BIOTROPICA 33(3): 393–408 2001

Hurricane Impacts on a Mangrove Forest in the Dominican Republic: Damage Patterns and Early Recovery[1]

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ABSTRACT

On 22 September 1998, Hurricane Georges passed over the Dominican Republic causing extensive damage to a 4700 ha mangrove forest that has been the site of a detailed study of vegetation and ecosystem dynamics since 1994. We resurveyed the vegetation in permanent plots at 7 and 18 months after the hurricane to document structural damage of the forest and evaluate early recovery patterns. The intensity of damage was patchy across the landscape. Mortality (≥5 cm DBH) ranged from 14 to 100 percent (by density) among the 23 different plots and averaged 47.7 percent across all plots. Reductions in total basal area ranged from 9 to 100 percent, averaging 42.4 percent. Mortality increased by 9 percent between surveys at 7 and 18 months post-hurricane. Interspecific differences in susceptibility to wind damage appeared to be a primary factor contributing to spatial patterns in mortality. *Laguncularia racemosa* experienced much less mortality (26%) than either *Rhizophora mangle* (50%) or *Avicennia germinans* (64%), and plot-level mortality was strongly associated with differences in species composition. There were no clear relationships between canopy height and tree damage at this site. Over 80 percent of the of the surviving *R. mangle* trees exhibited less than 50 percent crown damage, whereas *ca* 60 percent of the *L. racemosa* survivors suffered almost complete (75–100%) crown loss. By 18 months after the hurricane, the percentage of *L. racemosa* trees in the 75 to 100 percent damage class was reduced to 20 percent; in contrast, the health of many *R. mangle* individuals appeared to be declining, as the percentage of trees in the 50 to 100 percent damage class increased from 16 to 36 percent. Understory light levels, as measured by the gap light index, increased from an average value of 3 percent in the pre-hurricane forest to 51 percent at 7 months after the hurricane and decreased slightly to 47 percent at 18 months. Few saplings (>1 m tall and <5 cm DBH) survived the hurricane; 72 percent of the tagged individuals in transect-based plots and 66 percent of saplings in pre-hurricane canopy gaps were killed. Seedling and sapling populations of all three species appear to be recovering rapidly although their densities still are lower than in the pre-hurricane forest. It is too early to predict the trajectory of forest recovery, and continued monitoring of the spatial and temporal patterns of forest development is needed to improve our understanding of the role that large-scale disturbance events play on the dynamics of mangrove forest ecosystems.

RESUMEN

El 22 de septiembre de 1998, el huracán Georges pasó sobre la República Dominicana causando daños extensos a 47 km^2 de manglar que ha sido objeto un estudio detallado de vegetación y dinámica de la communidad desde 1994. Se tomarón muestras de la vegetación en parcelas permanentes 7 y 18 meses después de paso del huracán para documentar los daños estructurales del bosque y evaluar los modelos de recuperación temprana que siguieron posteriormente. La intensidad del daño fue irregular a través del paisaje. La mortalidad (≥5 cm de dap) fue de 14 a 100 por ciento (para la densidad) en las 23 parcelas con un promedio de 47.7 por ciento. La reducción en área basal total fue de 9 a 100 por ciento con un promedio de 42.4 por ciento. La mortalidad aumentó 9 por ciento a los 7 y 18 meses después del huracán. Las diferencias interspecíficas en la susceptibilidad a los daños causados por el viento fueron un factor contribuyente importante en los patrones espacios de mortalidad. *Laguncularia racemosa* sufrió menor mortalidad (26%) que *Rhizophora mangle* (50%) o *Avicennia germinans* (64%), la mortalidad en las parcelas estuvo asociada fuertemente con la diferencia en composición de especies. No hubo ningún patrón definido entre la altura del dosel y el daño del árbol. Más del 80 por ciento de los árboles sobrevivientes de *R. mangle* exhibieron daoñres menores de 50 por ciento en sus copas, mientras que *ca* 60 por ciento de los *L. racemosa* sobrevivientes sufrió una perdida casi total (75–100%). Dieciocho meses después del huracán, el porcentaje de árboles de *L. racemosa* con daños del 75–100 por ciento se redujó a 20 por ciento; en contraste, la salud de muchos individuos de *R. mangle* disminuyó conforme el porcentaje de árboles con daños del 50–100 por ciento aumentó de 16 a 36 por ciento. Los niveles de penetración de luz en el sotobosque, medidos como el índice de iluminacion en los claros, aumentó de un promedio de 3 por ciento antes del huracán. a 51 por ciento 7 meses después del huracán, y disminuyó ligeramente a 47 por

[1] Received 31 December 1999; revision accepted 8 October 2000.

ciento a los 18 meses. Pocos arbolillos (>1 m alto y <5 cm de dap) sobrevivieron el huracán; 72 por ciento de los individuos marcados en los transectos de las parcelas murieron al igual que el 66 por ciento de los arbolillos que habitaban en los claros del dosel antes del huracán. Las poblaciones de plántulas y arbolillos de las tres especies parecen recuperarse rápidamente aunque sus densidades todavía son menores que las anteriores al huracán. Es prematuro predecir la trayectoria de recuperación del bosque y se requiere del monituro continuo de los patrones espaciales y temporales del desarrollo forestal para mejorar nuestra comprensión del papel de eventos perturbadores de gran escala en la dinámica de las communidades de manglares.

Key words: *Dominican Republic; gap light index; hurricane; large-scale disturbance; mangrove forest; regeneration.*

CARIBBEAN LANDSCAPES ARE SUBJECT TO RELATIVELY FREQUENT LARGE-SCALE DISTURBANCE by hurricanes. For example, from 1899 through 1987, there was an average of five to nine hurricanes per decade near the islands of Hispaniola and Puerto Rico (Reading 1990). Because Caribbean landscapes have been struck repeatedly by hurricanes throughout recorded history, these disturbance events undoubtedly have played a major role in shaping the characteristics of Caribbean biotic communities. A clear understanding of forest dynamics in this region requires comprehensive information about how communities respond to hurricane disturbance. Nevertheless, the ecological effects of hurricanes on terrestrial ecosystems are not well understood (Walker *et al.* 1991, Zimmerman *et al.* 1996).

Mangrove forests are especially vulnerable to disturbance by the high winds of tropical cyclones because of their position in low-lying coastal regions; however, surprisingly little quantitative research exists on the role of hurricane disturbance on mangrove forest dynamics (Craighead & Gilbert 1962, Stoddart 1969, Craighead 1971, Roth 1992, Smith *et al.* 1994, Imbert *et al.* 1996). On 22 September 1998, Hurricane Georges passed over the island of Hispaniola causing extensive damage to a mangrove forest located at the west end of Samaná Bay on the northeastern coast of the Dominican Republic (Fig. 1). This large mangrove forest has been the site of a detailed vegetation and ecosystem dynamics study since 1994 (Sherman 1998; Sherman *et al.* 1998, 2000). The availability of data on the pre-hurricane forest provided us with an unusual opportunity to assess the impacts of a severe disturbance on mangrove forest structure, species composition, and the initial stages of ecosystem recovery.

The overall goal of this study was to quantify the hurricane damage to the Samaná Bay mangrove forest by comparing pre- and post-hurricane surveys of 23 permanent vegetation plots distributed along two transects that traversed the mangrove. Specific objectives included: (1) quantify patterns of damage across the mangrove landscape; (2) examine species differences in susceptibility to wind damage; (3) investigate hurricane damage to different forest types within the mangrove; and (4) document initial patterns of forest recovery in the mangrove. Our previous research at this site indicated that existing patterns of species distribution across the environmental complex in the mangrove were not reinforced by regeneration in small canopy disturbances (Sherman *et al.* 2000), leading to the hypothesis that large-scale disturbances, like hurricanes, may be required to generate and maintain species distribution patterns in these ecosystems.

HURRICANE GEORGES.—Hurricane Georges made landfall on the southeastern shore of the Dominican Republic on 22 September 1998, with a minimum central pressure of 962 Mb and estimated sustained surface winds of 194 km/h, a category 3 hurricane (Guiney 1999). Georges weakened as it moved slowly across the center of the island on a west–northwestward course over a 21-hr period (Fig. 1; Guiney 1999). The eye of the hurricane passed *ca* 50 km to the south of the mangrove study site, with maximum sustained wind speeds of *ca* 176 km/h and a central pressure of 970 Mb (Fig. 1). Wind speeds in the mangrove forest were estimated from calculations of sustained surface winds over water at 10 m height and presumed to be in the range of 110–120 km/h (Hurricane Research Division). Satellite-derived rainfall estimates suggest that as much as 99 cm of rain may have fallen over portions of the Dominican Republic and Haiti over a 24-hour period, although no land-based measurements are available (Guiney 1999)

STUDY AREA

This study was conducted in a 4700 ha mangrove forest located at the western end of Samaná Bay in the Los Haitises National Park, Dominican Republic, in the broad delta created at the mouths of the Yuna and Barracote Rivers (19°10'N, 69°40'W; Fig. 1). Before the hurricane, the forest was dominated by the red mangrove (*Rhizophora mangle* L.,

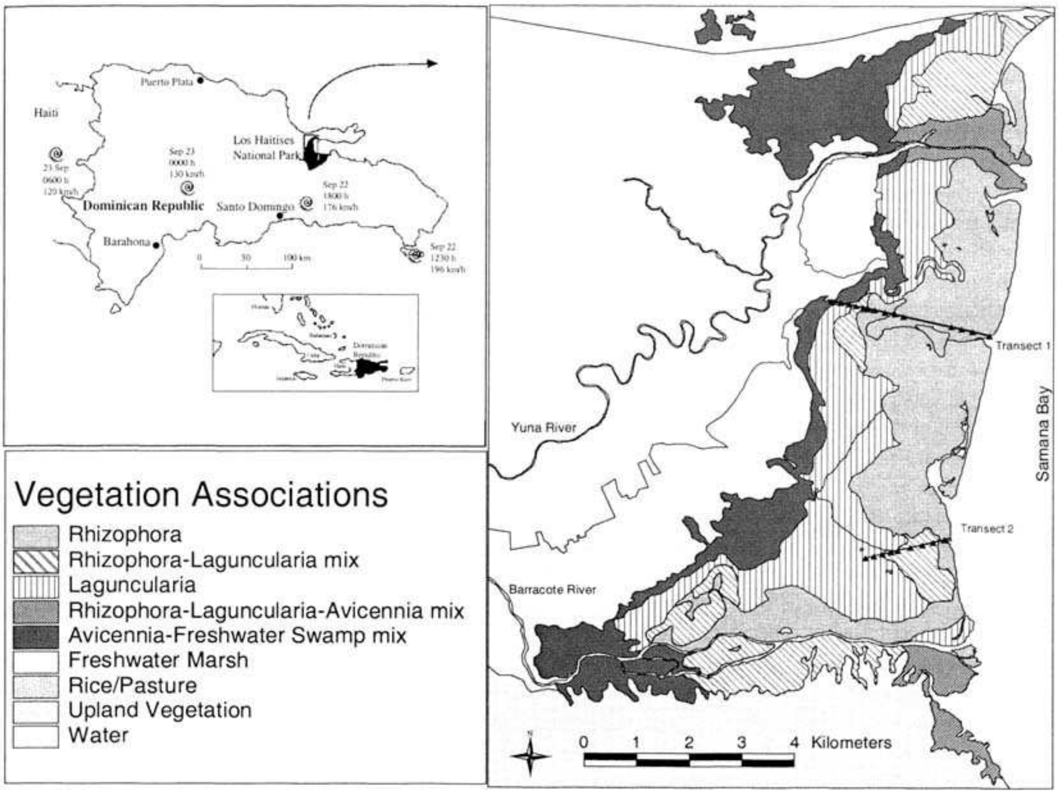

FIGURE 1. The mangrove forest study area in the Los Haitises national park, Dominican Republic, depicting the approximate track and wind speed of Hurricane Georges across the Dominican Republic, mangrove forest community associations, and transects and plots used for field sampling (heavy solid lines and triangles, respectively).

Rhizophoraceae) and white mangrove (*Laguncularia racemosa* Gaertn, Combretaceae) with a lesser amount of the black mangrove (*Avicennia germinans* L., Avicenniaceae; Fig. 1; Sherman *et al.* 2000). A freshwater swamp, cattail marsh, and an extensive rice production region forms the inland border to the mangrove forest. Mean annual temperature in the study area is 26.3°C and rainfall averages 2065 mm/yr, with the driest months of February and March averaging 100 mm/mo (Oficina Nacional de Meteorología, Dominican Republic). Mean tidal amplitude is *ca* 0.6 m. A tidal wave produced by an offshore earthquake destroyed much of the mangrove forest in 1946 (Sachtler 1973, Alvarez & Cintrón 1984).

Based on a series of aerial photographs, the forest reestablished quickly following the tidal wave and most of the current mangrove is dominated by an even-aged forest dating from soon after 1946. The mangrove extent, however, has expanded steadily (especially seaward), increasing in area from 32.7 km^2 in 1959 to 47.1 km^2 in 1996 (Sherman *et al.* 2000). The most recent aerial photographs were used in conjunction with plot sampling (see below) and qualitative ground-truthing to develop a map of forest zonation in the mangrove (Fig. 1; Sherman *et al.* 2000). The recent hurricane has been the first large-scale disturbance since the 1946 tidal wave; however, small-scale disturbances are common in the mangrove forest (Sherman *et al.* 2000). Lightning is an important mortality agent in many mangroves (Smith 1992, Smith *et al.* 1994, Sherman *et al.* 2000), and we estimated that in 1996, 1.9 percent of the prehurricane forest was in gaps associated with lightning mortality (Sherman *et al.* 2000).

To conduct a detailed investigation of forest structure across the tidal gradient, twenty-three 30 m diameter plots were established along two transects that traversed the mangrove forest (Sherman *et al.* 2000). One transect extended 3.1 km from the coast inland to the transition to the freshwater swamp (established January 1994) and a second transect extended from the coast inland for 1.8 km (established November 1994; Fig. 1). The lower tidal zone was dominated by *R. mangle* along both transects with a gradual transition to a *L. racemosa*-dominated forest (Fig. 2a). Near the inland margin, along transect 1, a sharp transition to an *A. germinans*-dominated forest occurred, followed by an abrupt transition to a freshwater marsh and rice production area (Fig. 2a). Transect 2 did not traverse the entire forest (Fig. 1), but field reconnaissance indicated that the *L. racemosa*-dominated forest extended beyond the end of the transect to the inland forest edge; although an *A. germinans*–freshwater swamp association occurred along the inland border, *A. germinans* was not a dominant species in this region of the freshwater swamp. Before the hurricane, the maximum forest canopy height averaged 24 m, ranging from *ca* 18 m near the coast to 30 m in the more inland plots (the four tallest trees in each plot were measured using a clinometer; Fig. 2b). Salinity of the surface water decreased across the tidal gradient from *ca* 30 g/kg near the coast to less than 5 g/kg at the inland forest margin (Fig. 2c). Salinity of the interstitial soil water collected at a depth of 50 cm was higher than the surface water and averaged 30.2 g/kg across most of the tidal gradient; however, pore water salinity decreased abruptly near the upper edge of the mangrove in the *A. germinans*-dominated forest (Fig. 2c; transect 1). Surface water and deep soil water nitrogen concentrations increased across the tidal gradient from *ca* 10 mM/liter near the coast to 40 mM/liter in the upper tidal forest; organic N accounted for 70 to 98 percent of the total N measured in samples (Sherman *et al.* 1998). Phosphorous concentrations ranged from 1 to 35 μM/liter across the tidal gradient, reaching maximum concentrations in the *L. racemosa*-dominated stands (Sherman *et al.* 1998).

METHODS

In 1994, all stems 5 cm diameter at breast height (DBH) or greater were measured with DBH tape and tagged in each plot to estimate density, basal area, diameter growth rates, and mortality rates. All saplings (>1 m tall and <5 cm DBH) were counted and identified in each plot, and seedlings (≤1 m tall) were enumerated by species in twelve 1 m^2 subplots spaced evenly along perpendicular transects set out north–south and east–west from the center of each plot. In November 1995, *ca* 25 saplings of each species were measured and tagged in each of the 23 permanent plots to estimate growth and mortality rates. In addition, seedling and sapling density was quantified in 17 canopy gaps and a subset of saplings tagged for growth and mortality estimates. All canopy gaps sampled were created by lightning and averaged 30.4 m in diameter (Sherman *et al.* 2000). Tagged trees were remeasured every two years, and tagged saplings, annually.

To quantify the disturbance associated with the hurricane, we resurveyed the vegetation in each of the permanent plots in April 1999, seven months after the hurricane. Tagged trees were remeasured and the extent of damage to each tree was assessed. For each living tree, crown disturbance was visually classified into five damage categories: 0–25; 25–50; 50–75; 75–99; and 100 percent crown loss (branches and leaves). Dead trees were classified as either tip-up, snap-off, or standing dead, and the direction of fall was recorded. Seedlings and saplings were identified and enumerated in 1 m wide strip plots along the N–S and E–W axes of each plot to estimate density. Tagged saplings were remeasured to estimate mortality rates. In March 2000, we resurveyed the vegetation in each of the plots and repeated measurements as described above; however, in this paper, we focus primarily on the initial measurements made 7 mo after the hurricane.

To quantify light availability to understory trees, we measured the gap light index (GLI) in each plot during April 1999 and March 2000 (Canham 1988, Canham *et al.* 1990) and compared these values to pre-hurricane measurements (Sherman *et al.* 2000). The GLI quantifies the percentage of photosynthetically active radiation transmitted to a particular point on the forest floor over the course of the growing season. The technique is based on predictable changes in solar geometry during the growing season. The GLI ranges from 0 for a completely closed canopy to 100 for a completely open site. One fisheye photograph was taken at a random location in each of four quadrats inside each plot for a total of four photographs per plot. The photographs were digitized and then analyzed using GLI/C software developed by Charles D. Canham (Institute of Ecosystem Studies, Millbrook, New York).

Individual plots were the experimental unit of study for statistical analysis. One-way ANOVAs were used to analyze differences in mortality rates among species and among vegetation zones. Chi-square analysis was used to test for differences in mortality patterns among tree size classes and differences in damage patterns among species. Nonparametric statistics were used to analyze changes in the sapling and seedling populations.

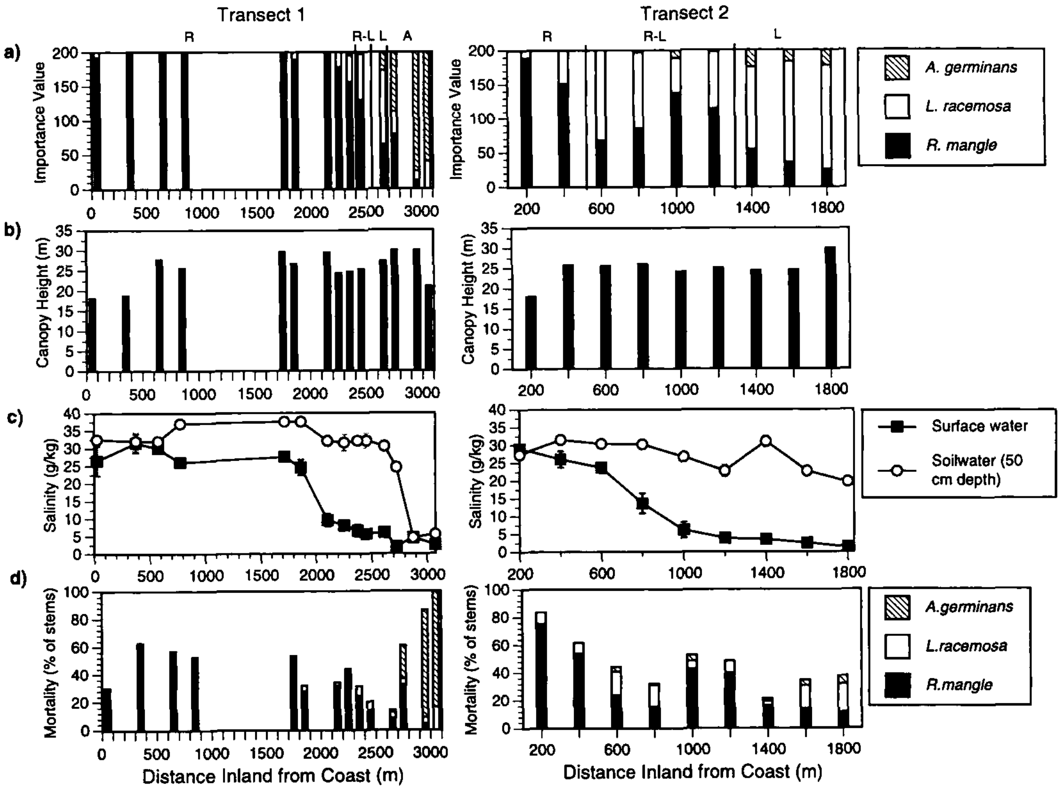

FIGURE 2. Importance value (relative dominance + relative density) of mangrove species (≥5 cm DBH) in the pre-hurricane forest (a), canopy height (b), salinity (c) and hurricane-induced mortality (d) measured in plots along two transects across the intertidal zone of a neotropical mangrove forest (see Figure 1 for location of transects). The different forest associations are delineated by the vertical lines in panel (a) (R = *R. mangle*, R-L = *R. mangle–L. racemosa*, L = *L. racemosa*, A = *A. germinans* dominated stands).

RESULTS

The intensity of damage associated with the hurricane was highly variable across the mangrove landscape (Fig. 2d). Tree mortality (≥5 cm DBH) ranged from 14 to 100 percent by density among the 23 different plots and averaged 47.7 percent across all plots (Fig. 2d). Reductions in total live basal area ranged from 9 to 100 percent, averaging 42.4 percent across all plots. *Avicennia germinans* suffered the greatest mortality, with 64 percent of its stems and 60 percent of its basal area killed. Mortality of *R. mangle* was intermediate, with 50 percent of its stems and 47 percent of its basal area killed. *Laguncularia racemosa* experienced the lowest mortality, losing 26 percent of its stems and 25 percent of its basal area.

Plots dominated by *L. racemosa* had much less damage than those dominated by either *A. germinans* or *R. mangle* (Fig. 3a, b), corresponding with observed differences in mortality among the three species. For example, in the upper tidal forest along transect 1, live basal area in the three plots dominated by *A. germinans* averaged 20.4 m^2/ha before the hurricane and only 6.6 m^2/ha following the hurricane, and density was reduced from an average of 377 to 99 stems/ha in these three plots. Similarly, in the 12 plots dominated by *R. mangle*, live basal area was reduced from 23.8 to 13.4 m^2/ha and density decreased from 1098 to 568 stems/ha. In contrast, in the 4 *L. racemosa*-dominated plots, basal area was reduced from an average of 40.9 to 33.0 m^2/ha and density decreased from 1171 to 852 stems/ha.

Surprisingly, spatial variation in mortality for each species across the 23 sample plots was relatively low (*R. mangle*, 50.1 ± 3.6% [±SE]; *L. racemosa*, 26.4 ± 4.5%; *A. germinans*, 63.7 ± 9.5%). Hence, the absolute amount of mortality, expressed as the number of stems or basal area dying per unit area, was well predicted simply by the pre-hurricane density or basal area for a particular species

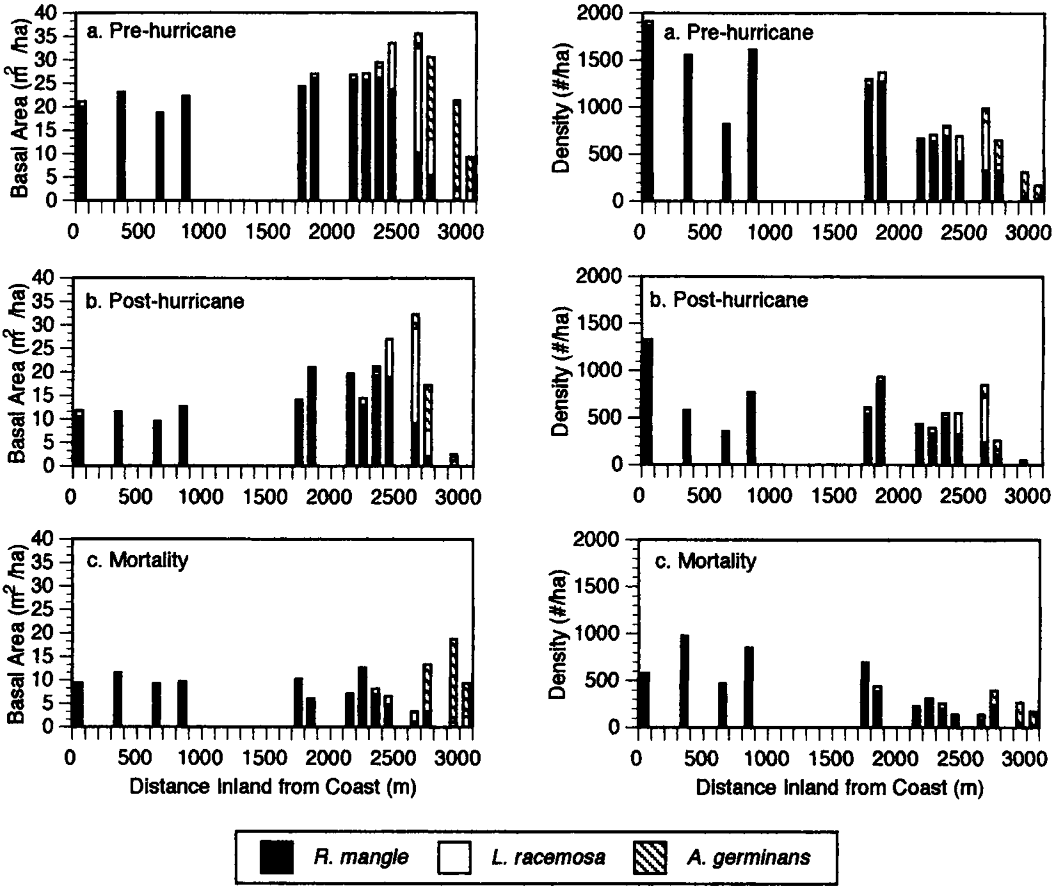

FIGURE 3a. Basal area and density of trees ≥5 cm DBH measured in plots along transect 1 across the intertidal zone in the pre-hurricane forest (a) and live (b) and dead (c) trees in the post-hurricane forest.

(Table 1). The slopes of these relationships were indicative of susceptibility to hurricane mortality and increased strongly ($F_{2,5}$ = 46.04, P = 0.006) in the order of *L. racemosa* < *R. mangle* < *A. germinans*. Species composition also was strongly associated with mortality patterns across the tidal gradient. A linear model of plot-level mortality (%) regressed against the basal area or density of the three species in each plot was associated with 82.2 percent (P < 0.001) of the between-plot variation in basal area mortality and 46.8 percent (P = 0.006) of the mortality by density. Mortality patterns among plots were not correlated with canopy height (r = 0.19).

To further test the effects of stand composition and structure on mortality patterns, we compared mortality rates among vegetation zones of the pre-hurricane forest (Figs. 1 and 2) and across tree diameter classes (Fig. 4). Each plot was classified into a stand type based on the dominant species, which was determined by importance values (relative basal area + relative density); four forest types were represented among our 23 plots: *R. mangle-*, *L. racemosa-*, *R. mangle–L. racemosa* mix, and *A. germinans*-dominated plots (Fig. 2a). Overall, mortality rates differed significantly among forest zones (one-way ANOVA $F_{3,21}$ = 5.23, P = 0.009), corresponding with the previous observations about species differences (Fig. 4b). In addition, the mortality rates of each species differed among forest zones. For example, mortality rates of *R. mangle* tended to be lowest in the *L. racemosa*-dominated stands (43%), intermediate in *R. mangle–L. racemosa* mixed plots (46%) and the *R. mangle*-dominated plots (49%), and highest in the *A. germinans*-dominated plots (64%), although these were not sig-

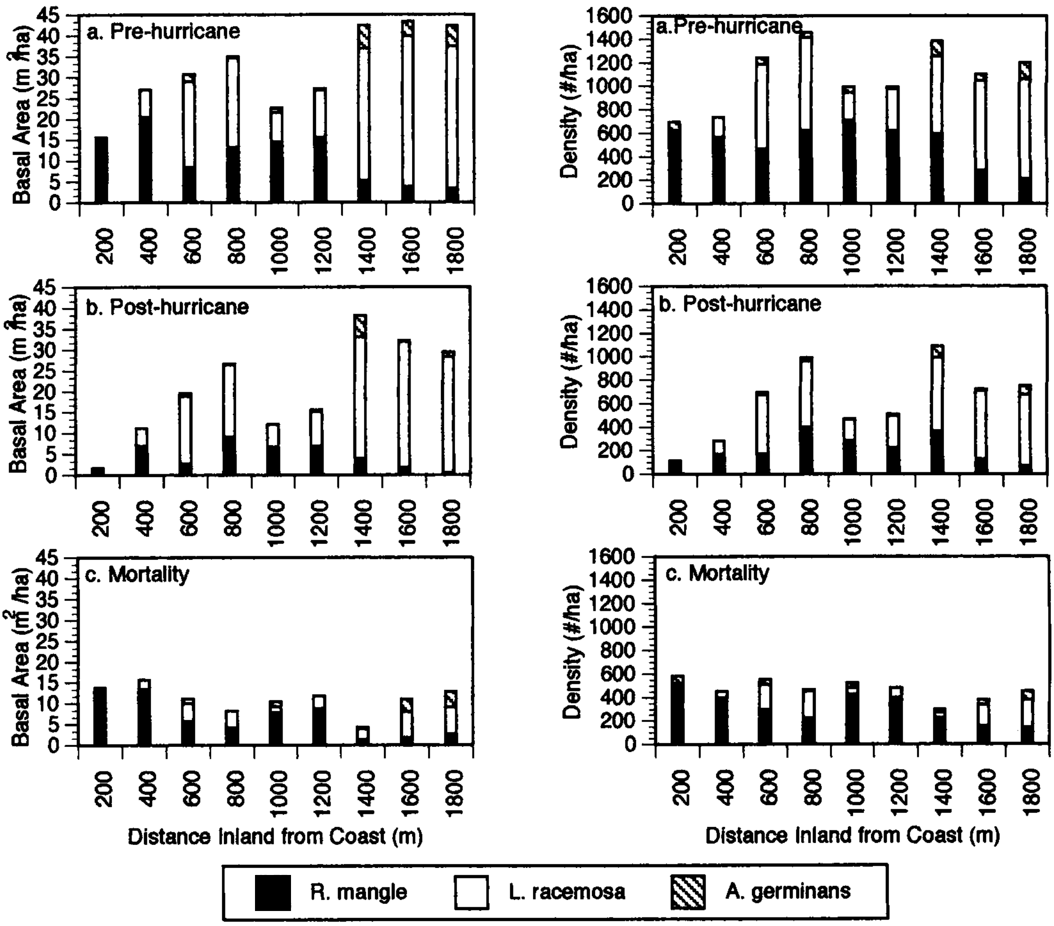

FIGURE 3b. Basal area and density of trees ≥5 cm DBH measured in plots along transect 2 across the intertidal zone in the pre-hurricane forest (a) and live (b) and dead (c) trees in the post-hurricane forest.

nificantly different (χ^2 = 5.2, P = 0.16, df = 3; χ^2 = 0.39, P = 0.82, df = 2, *A. germinans*- dominated plots excluded). Mortality rates of *L. racemosa* were lowest in the *L. racemosa*-dominated stands (18%), slightly greater in the mixed forest (22%), higher in the *R. mangle*-dominated stands (27%), and greatest in the *A. germinans*-dominated plots (64%); differences in mortality rates were not significant when the *A. germinans*-dominated plots were excluded from analysis (χ^2 = 1.83, P = 0.40, df = 2). Mortality of *A. germinans* was much more variable across forest zones, most likely due to the small sample size.

TABLE 1. *Linear relationships between basal area and density for three mangrove species (≥5 cm DBH) and their mortality following Hurricane Georges (measured as basal area and density, measured in 23 plots across the tidal gradient).*

	Basal area		Density	
	R^2	Slope	R^2	Slope
R. mangle	51.2	0.341	74.3	0.442
L. racemosa	79.3	0.143	78.2	0.228
A. germinans	84.4	0.717	78.8	0.695

The patterns of tree mortality by size class within the four forest zones (Fig. 4) suggested that, with a few exceptions, hurricane-caused mortality was not strongly segregated across tree size within the mangrove. The population size structure of trees that died within the four forest zones was not significantly different than the population size structure of the pre-hurricane forest in the respective forest zone (Fig. 4c; *R. mangle* plots: χ^2 = 1.14, P = 0.98; *R. mangle–L. racemosa* plots: χ^2 = 7.46, P = 0.19; *L. racemosa* plots: χ^2 = 7.86, P

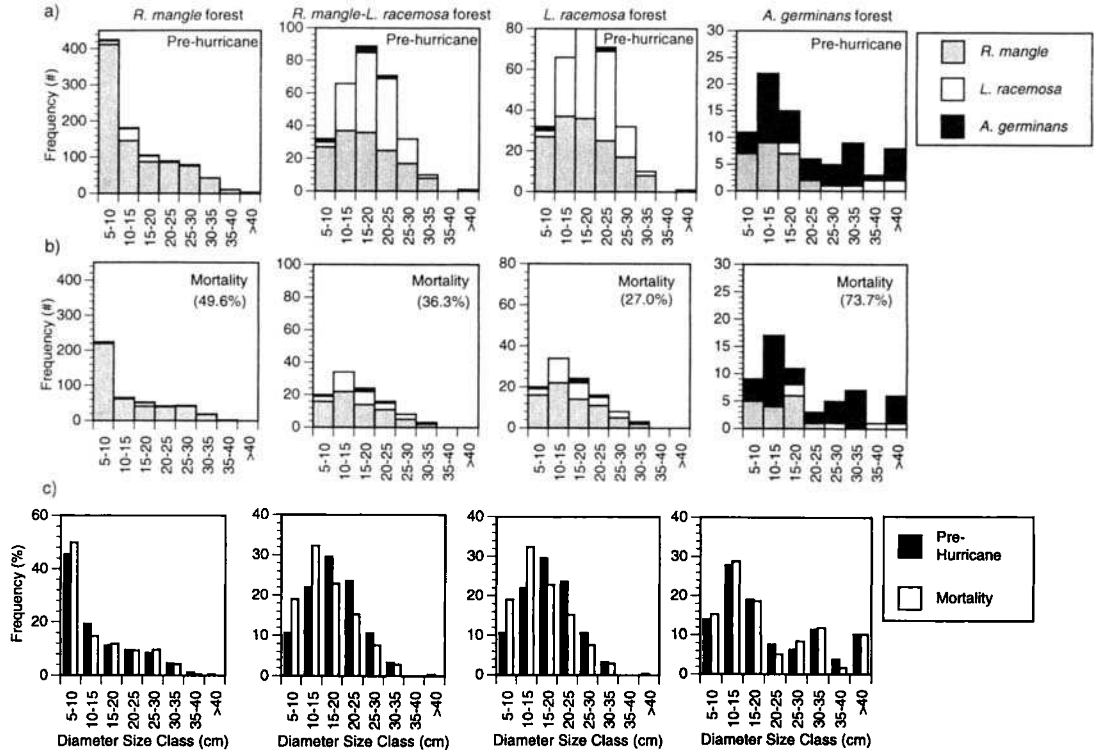

FIGURE 4. Diameter size class distribution of mangrove trees by species within the different forest types in the pre-hurricane forest (a), dead trees in the post-hurricane forest (total percent mortality in parentheses) (b), and the population size structure of the pre-hurricane forest and mortality within forest types (c).

= 0.16; *A. germinans* plots: $\chi^2 = 3.78$, $P = 0.78$), indicating that relative mortality was constant among most size classes. The notable deviations were in the *L. racemosa*-dominated and the *R. mangle–L. racemosa* mix plots in the two smallest size classes, in which greater relative mortality occurred (5–15 cm) and mortality was lower (15–25 cm). When total percent mortality was examined within size classes by species, slightly different patterns emerged (Fig. 5). Most notable was the significantly lower mortality (<15%) in the largest size class (>35 cm DBH) of *R. mangle* ($\chi^2 = 70.42$, $P < 0.001$, df = 1) and the significantly greater mortality recorded for *L. racemosa* in the 20–25 cm DBH size class ($\chi^2 = 18.02$, $P < 0.0001$, df = 1). Mortality rates of *A. germinans* were significantly lower for trees that ranged in size from 15 to 25 cm DBH ($\chi^2 = 60.62$, $P < 0.001$, df = 1).

The number of dead trees that snapped, uprooted, or were left standing dead differed among species (Fig. 6). Only 15 percent of the *R. mangle* trees tipped-up (69), whereas the number found standing dead (206) and broken (199) were similar ($\chi^2 = 75.35$, $P < 0.0001$). For *L. racemosa,* similar numbers were found in all three mortality classes (22 standing dead, 36 snapped, and 23 tip-ups; $\chi^2 = 4.52$, $P = 0.1$), while the greatest number of *A. germinans* were found standing dead (22), with the number of tip-ups intermediate (11) and only a few trees with their trunks snapped (6; $\chi^2 = 10.31$, $P = 0.006$). There was little variation in treefall orientation: 81 percent of the trees fell in a W–SW direction and 16 percent of the trees fell to the south. Patterns of tree mortality type (tip-up, snap-off, and standing dead) by size class within species (Fig. 6) suggested that the type of mortality sustained by trees was not strongly segregated across tree size. For example, the proportion of *R. mangle* trees in the three mortality classes was relatively constant among size classes even though the total number of trees decreased across size classes. Although the sample sizes for *L. racemosa* and *A. germinans* were small, no clear patterns emerged among mortality type and stem size for these two species.

The extent of damage to trees that survived the

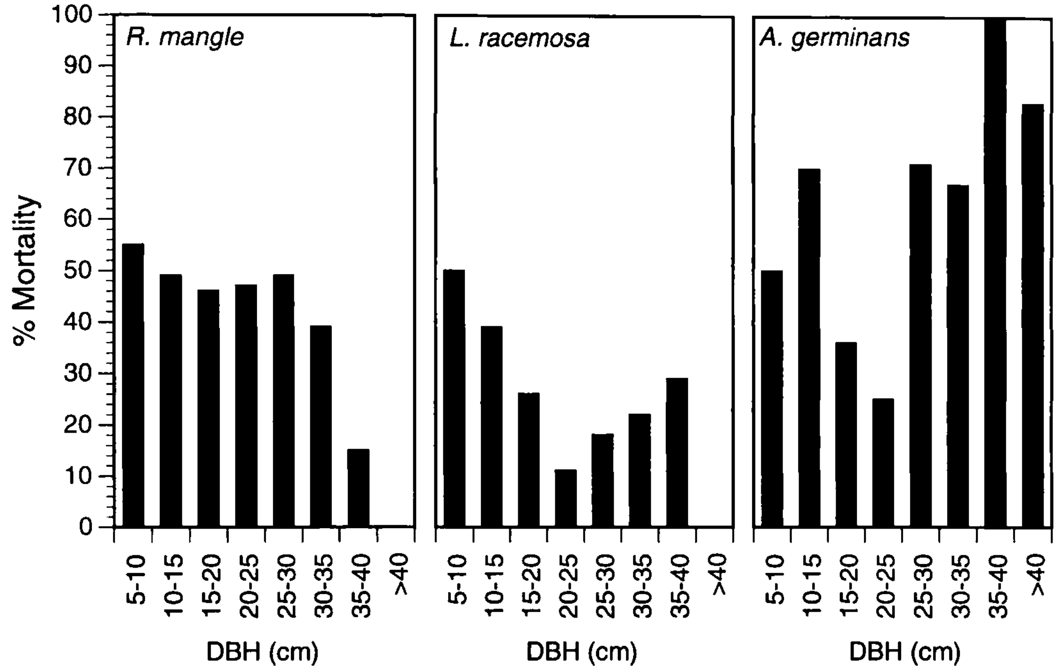

FIGURE 5. Percent mortality among diameter size classes of three mangrove species following Hurricane Georges.

hurricane differed significantly among species ($\chi^2 = 400.8$, $P < 0.001$, df = 8). Over 80 percent of the surviving *R. mangle* trees exhibited less than 50 percent crown damage, whereas *ca* 60 percent of the *L. racemosa* survivors suffered almost complete crown loss (75–100% damage; Fig. 7). Similar numbers of *A. germinans* survivors fell into the different crown disturbance classes. Crown damage and stem size were not related for either *R. mangle* or *L. racemosa,* while smaller individuals of *A. germinans* tended to experience less crown damage than larger size classes (Fig. 7).

Considerable additional mortality was observed for each species between 7 and 18 months after the hurricane; an additional 99 *R. mangle* trees (9%), 34 *L. racemosa* trees (6%), and 9 *A. germinans* trees (6%) died in the plots. The distribution of trees among crown damage classes also shifted considerably during this time interval as trees either recovered or declined. In particular, there was a considerable reduction in the number of *L. racemosa* trees in the 75 to 100 percent damage classes and a consequent increase in the number of trees in the 25 to 75 percent damage classes (Fig. 8); in contrast, many *R. mangle* individuals appeared to be declining as the number of trees in the 50 to 99 percent damage classes increased and the number of trees in the 0 to 50 percent canopy damage classes decreased.

Few saplings (>1 m tall and <5 cm DBH) survived the hurricane, with 71.8 percent (SE ± 3.8%) of the tagged individuals in understory plots and 66.3 percent (±7.3%) in preexisting gaps found dead. Sapling mortality in plots and gaps was not significantly different ($t = 0.66$, $P = 0.52$). Many saplings were killed by falling trees and branches and others were found standing dead. Both the seedling and sapling populations were significantly smaller in the post-hurricane forest at 7 months compared to the pre-hurricane population when pooled across all plots (Mann-Whitney *U*-test, $P < 0.05$). Both the seedling and sapling layers were dominated by *R. mangle* throughout the forest in the post-hurricane forest (Kruskal-Wallis test, $P < 0.001$); however, there was high spatial variation among plots and some plots were dominated by *L. racemosa,* whereas other plots had no regeneration in the post-hurricane forest (Fig. 9a, b). Most of the *L. racemosa* saplings were new basal sprouts. Very few *A. germinans* saplings were observed in either the pre-hurricane or post-hurricane forest at 7 months.

By 18 months after the hurricane, the density of seedlings and saplings had increased in most

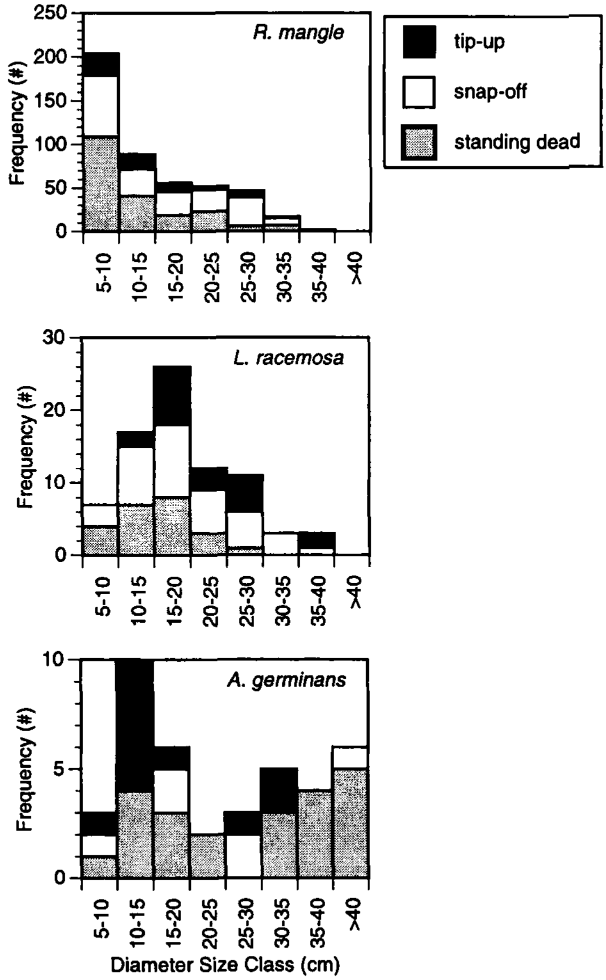

FIGURE 6. Mortality type among diameter size classes of three mangrove species following Hurricane Georges.

plots since the last survey, particularly along transect 2 (Fig. 9a, b) although this change was not significant due to the high spatial variation among plots (Mann-Whitney *U*-test, $P = 0.065$ for saplings and $P = 0.17$ for seedlings). Recruitment of *L. racemosa* was particularly striking in the 11 months between surveys, especially along transect 2 (Fig. 9b). Several saplings of *A. germinans* were found in one plot near the coast along transect 2; these were not present at 7 months.

Light levels in the forest understory were greatly enhanced following the hurricane. The GLI in the pre-hurricane forest averaged 2.9 ± 0.2 across all plots, and increased to an average of 51.1 ± 3.3 at 7 months post-hurricane and decreased slightly to an average of 46.8 ± 3.5 at 18 months post-hurricane. The GLI measured at 7 months post-hurricane ranged from 29 to 72 across the 23 plots and was positively correlated with plot-level percent mortality ($r = 0.89$ by density and $r = 0.78$ by basal area). The GLI tended to be lowest in the *L. racemosa*-dominated stands in the post-hurricane forest, coincident with the lower mortality of these stands, and highest in the *A. germinans* stands, although differences were not significant (Table 2). Mortality rates averaged across plots within forest types were highly correlated with the average GLI within these stands ($r = 0.99$ when mortality was measured as density or basal area). Decreases in GLI at 18 months post-hurricane were not significantly different from measurements at 7 months post-hurricane, although decreases tended to be greatest in the *L. racemosa*-dominated stands (Table 2).

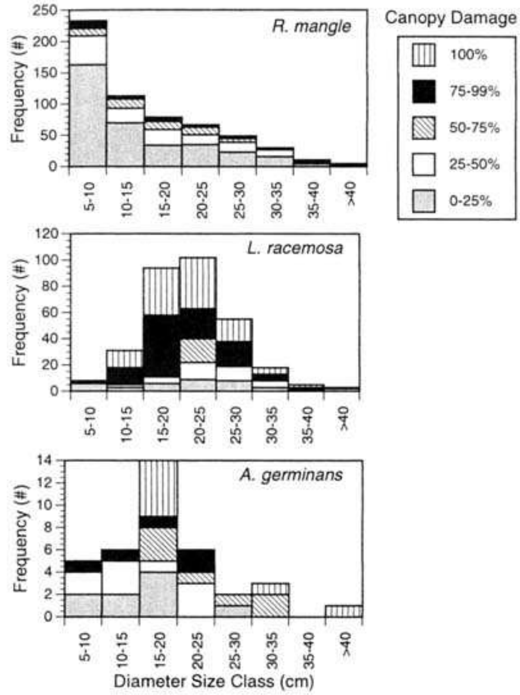

FIGURE 7. Extent of crown damage among diameter size classes of three mangrove species that survived Hurricane Georges.

DISCUSSION

Hurricanes are important large-scale disturbance events in the Caribbean and other subtropical regions of the world, and as a result of recent detailed studies, a better understanding of their effects on local and regional vegetation patterns is beginning to emerge (Walker *et al.* 1991, Boose *et al.* 1994, Zimmerman *et al.* 1996). Hurricanes can have a major effect on forest dynamics in terms of the age and size distribution of trees (Weaver 1986), forest composition (Crow 1980, Weaver 1986), forest biomass (Lodge & McDowell 1991), species diversity (Weaver 1986, Vandermeer *et al.* 1996), canopy structure (Brokaw & Gear 1991), and successional changes in species composition (Frangi & Lugo 1991, Walker 1991). Hence, understanding how the biotic community responds to hurricane disturbance may be essential for understanding the dynamics of many subtropical forest ecosystems.

The most immediate and obvious impact of a severe hurricane is the loss of live biomass and removal of the forest canopy. Even though the eye of Hurricane Georges tracked 50 km south of the mangrove forest (Fig. 1), *ca* 42 percent of the basal area of this mangrove forest was killed. Moreover, of the trees that survived, many experienced substantial damage; only *ca* 10% of the *L. racemosa* and 20 percent of the *A. germinans* individuals that survived experienced less than 25 percent crown loss. Crown damage to *R. mangle* was lower, with 60 percent of the survivors experiencing minimal canopy damage, but mortality was high (*ca* 50% by density). Hurricane-related mortality can continue for months (Smith *et al.* 1994) and even years (Craighead & Gilbert 1962, Dittus 1985, Bellingham *et al.* 1995). Tree mortality at our site increased by 9 percent (by density) between 7 and 18 months following the hurricane, and the full impact of Hurricane Georges will not be known for some time. Compared to tree mortality rates of less than 2 percent per year in the pre-hurricane forest (R. Sherman, pers. obs.), this massive and sudden mortality will be evident for decades as the forest recovers.

Hurricanes typically create heterogeneous damage patterns across forested landscapes as a result of complex interactions among meteorologic, topographic, and biotic factors (Boose *et al.* 1994). In this study, several lines of evidence suggest that interspecific differences in susceptibility to hurricane-induced mortality was an important factor contributing to spatial variability in damage across the mangrove landscape. *Laguncularia racemosa* experienced much lower mortality than either *R. mangle* or *A. germinans*, and total mortality at the plot level was strongly associated with differences in species composition. Moreover, the mortality rate for *L. racemosa* and *R. mangle* was relatively uniform across the different stand types within the mangrove ecosystem and between the two widely separated transects (the abundance of *A. germinans* was not high enough to be conclusive).

Site factors such as structure, tree age, tree height, tree health, rooting characteristics, and soil conditions also can influence wind susceptibility at the stand level (Foster 1988, Boose *et al.* 1994). In particular, the structural complexity of different forest types was found to play an important role in determining patterns of wind damage in other forests (Foster 1988, Imbert *et al.* 1996). Uneven-aged stands that have vertically differentiated canopies are more susceptible to wind damage because canopy surface roughness increases wind turbulence and overstory dominants have greater exposure to high winds (Foster 1988). Our study site was largely an even-aged forest, having arisen following a tidal wave in 1946 that destroyed most of the preexisting mangrove, and thus had low structural

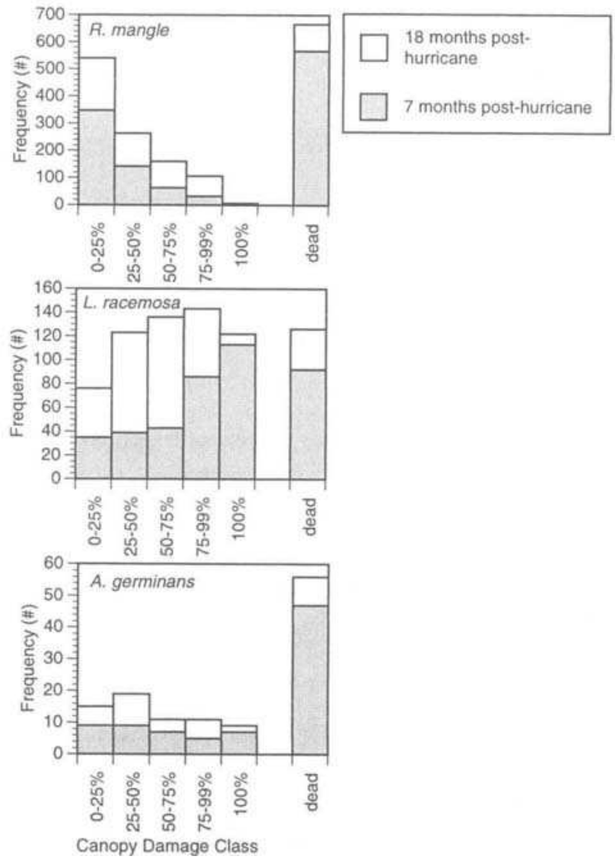

FIGURE 8. Extent of crown damage and mortality of three mangrove species surveyed at 7 months and 18 months following Hurricane Georges. Mortality is cumulative over the two time periods whereas crown damage is the total number of individuals at each sampling period in a category.

complexity. Imbert *et al.* (1996) concluded that in species-poor, structurally homogeneous forests such as mangroves, a species' susceptibility to wind is the major determinant of damage. Our results also suggest the strong role of species composition in regulating forest damage patterns; however, aerial photographs from our study site indicated that canopy surface roughness differs among forest types; the *L. racemosa*-dominated stands have a smooth, even canopy, *A. germinans*-dominated stands have a more open and uneven canopy, and *R. mangle*-dominated stands are intermediate. Observed mortality patterns among forest types at our site increased corresponding to changes in canopy surface roughness; hence, structural differences among forest types also may have contributed to observed damage patterns. Because heights were measured only on a small subsample of trees of each species, we could not directly assess the possible role of tree height and relative canopy position in regulating susceptibility to hurricane damage; thus, our conclusions must be considered tentative.

Local wind gusts and turbulence can produce complex patterns of damage. Although we have no information on the actual wind fields during the hurricane, it is notable that treefall orientation was consistently in a W–SW direction, suggesting little wind turbulence at the stand level (Boose *et al.* 1994). In contrast, wind micro-bursts during Hurricane Andrew were reported as contributing to damage patterns in a south Florida mangrove (Smith *et al.* 1994).

It was surprising that no clear patterns emerged between canopy height and tree damage at our site because other studies of mangrove forests have found tall stands to be more vulnerable to wind damage than shorter stands (Smith *et al.* 1994, Imbert *et al.* 1996). Moreover, rates of mortality among DBH classes observed at our site differed greatly from those reported for the Floridian man-

TABLE 2. *Understory light levels measured by the gap light index (% ± standard error of the mean) among the different forest types in the pre-hurricane forest and in the post-hurricane forest at 7 months and 18 months after Hurricane Georges.*

Vegetation association	Pre-hurricane	Post-hurricane	
		7 Months	18 Months
R. mangle-dominated stands	3.1 ± 0.35	54.4 ± 4.58	49.5 ± 4.57
R. mangle–L. racemosa mix stands	3.4 ± 0.94	48.1 ± 7.24	45.9 ± 7.39
L. racemosa-dominated stands	1.8 ± 0.18	38.0 ± 3.50	29.5 ± 2.80
A. germinans-dominated stands	3.3 ± 1.85	68.8 ± 3.62	67.2 ± 0.88

grove following Hurricane Andrew (Smith *et al.* 1994). At our site, mortality of *A. germinans* was lowest in the 20 to 25 cm DBH size class and mortality of *L. racemosa* was lowest in the 15 to 25 cm DBH class, but maximum mortality was recorded in these size classes for these two species at the Florida site (Smith *et al.* 1994). Smith *et al.* (1994) also reported that mortality of *R. mangle* was greatest in the mid-sized DBH classes, whereas we saw little variation in mortality across size classes. Saplings (>1 m tall and <5 cm DBH) at our site suffered very high mortality (>70%), but sapling mortality at the Florida site (<5 cm DBH) was less than 10 percent (Smith *et al.* 1994). Wadsworth (1959) and Craighead (1971) also indicated that smaller-sized trees (<2 m tall) were the least damaged in mangrove forests following hurricanes. Because forest damage is dependent partially upon storm characteristics, it is difficult to draw specific conclusions from these results without more information regarding local meteorological data specific to the different sites.

Smith *et al.* (1994) observed that survival of individuals growing in preexisting lightning-created canopy gaps was higher than for trees growing in the surrounding canopy following Hurricane Andrew, and suggested that these gap survivors may be an important seed source for recolonization of the forest. At our site, mortality of saplings growing in lightning gaps (Sherman *et al.* 2000) was *ca* 66 percent, which was not different than sapling mortality under the intact forest canopy (72%). The estimate of sapling mortality in gaps was based on a small sample size ($N = 10$ gaps) because we were not able to find the other gaps with tagged saplings; however, there was no indication to suggest that sapling survival was greater in preexisting canopy gaps than under the forest canopy.

Although it is not entirely clear what characteristics determine a mangrove species vulnerability to wind damage, the relatively low mortality of *L. racemosa* can be explained in part by its ability to resprout from epicormic shoots. Numerous individuals of this species that suffered complete canopy loss during the hurricane were refoliating and appeared healthy. Similar observations were reported following hurricane wind damage for mangroves in Nicaragua (Roth 1992) and Florida (Smith *et al.* 1994). In fact, some individuals that we initially classified as dead in the first survey 7 months post-hurricane had resprouted and appeared healthy at 18 months; we adjusted our initial mortality estimates accordingly. Defoliation and subsequent rapid refoliation may be an adaptation to reduce wind resistance and decrease stem breakage during hurricanes. The large decrease in the number of *L. racemosa* individuals that exhibited extensive crown damage (75–100% crown loss) between our surveys at 7 months (63% of the population) and 18 months (20%) post-hurricane was indicative of the rapid canopy recovery rate for this species. Similarly, understory light levels in the post-hurricane forest appeared to be decreasing at a more rapid rate in stands dominated by *L. racemosa* compared to the other forest types within the mangrove.

In contrast to *L. racemosa*, *R. mangle* has little ability to resprout (Tomlinson 1986) and few of the individuals that experienced heavy crown damage survived. Similarly, Imbert *et al.* (1996) attributed the high mortality (>50%) of *R. mangle* in a mangrove in Guadaloupe to its inability to coppice or resprout. *Avicennia germinans* has the ability to resprout (Wadsworth 1959, Tomlinson 1986, Roth 1992, Smith *et al.* 1994), but few individuals at our site had refoliated and many were found standing dead. In contrast to our findings, *A. germinans* experienced significantly lower mortality from hurricane wind damage than other species in both Florida (Smith *et al.* 1994) and Guadeloupe (Imbert *et al.* 1996). The distribution of *A. germinans* at our site was limited, and it was most abundant in a narrow band along the inland freshwater margin of the forest in the first three plots along transect 1. It is notable that both *L. racemosa*

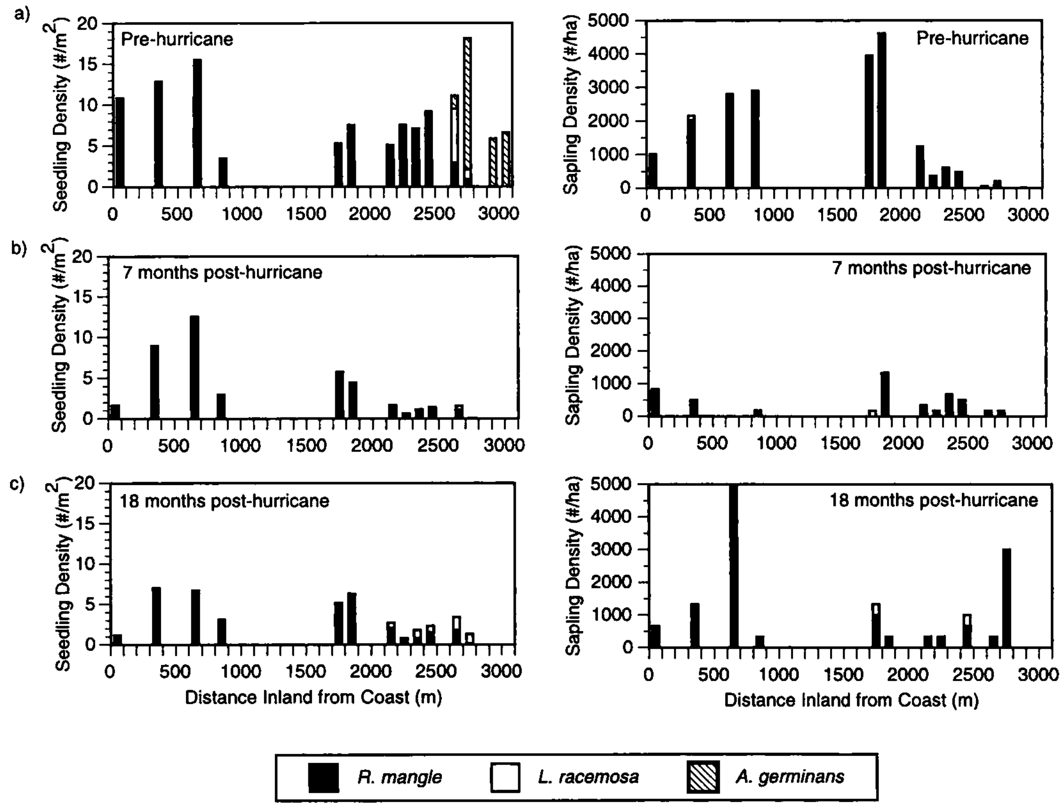

FIGURE 9a. Seedling (≤1 m tall) and sapling (>1 m tall and <5 cm DBH) density measured in plots along transect 1 in the pre-hurricane (a) and post-hurricane forest at 7 months (b) and 18 months (c) following Hurricane Georges.

and *R. mangle* experienced somewhat higher than average mortality in these plots, suggesting that wind exposure may have been higher in this area of the mangroves related either to position in the forest or canopy surface roughness; however, individuals of *A. germinans* that occurred in other stands throughout the forest also experienced high mortality, and we cannot explain the exceptional mortality of this species at our site.

One of the most dramatic effects of the hurricane on the forest was the loss of canopy leaf area and consequent increases in understory light levels. The high light levels in the understory should facilitate mangrove regeneration and recovery of the forest because both survival and growth rates of these species are enhanced in high light environments (Smith 1987, Clarke and Allaway 1993, Ellison & Farnsworth 1993, Sherman *et al.* 2000). Although early recruitment (7 mo post-hurricane) was dominated by *R. mangle,* there was a marked increase in regeneration of both *L. racemosa* and *A. germinans* by 18 months. Thus, seedling and sapling populations of all three species appeared to be recovering rapidly. Other plant species, however, also are becoming established in parts of the forest. In particular, the mangrove fern (*Acrostichum* sp.), which was present at low densities before the hurricane, increased in abundance in the low-salinity regions of the upper tidal forest to densities as high as 3000/ha after the hurricane. The mangrove fern can inhibit mangrove tree regeneration (Roth 1992) and may have long-term effects on forest recovery processes. Other notable invading species include *Cecropia* sp., an early successional tree common throughout the Neotropics. This species was not present in the pre-hurricane forest but individuals have already reached heights of *ca* 5 m in the upper tidal forest. Also, a liana (*Pavonia* sp.), which was present in the pre-hurricane forest, has increased its abundance dramatically since the hurricane.

The sapling layer throughout our site was dom-

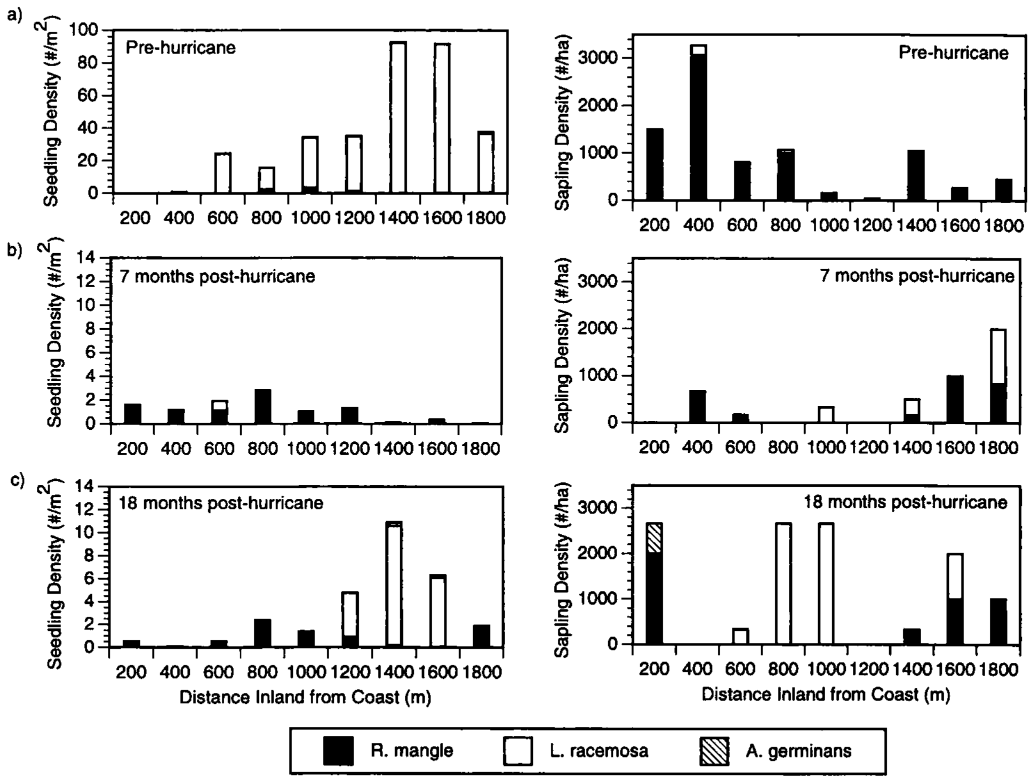

FIGURE 9b. Seedling (≤1 m tall) and sapling (>1 m tall and <5 cm DBH) density measured in plots along transect 2 in the pre-hurricane (a) and post-hurricane forest at 7 months (b) and 18 months (c) following Hurricane Georges.

inated by *R. mangle* before the hurricane, both under the intact forest canopy and in small canopy gaps. Sherman *et al.* (2000) have suggested that the forest would eventually be replaced by *R. mangle* under the current disturbance regime and that large-scale disturbances may be necessary to initiate or maintain the natural patterns in this mangrove forest. Mangrove species have many life history traits characteristic of pioneer species (Tomlinson 1986), suggesting that large-scale disturbances have been an important driving force in their evolution; however, the processes by which mangrove ecosystems recover from large-scale disturbance events and the rates and patterns of recovery are still largely unknown. It is too early to predict the trajectory of forest recovery following this large-scale disturbance, and continued monitoring of the spatial and temporal patterns of development in the post-hurricane forest will be needed to improve our understanding of the role that large-scale disturbance events play on the dynamics of mangrove forest ecosystems.

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