are recruited into larger size classes and to what extent they may lead to compositional changes (cf. Glitzenstein et al. 1986, Foster 1988b). Our current interpretation of dynamics in this forest is that the low level of mortality among most species, the generally low level of damage (Bellingham 1991, Bellingham et al. 1992, this study), and rapid vegetative recovery of many adults (Bellingham et al. 1994) after Hurricane Gilbert means that, at present, hurricanes have few long-term effects on the forests (cf. Yih et al. 1991). However, a change in the disturbance regime may alter this.

LITERATURE CITED

Adams, C. D. 1972. Flowering plants of Jamaica. University of the West Indies, Mona, Jamaica.

Alaka, M. A. 1976. Climatology of Atlantic tropical storms and hurricanes. Pages 479–509 *in* W. Schwerdtfeger, editor. Climates of Central and South America. (World survey of climatology. Volume 12). Elsevier Scientific Publishing Company, Amsterdam, The Netherlands.

Basnet, K., F. N. Scatena, G. E. Likens, and A. E. Lugo. 1993. Ecological consequences of root grafting in tabonuco (*Dacryodes excelsa*) trees in the Luquillo Experimental Forest, Puerto Rico. Biotropica **25**:28–35.

Bellingham, P. J. 1991. Landforms influence patterns of hurricane damage: evidence from Jamaican montane forests. Biotropica 23:427–433.

———. 1993. The effects of a hurricane on Jamaican montane rain forests. Dissertation. University of Cambridge, Cambridge, UK.

Bellingham, P. J., V. Kapos, N. Varty, J. R. Healey, E. V. J. Tanner, D. L. Kelly, J. W. Dalling, L. S. Burns, D. Lee, and G. Sidrak. 1992. Hurricanes need not cause high mortality: the effects of Hurricane Gilbert on forests in Jamaica. Journal of Tropical Ecology 8:217–223.

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

Boose, E. R., D. R. Foster, and M. Fluet. 1994. Hurricane impacts to tropical and temperate forest landscapes. Ecological Monographs 64:369–400.

Bormann, F. H., and G. E. Likens. 1979. Pattern and process in a forested ecosystem. Springer-Verlag, Berlin, Germany.

Boucher, D. H., J. H. Vandermeer, M. A. Mallona, N. Zamora, and I. Perfecto. 1994. Resistance and resilience in a directly regenerating rainforest: Nicaraguan trees of the Vochysiaceae after Hurricane Joan. Forest Ecology and Management 68:127–136.

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

Brokaw, N. V. L., and L. R. Walker. 1991. Summary of the effects of Caribbean hurricanes on vegetation. Biotropica 23:442–447.

Brown, N. D., and T. C. Whitmore. 1992. Do dipterocarp seedlings really partition tropical rain forest gaps? Philosophical Transactions of the Royal Society of London B 335:369–378.

Connell, J. H., and W. P. Sousa. 1983. On the evidence needed to judge ecological stability or persistence. American Naturalist 121:789–824.

Coutts, M. P. 1983. Root architecture and tree stability. Plant and Soil 71:171–188.

Crow, T. R. 1980. A rainforest chronicle: a 30-year record of change and structure and composition at El Verde, Puerto Rico. Biotropica 12:42–55.

Dalling, J. W. 1992. Regeneration on landslides in the Blue Mountains, Jamaica. Dissertation. University of Cambridge, Cambridge, UK.

———. 1994. Vegetation colonization of landslides in the Blue Mountains, Jamaica. Biotropica 26:392–399.

Dalling, J. W., and E. V. J. Tanner. 1995. An experimental study of regeneration on landslides in montane rain forest in Jamaica. Journal of Ecology 83:55–64.

Dittus, W. P. J. 1985. The influence of cyclones on the dry evergreen forest of Sri Lanka. Biotropica 17:1–14.

Emanuel, K. A. 1987. The dependence of hurricane intensity on climate. Nature 326:483–485.

Foster, D. R. 1988a. Species and stand response to catastrophic wind in central New England. Journal of Ecology 76:135–151.

———. 1988b. Disturbance history, community organisation and vegetation dynamics of the old-growth Pisgah Forest, south-western New Hampshire, U.S.A. Journal of Ecology 76:105–134.

Frangi, J. L., and A. E. Lugo. 1991. Hurricane damage to a flood plain forest in the Luquillo Mountains of Puerto Rico. Biotropica 23:324–335.

Fraser, A. I. 1962. The roots and soil as factors in tree stability. Forestry 35:117–127.

Glitzenstein, J. S., and P. A. Harcombe. 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.

Glitzenstein, J. S., P. A. Harcombe, and D. A. Streng. 1986. Disturbance, succession, and maintenance of species diversity in an east Texas forest. Ecological Monographs 56:243–258.

Gresham, C. A., T. M. Williams, and D. J. Lipscomb. 1991. Hurricane Hugo wind damage to southeastern U.S. coastal forest tree species. Biotropica 23:420–426.

Grubb, P. J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biological Reviews 52:107–145.

Grubb, P. J., and A. J. M. Hopkins. 1986. Resilience at the level of the plant community. Pages 21–38 in B. Dell, A. J. M. Hopkins, and B. B. Lamont, editors. Resilience in Mediterranean-type ecosystems. Dr W. Junk Publishers, Dordrecht, The Netherlands.

Grubb, P. J., and E. V. J. Tanner. 1976. The montane forests and soils of Jamaica: a reassessment. Journal of the Arnold Arboretum 57:313–368.

Hall, J. B. 1991. Multiple-nearest-tree sampling in an ecological survey of Afromontane catchment forest. Forest Ecology and Management 42:245–266.

Halpern, C. B. 1988. Early successional pathways and the resistance and resilience of forest communities. Ecology 69:1703–1715.

Harper, J. L. 1977. Population biology of plants. Academic Press, London, UK.

Healey, J. R. 1990. Regeneration in a Jamaican montane tropical rain forest. Dissertation. University of Cambridge, Cambridge, UK.

Kelly, D. L., E. V. J. Tanner, E. NicLughadha, and V. Kapos. 1994. Floristics and biogeography of a rain forest in the Venezuelan Andes. Journal of Biogeography 21:421–440.

King, D. A. 1986. Tree form, height growth, and susceptibility to wind damage in Acer saccharum. Ecology 67:980–990.

Knowlton, N., J. C. Lang, M. C. Rooney, and P. Clifford. 1981. Evidence for delayed mortality in hurricane-damaged Jamaican staghorn corals. Nature 294:251–252.

Lawrence, M. B., and J. W. Gross. 1989. Atlantic hurricane season of 1988. Monthly Weather Review 117:2248–2259.

Lawton, R. O. 1984. Ecological constraints on wood density in a tropical montane rain forest. American Journal of Botany 71:261–267.

Leps, J., J. Osbornová-Kosinová, and M. Rejmánek. 1982. Community stability, complexity and species life-history strategies. Vegetatio 50:53–63.

Lugo, A. E., M. Applefield, D. J. Pool, and R. B. McDonald. 1983. The impact of Hurricane David on the forests of Dominica. Canadian Journal of Forest Research 13:201–211.

Lugo, A. E., and C. T. Rivera Batlle. 1987. Leaf production, growth rate, and age of the palm Prestoea montana in the Luquillo Experimental Forest, Puerto Rico. Journal of Tropical Ecology 3:151–161.

Merrens, E. J., and D. R. Peart. 1992. Effects of hurricane damage on individual growth and stand structure in a hardwood forest in New Hampshire, U.S.A. Journal of Ecology 80:787–795.

Naughton, P. W. 1982. The Jamaican hurricane season—changing the rhyme. Caribbean Journal of Science 18:107–111.

Neumann, C. J., G. W. Cry, E. L. Caso, and B. R. Jarvian. 1978. Tropical cyclones of the North Atlantic Ocean. 1871–1977. National Climatic Center, Asheville, North Carolina, USA.

Oliver, C. D., and E. P. Stephens. 1977. Reconstruction of a mixed species forest in central New England. Ecology 58:562–572.

Parotta, J. A., and D. J. Lodge. 1991. Fine root dynamics in

a subtropical wet forest following hurricane disturbance in Puerto Rico. Biotropica 23:343–347.

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

Petty, J. A., and C. Swain. 1985. Factors influencing stem breakage of conifers in high winds. Forestry 58:75–84.

Proctor, G. R. 1985. Ferns of Jamaica. British Museum (Natural History), London, UK.

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

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

Putz, F. E., and 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.

Reading, A. J. 1990. Caribbean tropical storm activity over four centuries. International Journal of Climatology 10:365–376.

Ryan, B. F., I. G. Watterson, and J. L. Evans. 1992. Tropical cyclone frequencies inferred from Gray's Yearly Genesis Parameter: validation of GCM tropical climates. Geophysical Research Letters 19:1831–1834.

Sauer, J. D. 1962. Effects of recent tropical cyclones on the coastal vegetation of Mauritius. Journal of Ecology 50:275–290.

Shreve, F. 1914. A montane rain-forest. A contribution to the physiological plant geography of Jamaica. Publication No. 199. Carnegie Institute of Washington, Washington, D.C., USA.

Sugden, A. M., E. V. J. Tanner, and V. Kapos. 1985. Regeneration following clearing in a Jamaican montane forest: results of a ten-year study. Journal of Tropical Ecology 1:329–351.

Swaine, M. D., and T. C. Whitmore. 1988. On the definition of ecological species groups in tropical rain forests. Vegetatio 75:81–86.

Tanner, E. V. J. 1977. Four montane rain forests of Jamaica: a quantitative characterization of the floristics, the soils and the foliar mineral levels, and a discussion of the interrelations. Journal of Ecology 65:883–918.

———. 1980. Studies on the biomass and productivity in a series of montane rain forests in Jamaica. Journal of Ecology 68:573–588.

———. 1982. Species diversity and reproductive mechanisms in Jamaican trees. Biological Journal of the Linnaean Society 18:263–278.

———. 1985. Jamaican montane forests: nutrient capital and cost of growth. Journal of Ecology 73:553–568.

Tanner, E. V. J., and V. Kapos. 1982. Leaf structure of Jamaican upper montane rain-forest trees. Biotropica 14:16–24.

Tanner, E. V. J., V. Kapos, S. Freskos, J. R. Healey, and A. M. Theobald. 1990. Nitrogen and phosphorus fertilization of Jamaican montane forest trees. Journal of Tropical Ecology 6:231–238.

Thomas, J. L. 1960. A monographic study of the Cyrillaceae. Contributions from the Gray Herbarium of Harvard University 186:1–114.

Thompson, D. A. 1983. Effects of Hurricane Allen on some Jamaican forests. Commonwealth Forestry Review 62:107–115.

Uhl, C., K. Clark, N. Dezzeo, and P. Maquirino. 1988. Vegetation dynamics in Amazonian treefall gaps. Ecology 69:751–763.

Wadsworth, F. H., and G. H. Englerth. 1959. Effects of the 1956 hurricane on forests in Puerto Rico. Caribbean Forester 20:38–51.

Walker, L. R. 1991. Tree damage and recovery from Hurricane Hugo in Luquillo Experimental Forest, Puerto Rico. Biotropica 23:379–386.

Walker, L. R., J. Voltzow, J. D. Ackerman, D. S. Fernández, and N. Fetcher. 1992. Immediate impact of Hurricane Hugo on a Puerto Rican rain forest. Ecology 73:691–694.

Weaver, P. L. 1986a. Hurricane damage and recovery in the montane forests of the Luquillo Mountains of Puerto Rico. Caribbean Journal of Science 22:53–70.

———. 1986b. Growth and age of Cyrilla racemiflora L. in montane forests of Puerto Rico. Interciencia 11:221–228.

———. 1989. Forest changes after hurricanes in Puerto Rico's Luquillo Mountains. Interciencia 14:181–192.

Webb, S. L. 1988. Windstorm damage and microsite colonization in two Minnesota forests. Canadian Journal of Forest Research 18:1186–1195.

———. 1989. Contrasting windstorm consequences in two forests, Itasca State Park, Minnesota. Ecology 70:1167–1180.

Whitmore, T. C. 1974. Change with time and the role of cyclones in tropical rain forest on Kolombangara, Solomon Islands. Commonwealth Forestry Institute Paper 46, Oxford, UK.

Wood, T. W. W. 1970. Wind damage in the forest of Western Samoa. The Malayan Forester 33:92–99.

Woodley, J. D., E. A. Chornesky, P. A. Clifford, J. B. C. Jackson, L. S. Kaufman, N. Knowlton, J. C. Lang, M. P. Pearson, J. W. Porter, M. C. Rooney, K. W. Rylaarsdam, V. J. Tunnicliffe, C. M. Wahle, J. L. Wulff, A. S. G. Curtis, M. D. Dallmeyer, B. P. Jupp, M. A. R. Koehl, J. Neigel, and E. M. Sides. 1981. Hurricane Allen's impact on Jamaican coral reefs. Science 214:749–755.

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

Zimmerman, J. K., E. M. Everham, III, R. B. Waide, D. J. Lodge, C. M. Taylor, and N. V. L. Brokaw. 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.