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Hurricane Damage and Regeneration in Fringe Mangrove Forests of Southeast Florida, USA

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ABSTRACT



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Hurricane damage was surveyed at two sites in mangrove forests fringing Biscayne Bay in south Florida that were hit by Hurricane Andrew on 24 August 1992. Two sites not impacted by Andrew and last hit by a major hurricane in 1965 were also surveyed. *Avicennia germinans* (L.) Stearn (black mangrove), *Laguncularia racemosa* Gaertn.f. (white mangrove), and *Rhizophora mangle* L. (red mangrove) were found to differ in their susceptibility to hurricane-related damage and mortality and in their mechanism of regeneration following hurricanes. The highest mortality associated with Hurricane Andrew was observed in *R. mangle* (85.1%); mortality was lower in *A. germinans* (65.0%) and *L. racemosa* (59.5%), values nonetheless much higher than tree mortality rates in other communities in south Florida. The ability to resprout epicormically in *A. germinans* and *L. racemosa* following the hurricane is probably the primary reason for their higher survival; epicormic sprouts were not observed in *R. mangle*. Despite its higher mortality, *R. mangle* sustained proportionally less severe structural damage than *A. germinans* and *L. racemosa*. Reestablishment of the population of *R. mangle* is occurring primarily through seedling recruitment, while regeneration of *A. germinans* and *L. racemosa* is primarily via epicormic sprouting. At the two sites not impacted by Hurricane Andrew, patterns of regeneration similar to those observed following Hurricane Andrew appear to have occurred following Hurricane Betsy in 1965.

ADDITIONAL INDEX WORDS: *Avicennia germinans*, *Laguncularia racemosa*, *Rhizophora mangle*, Hurricane Andrew, mortality, recruitment, resprouting, seedlings, wind direction.

INTRODUCTION

Mangrove forests in south Florida and much of the Caribbean region experience frequent hurricanes (JIMENEZ *et al.*, 1985; CHAPMAN, 1976; LUGO and SNEDAKER, 1974; NEUMANN *et al.*, 1993; SIMPSON and LAWRENCE, 1971; GENTRY, 1974), and there have been numerous qualitative reports of hurricane damage to neotropical mangroves over the past several decades (*e.g.*, DAVIS, 1940; EGLER, 1952; CRAIGHEAD and GILBERT, 1962; STODDART, 1971; OGDEN, 1992). Significantly higher mortality was recorded for larger than for smaller trees in mangroves in Nicaragua affected by Hurricane Joan (ROTH, 1992), but no significant differences in

mortality or recovery were found among the species studied, possibly because of small sample size (66 trees total). In a more extensive study of initial mangrove mortality following Hurricane Andrew, SMITH *et al.* (1994) reported a non-linear increase in mortality with increasing size and lower mortality in *Avicennia germinans*, (L.) Stearn (black mangrove) than in other species. Other than these studies, little quantitative information exists concerning the effects of hurricanes on mangroves.

Hurricane Andrew passed over south Florida on 24 August 1992. Observations made by W.J. Platt in December 1992 in mangrove forests fringing Biscayne Bay suggested that *Rhizophora mangle* L. (red mangrove), *A. germinans*, and *Laguncularia racemosa* (L.) Gaertn.f. (white mangrove), the three mangrove tree species present,

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exhibited differences in mortality and recovery. *Rhizophora mangle* appeared to experience higher mortality than *A. germinans* or *L. racemosa*, but seedlings of *R. mangle* appeared to be more abundant than seedlings of *A. germinans* and *L. racemosa*. These field observations led to several questions. First, are there differences in hurricane-induced structural damage or mortality among the three species of mangroves? Second, are there differences in mechanisms of regeneration among the three species? And third, will the structure of forests hit by Andrew eventually resemble the structure of other forests in south Florida that have not been recently impacted by hurricanes (*e.g.*, within the last 30 years)?

To address the first two questions, we examined patterns of damage, mortality, and recovery in trees, saplings, and seedlings in mangrove forests on Biscayne Bay that experienced high winds and storm tides during Hurricane Andrew. To address the third question, we studied intact mangrove forests last impacted by a major hurricane in 1965 (Betsy). Our results indicate that the three species of mangroves differ both in susceptibility to hurricane-induced damage and mortality and in mechanisms of regeneration following hurricanes. Interspecific variation in response to hurricanes can be attributed to fundamental differences in life history and anatomy.

STUDY SITES

Hurricane Andrew crossed the southeastern coast of Florida at Biscayne Bay at 5:05 A.M. EDT (0905 Greenwich Mean Time) on 24 August 1992 (RAPPAPORT, 1993), heading west at a speed of approximately 16 km/h (STONE *et al.*, 1993). A minimum recorded central barometric pressure of 922 mb, maximum sustained wind speed of 232 km/h with gusts to at least 280 km/h (Category 4 on the Saffir/Simpson hurricane scale), and a storm tide up to 5.2 m above mean sea level (AMSL) all occurred about the time the eye of the hurricane crossed the west coast of Biscayne Bay (RAPPAPORT, 1993; STONE *et al.*, 1993). Storm tide is the sum of the storm surge and the astronomical tide, which was near high tide (0.61–0.76 m AMSL) at landfall (RAPPAPORT, 1993). Mangrove forests along Biscayne Bay were directly in the path of the storm as it came ashore (Figure 1).

Mangrove forests were studied in March 1993 (seven months after Hurricane Andrew) and Jan-

uary 1994 at four sites in Dade and Monroe Counties in south Florida: Cutler Canal, Mowry Canal, Coot Bay Pond, and Key Largo Sound (Figure 1). These sites were selected based on their hydrogeologic characteristics and location relative to the path of Hurricane Andrew. They are located in the middle to lower intertidal zone along the shorelines of bays, are not impounded by natural or man-made berms or levees (*i.e.*, they drain freely following tidal inundation), and at the time of Hurricane Andrew contained mangrove trees 15 m or more in height. The mangrove forests at these sites are similar to the “fringe” forest type described by LUGO and SNEDAKER (1974).

The Cutler Canal site (25°37'N, 80°18'W) is on the southern end of the Charles Deering Estate just north of Biscayne National Park. The right (northern) eye wall of Hurricane Andrew passed over this site. Recorded barometric pressures in the vicinity of this site were about 940 mb, and wind gusts were estimated to be as high as 280 km/h (RAPPAPORT, 1993). Cutler Canal was within the zone of maximum damage reported by WAKIMOTO and BLACK (1994). The site is located less than 1 km from the site where the maximum storm tide of 5.2 m was recorded (RAPPAPORT, 1993); we found storm debris as high as 5.5 m above the ground in trees at Cutler Canal.

The eye of the hurricane passed over the Mowry Canal site (25°28'N, 80°21'W) in Biscayne National Park. This site is located in an area where sustained winds were estimated to fall within a range of 184–240 km/h, and storm tides were about 2.1 m (RAPPAPORT, 1993). The last major hurricanes to pass over or near the Cutler Canal and Mowry Canal sites prior to Hurricane Andrew occurred in 1926, 1945, and 1950 (Figure 2; JARVINEN *et al.*, 1984; PERKINS and ENOS, 1968; GENTRY, 1974; NEUMANN *et al.*, 1993). Major hurricanes are defined here as hurricanes of class 3, 4, or 5 on the Saffir/Simpson scale (winds ≥ 178 km/h and/or storm surge ≥ 2.74 m above normal; NEUMANN *et al.*, 1993).

The Coot Bay Pond (25°11'N, 80°54'W) and Key Largo Sound (25°08'N, 80°24'W) sites were relatively unaffected by winds and storm tides associated with Hurricane Andrew. These sites are located near the south edge of Coot Bay Pond in Everglades National Park and on the western shore of Largo Sound in John Pennekamp Coral

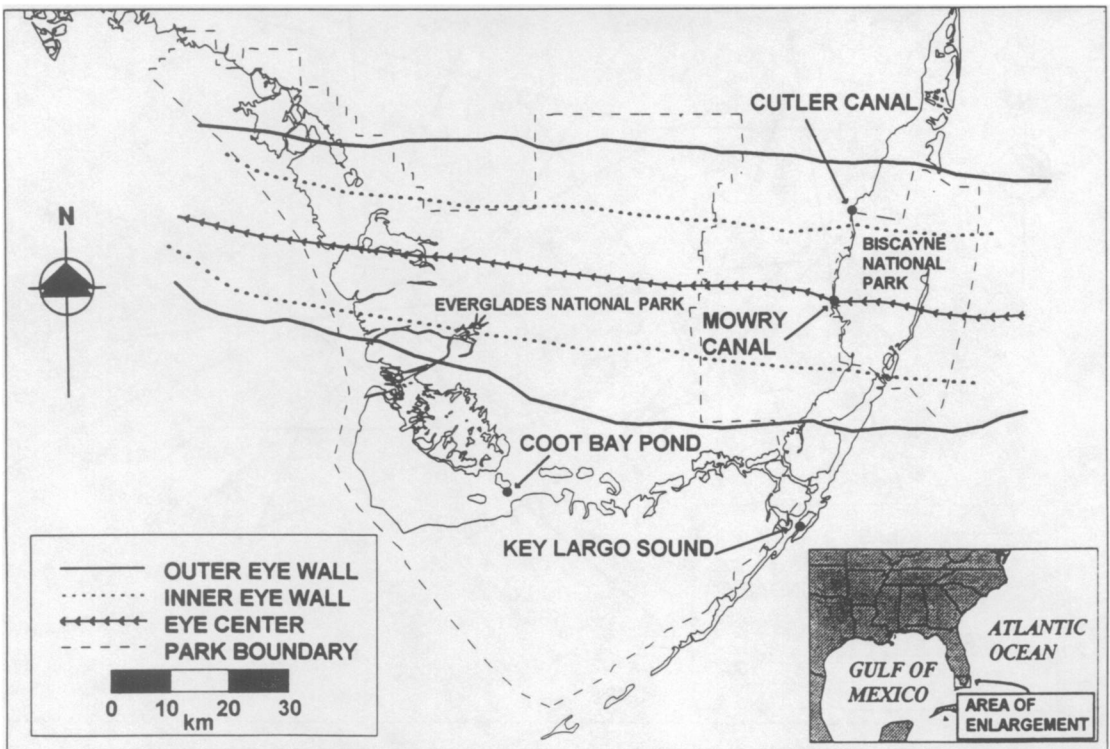


Figure 1. Path of Hurricane Andrew across south Florida and location of mangrove study sites. Tracks of eye and eyewalls based on National Weather Service radar images taken at 18-minute intervals (see Armentano *et al.*, 1995). Base map provided by Everglades National Park.

Reef State Park on Key Largo. The last major hurricanes to pass over or near these sites occurred in 1909, 1929, 1935, 1960 (Donna), and 1965 (Betsy) (Figure 2; JARVINEN *et al.*, 1984; BALL *et al.*, 1967; CRAIGHEAD and GILBERT, 1962; PERKINS and ENOS, 1968; GENTRY, 1974; NEUMANN *et al.*, 1993).

METHODS

Vegetation Sampling

At each of the four sites, two replicate 50 m by 10 m strip transects containing five 10 m by 10 m plots each were established in March 1993. The exact locations of the transects at each site were selected haphazardly within a region approximately 20 to 30 m from the shore of the adjacent bay. The transects were set up parallel to the shoreline in an approximately north-south orientation.

Species and diameter at breast height (DBH) were recorded for all trees (woody plants having ≥ 2.5 cm stem diameter) in each plot. One of the following six damage categories was assigned to each tree: trunk snap (above ground level), tip-up (roots pulled up when tree fell), severe lean ($>45^\circ$ from vertical), lean ($<45^\circ$ from vertical), severe branch removal, and branch removal. In addition, height of snaps and azimuth (compass direction of trunk from base to crown) of leans, tip-ups, or snaps were measured where direction of fall or lean was evident (*i.e.*, crowns were still present in the vicinity). Where trees had multiple trunks, separate measurements were made for each trunk. Trees hit by a falling tree were noted as such. Each tree was recorded as alive or dead and recovery status was noted (epicormic shoots, root shoots, or leaves present). For the Everglades and Key Largo sites, trees that had died prior to Andrew (generally evident as par-

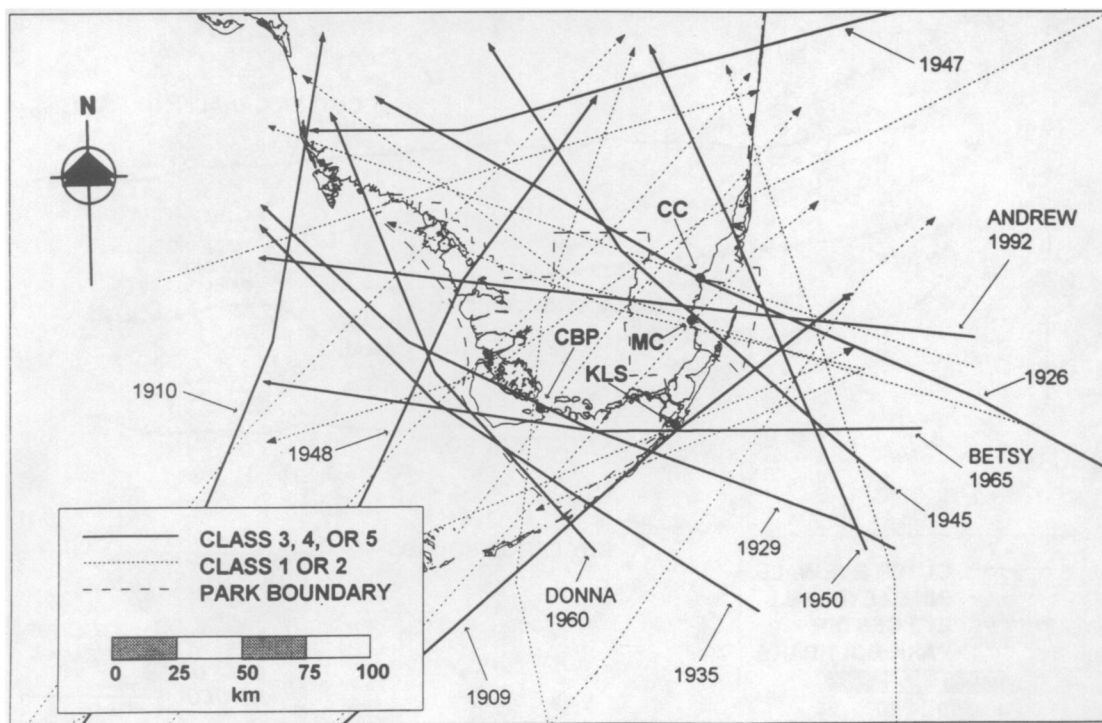


Figure 2. Paths of hurricanes making landfall in south Florida between 1886 and 1992. Storm tracks based on latitude and longitude data for storm position at 6-hour intervals in Jarvinen *et al.* (1984). Names and dates given only for hurricanes of Saffir/Simpson class 3 or higher. CC = Cutler Canal, MC = Mowry Canal, CBP = Coot Bay Pond, KLS = Key Largo Sound.

tially rotted standing, leaning, or fallen logs with bark gone) were included in the survey.

In addition to tree measurements, the number, species, and condition (alive or dead) of established (standing) seedlings (any juvenile <1 m in height) and saplings (≥ 1 m in height, <2.5 cm stem diameter) in a 5 m by 5 m quadrat in a randomly selected corner of each 10 m by 10 m plot were also recorded. Finally, measurements of Photosynthetically Active Radiation (PAR; 400 to 700 nm waveband) flux density, through the canopy and reflected off the sediment surface, were measured using a LICOR LI-185B meter equipped with an LI-190SA Quantum Sensor. Through-canopy and reflected flux densities were measured at various times during daylight hours with the sensor pointed upward and downward, respectively, at a height of 1 m in the center of each 10 m by 10 m plot. Flux density readings for full sunlight were made at each site by pointing the sensor toward the sun at a height

of approximately 2 m in areas where no canopy was present so that plot readings could be normalized.

In January 1994, height and number of branches were measured on approximately 200 seedlings per site in the transects at Cutler Canal, Mowry Canal, and Key Largo Sound. Additionally, seedlings in two 10 m by 10 m plots in the transects at each site were counted.

Data Analysis

Analyses were performed on: tree density, size (DBH), damage, mortality, multiple trunk, and azimuth data; seedling and sapling density and mortality data; seedling height and branch number data; and PAR flux density data. Data were analyzed using the SAS statistical package (SAS INSTITUTE, 1990); a significance level of $P = 0.05$ was used in interpreting results of all statistical tests.

Analysis of Variance (ANOVA) was used to examine differences in tree density and size among sites and species, in tree size among damage categories, and in PAR flux density among sites. Data were analyzed as a nested design with site, species, or damage considered the main effects. The Satterthwaite approximate F test (indicated as F^{**}) was used for tree size analyses, where sample sizes were unequal; otherwise, exact F tests were used. Seedling height and branch number data were analyzed as a one-way ANOVA with site as the main effect. Tukey's Studentized Range test was used to compare means for balanced analyses, and the Bonferroni method was used to make comparisons among least squares means for the unbalanced tree size analyses. Accordingly, least squares means are presented when summarizing tree size data.

To facilitate interpretation, the six damage classes assigned to trees in the field were grouped into three damage categories for data analysis. Trees with snapped trunks or that were tipped up were grouped in a "snap" damage category, leaning or severely leaning trees were grouped in a "lean" damage category, and trees with branch removal or severe branch removal were grouped in a "branch" damage category. Where more than one type of damage occurred on a single stem, the more severe damage category was used in analyses (snap more severe than lean, lean more severe than branch).

Data were transformed prior to analysis where necessary to reduce heterogeneity of variances or to reduce deviations from normality. Tree density and size data and seedling height and branch number data were log-transformed ($\ln(x + 1)$). PAR flux density data were normalized as a proportion of full sunlight and square root-transformed (for PAR through canopy) or logit-transformed [$\ln(p/(1 - p))$; p = proportion of full sunlight] (for PAR reflected off sediment).

Chi-square (χ^2) tests were used to test independence of species and mortality, species and damage category, site and seedling mortality, and species and presence of multiple trunks; z-tests for comparison of two probabilities were used where necessary. Logistic regression was performed to identify relationships between tree size and mortality; the -2 Log Likelihood test (HOSMER and LEMESHOW, 1989) was used in assessing model fit.

Azimuth data were analyzed by first determining the number of occurrences of trees with

azimuth values in each of eight azimuth categories (north = $338^\circ - 22^\circ$, northeast = $23^\circ - 67^\circ$, east = $68^\circ - 112^\circ$, etc.). Azimuth data were then bootstrapped by randomly assigning one of eight azimuth values ($N = 0^\circ$, $NE = 45^\circ$, $E = 90^\circ$, etc.) to each of n values (where n = the number of trees having azimuth readings at each site), and recording the maximum percentage of total occurrences in any direction. This procedure was repeated 1000 times for each n , and the number of times out of 1000 repetitions that the simulated maximum percentage exceeded the observed maximum percentage in any of the eight azimuth categories was recorded. This value represented the likelihood that values as large or larger than those recorded in the field could be expected by chance.

Where trees had multiple trunks originating from a common base, each trunk was considered as a separate tree stem in analyses of damage, size, density, and azimuths. However, trees with multiple trunks were considered as single individuals (genets) in tree mortality and multiple trunk analyses (except in logistic regression of tree mortality on size, where individual trunks on the same tree were of different sizes). Dead trees that could not be identified to species were excluded from all analyses.

RESULTS

Pre-Hurricane Structure

All four sites contained mixtures of *R. mangle*, *A. germinans*, and *L. racemosa*. A total of 1257 tree stems were censused, of which 1030 were living and 227 were dead at the time of Hurricane Andrew; 29 of the dead trees were excluded from analyses because they could not be differentiated as *A. germinans* or *L. racemosa* due to a lack of bark or other distinguishing features. Densities and sizes of the 1030 living tree stems are presented in Table 1.

In general, the sites were characterized by a few large *A. germinans* or *L. racemosa* trees interspersed among an abundance of small *R. mangle* trees. The mean density of *R. mangle* was higher than that of *A. germinans* or *L. racemosa* at Cutler Canal, Coot Bay Pond, and Key Largo Sound; *L. racemosa* occurred at a higher density than the other species at Mowry Canal (Table 1). Analysis of variance indicated densities of each of the three species varied significantly among

Table 1. Densities and sizes of three species of mangroves at four sites in southeast Florida alive at the time of impact of Hurricane Andrew. Density values are mean \pm SE of tree density in ten plots of 100 m² at each site. DBH values are mean \pm SE (number of trees); range of DBH values also given.

Site	Species			TOTAL
	<i>Avicennia germinans</i>	<i>Laguncularia racemosa</i>	<i>Rhizophora mangle</i>	
Density (number/100 m ²)				
Impacted by Andrew				
Cutler Canal	2.00 \pm 0.650	7.00 \pm 1.63	25.8 \pm 2.51	34.8 \pm 2.64
Mowry Canal	0.1 \pm 0.1	17.1 \pm 1.54	6.30 \pm 1.30	23.5 \pm 2.69
Not impacted by Andrew				
Coot Bay Pond	5.30 \pm 0.844	1.0 \pm 0.447	12.0 \pm 0.843	18.3 \pm 1.36
Key Largo Sound	2.10 \pm 0.348	0.1 \pm 0.1	24.2 \pm 1.97	26.4 \pm 2.20
DBH (cm)				
Impacted by Andrew				
Cutler Canal	11.2 \pm 1.29 (20) Range = 2.9-32.2	16.1 \pm 1.10 (70) Range = 3.1-35.1	7.76 \pm 0.295 (258) Range = 2.5-29.0	11.0 \pm 0.486 (348) Range = 2.5-35.1
Mowry Canal	14.0 \pm 4.97 (1) Range = 14.0	12.7 \pm 0.483 (171) Range = 4.1-45.0	10.6 \pm 0.672 (63) Range = 2.5-29.0	11.3 \pm 1.89 (235) Range = 2.5-45.0
Not impacted by Andrew				
Coot Bay Pond	16.9 \pm 0.785 (53) Range = 3.0-34.2	10.6 \pm 2.30 (10) Range = 3.4-15.4	9.09 \pm 0.419 (120) Range = 2.5-24.9	12.5 \pm 0.681 (183) Range = 2.5-34.2
Key Largo Sound	19.0 \pm 1.18 (21) Range = 5.8-57.0	12.7 \pm 6.08 (1) Range = 12.7	11.1 \pm 0.296 (242) Range = 2.9-32.1	14.9 \pm 1.90 (264) Range = 2.9-57.0

the four sites (*A. germinans*: $MS = 4.79$, $F_{3,4} = 15.3$, $P = 0.0118$; *L. racemosa*: $MS = 16.3$, $F_{3,4} = 87.6$, $P = 0.0004$; *R. mangle*: $MS = 4.26$, $F_{3,4} = 8.68$, $P = 0.0317$). Tukey's Studentized Range test indicated that *R. mangle* occurred at significantly higher densities at Cutler Canal and Key Largo Sound than at Mowry Canal (densities at Coot Bay Pond were intermediate and not significantly different from the other sites). *Laguncularia racemosa* occurred at significantly higher densities at Mowry Canal than at Cutler Canal which had significantly higher densities than Coot Bay Pond or Key Largo Sound. *Avicennia germinans* occurred at significantly higher densities at Coot Bay Pond than at Mowry Canal (densities at Key Largo Sound and Cutler Canal were intermediate and not significantly different from the other sites). Few *A. germinans* occurred at Mowry Canal and few *L. racemosa* occurred at Key Largo Sound. At the time of the hurricane, total tree density did not vary significantly among sites ($MS = 0.676$, $F_{3,4} = 3.48$, $P = 0.1300$).

Avicennia germinans and *L. racemosa* tended to be larger than *R. mangle* at all four sites (Table 1). For the four sites combined, *A. germinans* and *L. racemosa* did not differ significantly in size, but both were significantly larger than *R.*

mangle (Bonferroni multiple comparison procedure). However, mean tree sizes within species did not vary significantly among sites (*A. germinans*: $MS = 1.82$, $F_{3,4.42}^{**} = 3.92$, $P = 0.0994$; *L. racemosa*: $MS = 0.807$, $F_{3,4.86}^{**} = 1.71$, $P = 0.2823$; *R. mangle*: $MS = 5.04$, $F_{3,4.05}^{**} = 1.92$, $P = 0.2660$).

Larger proportions of *A. germinans* and *L. racemosa* than *R. mangle* had multiple trunks. While 6.38% of *A. germinans* trees and 5.69% of *L. racemosa* trees had multiple trunks, they occurred in only 0.876% of *R. mangle* trees. Numbers of multiple trunks were not independently distributed among the three species ($\chi^2_2 = 27.3$, $P < 0.0005$).

Although not impacted by Hurricane Andrew, 88 dead trees were present in plots at Coot Bay Pond and 110 dead trees were present in plots at Key Largo Sound. These dead trees comprised both fallen logs and standing dead trees in varying states of decomposition, and included long-dead large trees as well as smaller trees that had died more recently. The mean sizes of dead trees at Coot Bay Pond and Key Largo Sound were similar and tended to be slightly smaller than mean sizes of living trees shown in Table 1.

Densities of seedlings and saplings at the four sites seven months after Hurricane Andrew, as

well as the proportion that were standing but dead, are presented in Table 2. Seedlings of *R. mangle* vastly outnumbered seedlings of the other two species at both impacted and non-impacted sites, and the ANOVA of seedling density indicated a highly significant effect of species ($MS = 195$, $F_{2,8} = 83.7$, $P < 0.0001$). The density of *R. mangle* and *A. germinans* seedlings did not vary significantly among the four sites (*A. germinans*: $MS = 3.74$, $F_{3,4} = 4.20$, $P = 0.0998$; *R. mangle*: $MS = 4.44$, $F_{3,4} = 1.18$, $P = 0.4222$). However, the density of *L. racemosa* seedlings was greater at Coot Bay Pond than at the other sites (Table 2), and the effect of site was significant ($MS = 3.86$, $F_{3,4} = 7.63$, $P = 0.0394$). Total seedling density did not vary significantly among sites ($MS = 4.27$, $F_{3,4} = 1.51$, $P = 0.3404$). Saplings of all species occurred infrequently at low densities, with only *A. germinans* saplings at Cutler Canal and Mowry Canal, *R. mangle* and *L. racemosa* saplings at Coot Bay Pond, and no saplings at Key Largo Sound (Table 2).

Hurricane Damage

Hurricane Andrew resulted in high mortality in all three mangrove species at Cutler Canal and Mowry Canal. Mortality of *R. mangle* for these sites combined (85.1%) was greater than mortality of *A. germinans* (65.0%) and *L. racemosa*

(59.5%). Numbers of dead and living trees were not independently distributed among the three species ($\chi^2_2 = 43.7$, $P < 0.0005$). The proportion of dead *R. mangle* trees was significantly greater than the proportion of dead *A. germinans* and *L. racemosa* trees combined ($z = 6.50$, $P < 0.0002$), and the proportion of dead *A. germinans* trees was not significantly different from the proportion of dead *L. racemosa* trees ($z = 0.490$, $P = 0.6879$).

Results of logistic regression analysis indicated significant relationships between size (DBH) and hurricane-induced mortality for two of the three species. No significant relationships between DBH and mortality occurred for *A. germinans* (-2 Log Likelihood test: $\chi^2_3 = 5.53$, $P = 0.1370$), although the sample size was only 21 trees. For *L. racemosa* ($n = 222$ trees), mortality increased as tree size increased, and logistic regression indicated a best-fit non-linear relationship. The -2 Log Likelihood test ($\chi^2_3 = 9.37$, $P = 0.0248$) indicates a significant non-linear relationship between mortality and DBH for *L. racemosa* ($\text{logit}[p] = -2.16 + 0.666 * \text{DBH} - 0.0490 * \text{DBH}^2 + 0.00108 * \text{DBH}^3$, where p = probability of being killed by the hurricane). In this model, 54.3% of the predicted probabilities and observed responses were concordant.

Mortality also increased as tree size increased for *R. mangle* ($n = 318$ trees), and logistic regression indicated a best fit non-linear relationship.

Table 2. Densities of mangrove seedlings and saplings (number per 100 m²) at four sites in southeast Florida seven months after Hurricane Andrew. All values are mean \pm SE of seedling density in 10 plots of 25 m². Percent dead but still standing given in parentheses.

	Site	Species		
		<i>Avicennia germinans</i>	<i>Laguncularia racemosa</i>	<i>Rhizophora mangle</i>
Seedlings	Impacted by Andrew			
	Cutler Canal	2.40 \pm 1.07 (16.7%)	4.80 \pm 2.05 (8.33%)	174 \pm 32.4 (51.8%)
	Mowry Canal	1.20 \pm 0.854 (0%)	1.60 \pm 0.884 (0%)	530 \pm 124 (23.0%)
	Not impacted by Andrew			
	Coot Bay Pond	5.60 \pm 2.99 (0%)	22.4 \pm 8.20 (1.79%)	493 \pm 158 (12.0%)
Saplings	Key Largo Sound	19.2 \pm 5.23 (2.08%)	0.400 \pm 0.400 (0%)	806 \pm 106 (25.6%)
	Impacted by Andrew			
	Cutler Canal	0.400 \pm 0.400 (0%)	0	0
	Mowry Canal	0.400 \pm 0.400 (0%)	0	0
	Not impacted by Andrew			
	Coot Bay Pond	0	1.20 \pm 0.611 (0%)	5.60 \pm 2.54 (0%)
	Key Largo Sound	0	0	0

The -2 Log Likelihood test ($\chi^2_2 = 17.0$, $P = 0.0002$) indicates a significant non-linear relationship between mortality and DBH ($\text{logit}[p] = 0.787 + 0.0275 * \text{DBH}^2 - 0.00097 * \text{DBH}^3$). For the *R. mangle* model, 67.7% of the predicted probabilities and observed responses were concordant, indicating better model fit than for the *L. racemosa* model.

In addition to interspecific differences in mortality, severity of hurricane damage varied among the three species. The degree of damage sustained was not independently distributed among species ($\chi^2_4 = 78.4$, $P < 0.0005$). Higher percentages of stems occurred in the snap damage category for *A. germinans* and *L. racemosa* than for *R. mangle* (Figure 3). In contrast, *R. mangle* had larger percentages of trees that sustained lean or branch damage than did *A. germinans* or *L. racemosa*. Practically all trees at the hurricane-impacted sites sustained some type of damage, with only four trees at Cutler Canal and no trees at Mowry Canal sustaining no visible damage.

The sizes of trees in the snap damage category tended to be larger than sizes of trees in the lean or branch damage categories (Table 3). However, significant differences in size among damage categories occurred only in *L. racemosa* at Cutler Canal and in *R. mangle* at Cutler Canal and Mowry Canal. The snap damage category contained significantly larger trees of these species

than the lean category at Cutler Canal but not at Mowry Canal. For *R. mangle*, trees in the branch damage category were significantly smaller than those in other damage categories at Mowry Canal but not at Cutler Canal. Although *A. germinans* trees in the snap damage category tended to be larger than trees in other damage categories, this relationship was not significant.

Almost half of the *A. germinans* and *L. racemosa* trees in the snap, lean, or branch damage categories resprouted epicormically following the hurricane (*A. germinans* = 42.9%, *L. racemosa* = 46.4%). Of the trees that resprouted, 11.1% of the *A. germinans* and 21.4% of the *L. racemosa* trees had died by the time we sampled the trees. In contrast, epicormic sprouts were not observed in *R. mangle*. Root sprouts were not observed in any species during the March 1993 sampling but were noted on several *A. germinans* in January 1994.

Azimuths of trees that were leaning or snapped were primarily aligned within a 90° range at both Cutler Canal and Mowry Canal (Figure 4). At Cutler Canal, located directly beneath the right (northern) eye wall (Figure 1), 47.0% of all tree stems fell or leaned toward the southwest ($203^\circ - 247^\circ$), and 79.1% were aligned between 180° and 270° . At Mowry Canal, located almost directly beneath the center of the eye (Figure 1), 47.1% of all trees stems fell or leaned toward the southeast ($113^\circ - 157^\circ$), and 66.2% were aligned between 90° and 180° . Based on a bootstrapping analysis of azimuth data, the probability that the maximum observed percentage of trees would occur in one of the eight azimuth categories by chance alone was less than 0.001 for both Cutler Canal and Mowry Canal.

Also shown in Figure 4 are radar graphs of tree stem azimuths for Coot Bay Pond and Key Largo Sound, which were both last hit by major hurricanes in 1965 (Betsy) and 1960 (Donna). Although the pattern is not as well-defined as at the sites hit by Andrew, tree stems at these sites still show alignment primarily in one direction. Trees at Coot Bay Pond were aligned primarily toward the south (29.2%) or southwest (22.2%); 52.8% were aligned between 135° and 225° . Trees at Key Largo Sound fell or leaned primarily toward the southwest (31.8%); 50.0% were aligned between 180° and 270° . The probabilities of exceeding the maximum observed percentages of trees falling in one of the eight azimuth categories by chance alone are approximately 0.006 for

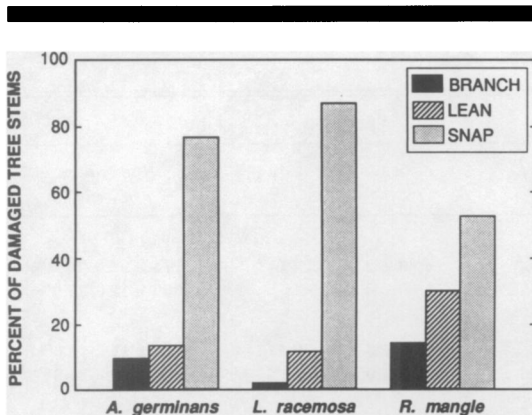


Figure 3. Percent of damaged tree stems in each of three damage categories at mangrove study sites impacted by Hurricane Andrew (Cutler Canal and Mowry Canal). BRANCH = branches removed, LEAN = trunk leaning, SNAP = trunk snapped or tipped up.

Table 3. Sizes of trees at Cutler Canal and Mowry Canal by hurricane damage category. Values are mean DBH (cm) \pm SE (number of trees). Within a site and species, means having the same letter are not significantly different using the Bonferroni multiple comparison method.

Species	Damage Category		
	Branch	Lean	Snap
<i>Cutler Canal</i>			
<i>A. germinans</i>	4.06 \pm 5.49 (2)a	5.31 \pm 4.62 (3)a	11.2 \pm 1.89 (15)a
<i>L. racemosa</i>	18.1 \pm 6.43 (1)ab	9.38 \pm 2.04 (10)b	16.7 \pm 0.855 (59)a
<i>R. mangle</i>	7.39 \pm 0.667 (40)ab	6.63 \pm 0.442 (88)b	8.00 \pm 0.376 (126)a
<i>Mowry Canal</i>			
<i>A. germinans</i>	No trees	No trees	14.0 \pm 7.30 (1)
<i>L. racemosa</i>	5.30 \pm 6.40 (1)a	11.3 \pm 1.66 (16)a	12.7 \pm 0.517 (154)a
<i>R. mangle</i>	4.99 \pm 1.63 (7)b	10.8 \pm 1.51 (9)a	11.8 \pm 0.636 (47)a

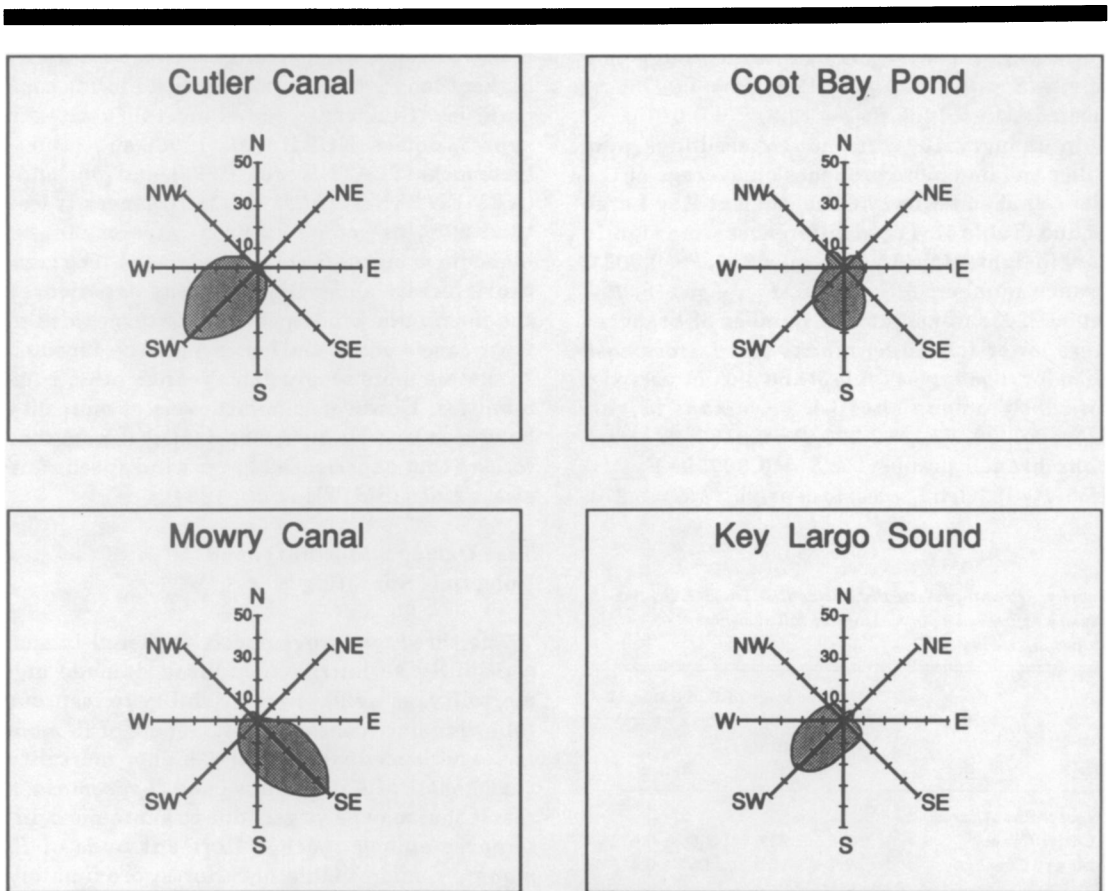


Figure 4. Percentage of all snapped or leaning trees having azimuth readings in each of eight azimuth categories at the four mangrove study sites.

Coot Bay Pond and less than 0.004 for Key Largo Sound.

Analyses of seedling mortality were limited to *R. mangle* because of the low densities of *A. germinans* and *L. racemosa* seedlings. Larger proportions of dead *R. mangle* seedlings occurred at Cutler Canal (51.8%) than at other sites (Table 2). Numbers of dead and alive seedlings were not distributed independently among Cutler Canal and the other three sites combined ($\chi^2_1 = 206$, $P < 0.0005$), and the proportion of dead seedlings was significantly greater at Cutler Canal than at the other three sites combined ($z = 12.4$, $P < 0.0002$). No dead saplings were observed in plots at any site. Photosynthetically Active Radiation flux density measurements expressed as a percentage of full sunlight through the canopy (sensor pointed up at 1 m height) and reflected off the sediment surface (sensor pointed down at 1 m height) were higher at the impacted sites than at the non-impacted sites (Table 4). Flux density varied significantly among sites (through canopy: $MS = 0.804$, $F_{3,4} = 19.8$, $P = 0.0073$; reflected: $MS = 14.3$, $F_{3,4} = 12.2$, $P = 0.0175$).

In January 1994, *R. mangle* seedlings were taller and had more branches on average at Cutler Canal and Mowry Canal than at Key Largo Sound (Table 5). These differences were significant (height: $MS = 15.3$, $F_{2,422} = 212$, $P < 0.0001$; branch number: $MS = 15.8$, $F_{2,422} = 118$, $P < 0.0001$). Mean height and number of branches were lower for *A. germinans* and *L. racemosa* than for *R. mangle* (Table 5) and did not vary significantly among sites (*A. germinans* height: $MS = 0.0399$, $F_{2,62} = 0.200$, $P = 0.8157$; *A. germinans* branch number: $MS = 0.00759$, $F_{2,62} = 1.55$, $P = 0.2204$; *L. racemosa* height: $MS = 0.274$,

$F_{2,95} = 2.36$, $P = 0.1002$; *L. racemosa* branch number: $MS = 0.00832$, $F_{2,95} = 0.250$, $P = 0.7812$). In addition to being taller and having more branches, some *R. mangle* seedlings had developed aerial roots, and some were flowering.

Densities of living seedlings sampled in January 1994 at Cutler Canal, Mowry Canal, and Key Largo Sound are summarized in Table 6. Recruitment of *A. germinans* and *L. racemosa* seedlings appears to have occurred between March 1993 and January 1994, based on observed increases in seedling density during this period. Densities of *R. mangle* decreased at Cutler Canal and remained about the same at Mowry Canal. Seedling densities of all species decreased at Key Largo Sound.

DISCUSSION

Mangroves along Biscayne Bay were greatly impacted by Hurricane Andrew. For all three mangrove species, mortality was substantially higher than for trees in other south Florida communities. Hurricane-related mortality rates in cypress domes (NOEL *et al.*, 1995), subtropical hammocks (SLATER *et al.*, 1995), and pinelands (ARMENTANO *et al.*, 1995) were generally less than 20%, as compared with rates of 60% or higher in mangroves at our study sites. The mangrove forests along Biscayne Bay experienced the maximum wind speeds and storm tides of Hurricane Andrew and hence might be expected to sustain more severe damage than other communities. However, similar levels of mortality have been noted in hurricane-damaged mangrove forests that experienced lower wind speeds and storm tides (SMITH *et al.*, 1994).

Tree Damage, Mortality, and Epicormic Sprouting

The three mangrove species differed in susceptibility to hurricane-induced damage and mortality, as well as in their ability to resprout following hurricane damage. Genets of *R. mangle* experienced significantly higher mortality than genets of *A. germinans* and *L. racemosa*, a result that may be largely due to anatomical differences among species. Dormant buds of *R. mangle* remain viable only for approximately three years (TOMLINSON, 1986), so that older stems cannot resprout when stem tips are broken off or killed; we observed no epicormic sprouting

Table 4. Photosynthetically Active Radiation (PAR) flux density expressed as percentage of full sunlight. Values are means \pm SE.

Site	Percentage of Full Sunlight	
	Through Canopy	Reflected
<i>Impacted by Andrew</i>		
Cutler Canal	69.5 \pm 7.32%	3.60 \pm 0.571%
Mowry Canal	49.7 \pm 5.16%	2.57 \pm 0.416%
<i>Not impacted by Andrew</i>		
Coot Bay Pond	8.15 \pm 2.34%	0.419 \pm 0.0862%
Key Largo Sound	9.23 \pm 1.03%	0.397 \pm 0.0540%

Table 5. Height and number of branches for mangrove seedlings sampled in January 1994. Values are means \pm SE (n); range also given.

Site	Species		
	<i>A. germinans</i>	<i>L. racemosa</i>	<i>R. mangle</i>
Height (cm)			
Cutler Canal	16.5 \pm 1.75 (26) Range = 10-40	12.0 \pm 0.840 (82) Range = 10-70	42.5 \pm 1.23 (84) Range = 20-70
Mowry Canal	20.0 (1) Range = 20	15.0 \pm 2.92 (14) Range = 10-40	50.7 \pm 1.05 (182) Range = 20-90
Key Largo Sound	16.6 \pm 1.57 (38) Range = 10-60	20.0 \pm 10.0 (2) Range = 10-30	27.2 \pm 0.527 (159) Range = 10-40
Number of Branches			
Cutler Canal	1.08 \pm 0.0533 (26) Range = 1-2	1.13 \pm 0.0881 (82) Range = 1-7	2.30 \pm 0.186 (84) Range = 1-8
Mowry Canal	1 (1) Range = 1	1 \pm 0 (14) Range = 1	3.07 \pm 0.131 (182) Range = 1-9
Key Largo Sound	1 \pm 0 (38) Range = 1	1 \pm 0 (2) Range = 1	1.01 \pm 0.00629 (159) Range = 1-2

in *R. mangle*. However, *A. germinans* and *L. racemosa* maintain viable dormant buds, and in our study most (>75%) trees of these species that resprouted epicormically survived for at least seven months following the hurricane. In January 1994, epicormic shoots 1-2 m long were common on *A. germinans* and *L. racemosa* trees at Cutler Canal and Mowry Canal. The ability of *A. germinans* and *L. racemosa* to resprout epicormically following disturbance, and the inability of *R. mangle* to do so, has been noted by GILL and TOMLINSON (1969).

The importance of the ability to produce epicormic shoots to genet survival is evident from the generally larger size and higher proportion of multiple trunks in *A. germinans* and *L. racemosa* than in *R. mangle*. The presence of some very large trees of *A. germinans* or *L. racemosa*

indicates that some individuals were from older cohorts, and multiple trunks are evidence of epicormic sprouting following severe branch or trunk damage. In mangrove forests fringing shorelines in south Florida, *A. germinans* and *L. racemosa* appear to be more likely to survive hurricanes and grow to older ages than *R. mangle*.

The pattern of mortality we observed at our study sites may not be occurring in other types of forests. In a survey of 43 plots located throughout mangrove forests damaged by Hurricane Andrew, SMITH *et al.* (1994) found significantly lower mortality in *A. germinans* than in *L. racemosa* or *R. mangle*. Our results clearly indicate higher mortality in *R. mangle*; possibly this reflects the restriction of our study to one type of forest, namely the fringe forest of the middle to

Table 6 Mean densities (number per 100 m²) of seedlings \pm SE in two 10 m by 10 m plots in January 1994. Mean densities of living seedlings in March 1993 shown in parentheses.

Site	Species		
	<i>A. germinans</i>	<i>L. racemosa</i>	<i>R. mangle</i>
Cutler Canal	6.0 \pm 2.0 (2.0)	15.5 \pm 2.5 (4.4)	34.5 \pm 10.5 (83.6)
Mowry Canal	6.0 \pm 2.0 (1.2)	4.0 \pm 0.0 (1.6)	568 \pm 140 (408)
Key Largo Sound	8.0 \pm 4.0 (18.8)	0.0 \pm 0.0 (0.4)	78 \pm 30 (600)

lower intertidal zone. Patterns of mortality would be expected to differ among basin, dwarf, overwash, fringe, and riverine forest types (after LUGO and SNEDAKER, 1974). For example, mortality of all three species may be high in basin forests or other areas surrounded by berms, where impoundment of water following hurricanes may result in anaerobic, strongly reducing conditions and the formation of toxic sulfides (MAZDA *et al.*, 1990; McKEE, 1993; JIMENEZ *et al.*, 1985; McKEE and MENDELSSOHN, 1987; PATRICK and JUGSUJINDA, 1992). Conversely, mortality of *R. mangle* in dwarf mangrove forests may be very low, with trees living for 40–50 years or more and surviving several hurricanes (LUGO and SNEDAKER, 1974; CRAIGHEAD and GILBERT, 1962; SMITH *et al.*, 1994; Karen McKee, personal communication).

Our results indicate a non-linear relationship between tree mortality and size, at least for *L. racemosa* and *R. mangle*. Larger trees were more likely to be killed by the hurricane, presumably because their taller crowns were exposed to higher wind velocities than small trees that have crowns closer to the ground or were surrounded by taller trees. Similar relationships between size and mortality or damage have been noted by other authors for mangroves (ROTH, 1992; SMITH *et al.*, 1994) and other tree species (GRESHAM *et al.*, 1991; REILLY, 1991; BASNET *et al.*, 1992; FOSTER, 1988 a,b; NOEL *et al.*, 1995; but see SLATER *et al.*, 1995).

While *R. mangle* sustained the highest mortality of the three species, *A. germinans* and *L. racemosa* sustained more severe structural damage than *R. mangle*. Proportionally more *A. germinans* and *L. racemosa* trees occurred in the snap damage category than *R. mangle* trees, which occurred in greater proportions in the branch or lean damage categories than the other species. Variation in damage among species may be partially explained by differences in size: snapped trees tended to be larger than trees in the branch or lean damage categories, and *A. germinans* and *L. racemosa* trees were significantly larger than *R. mangle* trees. However, differential response among Australian mangrove species to physical damage by wind or wave action has been attributed to differences in root architecture (SAENGER, 1982). Aerial roots (which are absent in *A. germinans* and *L. racemosa*) may reduce the susceptibility of *R. mangle* to trunk snap or tip-up.

Seedling Recruitment

Hurricane Andrew removed the vast majority of the forest canopy at Cutler Canal and Mowry Canal, resulting in much higher light levels near the forest floor as compared with sites not impacted by the hurricane. The higher light levels appear to have stimulated the release of *R. mangle* seedlings, which were present as advance recruits at high densities at the time of the hurricane. In March 1993, we observed little growth of advance recruits (except in lightning gaps near our plots, where the canopy had been killed prior to the hurricane [see SMITH *et al.*, 1994]). This observation is consistent with the low winter growth rates of *R. mangle* in Florida, which may be 2–4 times lower than summer growth rates (TOMLINSON, 1986). However in January 1994, we found that *R. mangle* seedlings at the hurricane-impacted sites were significantly taller and had more branches than seedlings below an intact canopy at Key Largo Sound, indicating that seedlings present at the hurricane-impacted sites were released and grew rapidly during the summer of 1993. Other authors have also reported that *R. mangle* seedlings in areas where canopy was removed grew at higher rates than seedlings below an intact canopy (ELLISON and FARNSWORTH, 1993).

Seedlings of *A. germinans* and *L. racemosa* occurred at low densities in March 1993, indicating that seedlings of these species were either not present at the time of the hurricane, did not survive the hurricane, succumbed to environmental stresses after the hurricane, or lacked sufficient resources to survive until March 1993. Seedlings of *A. germinans* and *L. racemosa* did become established during the 1993 growing season, as evidenced by the higher seedling densities of these species observed in January 1994. However, these seedlings were not as tall as those of *R. mangle*, which became established prior to the hurricane and at least one year before most *A. germinans* and *L. racemosa* seedlings.

Although total seedling densities did not vary significantly among sites, the proportion of *R. mangle* seedlings that became established but subsequently died (standing dead) was significantly higher at Cutler Canal than at the other sites. Cutler Canal experienced the maximum storm tide, while the storm tide at Mowry Canal was much smaller (RAPAPORT, 1993). The higher storm tide may have resulted in a greater

proportion of dead seedlings at Cutler Canal than at Mowry Canal (or the non-impacted sites) due to abrasion or removal of seedling leaves, increased siltation, or changes in soil chemistry.

Direction of High Winds

The predominant azimuth of tree fall or lean is indicative of the direction of highest wind velocities occurring during a hurricane. At Cutler Canal, located below the right (northern) eye wall of Hurricane Andrew, most tree stems having azimuth readings were aligned toward the southwest. At Mowry Canal, below the eye and less than 15 km south of Cutler Canal, a majority of the azimuth readings were toward the southeast. These patterns indicate that most damage occurred during a short time span when the eye of Hurricane Andrew was approaching the coast and just offshore, when northeasterly winds would have occurred at Cutler Canal and northwesterly winds would have occurred at Mowry Canal (see also WAKINOTO and BLACK, 1994).

At Coot Bay Pond and Key Largo Sound, the effects of high winds are still evident even though these sites have not been hit by a major hurricane since 1965. About half of the tree stems with azimuth readings were aligned toward the south at Coot Bay Pond and toward the southwest at Key Largo Sound. The observed azimuth readings are in concordance with the expected northerly or northeasterly high winds that would have occurred at these sites during Hurricane Betsy.

Forest Regeneration

A high density of large, rapidly growing seedlings, coupled with the inability of adult trees to resprout epicormically, suggests that recruitment of new adult genets from seedlings will be the primary means of regeneration of *R. mangle* in the middle to lower intertidal zone studied. While seedlings of *A. germinans* and *L. racemosa* were present in January 1994, seedlings of these species may be overtopped by the large numbers of taller *R. mangle* seedlings. Furthermore, *R. mangle* seedlings are better adapted for growth and survival than *A. germinans* and *L. racemosa* under the frequently inundated conditions of the middle to lower intertidal zone (ELLISON and FARNSWORTH, 1993; McKEE, 1993). *Avicennia germinans* and *L. racemosa* may persist in

the lower intertidal region, however, by resprouting epicormically following hurricanes, with only occasional recruitment of adults from seedlings.

The pattern of regeneration in forests at Coot Bay Pond and Key Largo Sound following Hurricane Betsy in 1965 appears to be similar to the pattern we observed in forests of similar structure damaged by Hurricane Andrew. The presence of a few large *A. germinans* and *L. racemosa* and an abundance of smaller *R. mangle* at Coot Bay Pond and Key Largo Sound suggests that most of the *R. mangle* trees at these sites were killed during a previous hurricane, while a greater proportion of the *A. germinans* and *L. racemosa* survived and resprouted epicormically. An abundance of *R. mangle* seedlings below the canopy at these sites suggests that the *R. mangle* population at these sites was recruited from advance recruits released after the canopy was removed by the hurricane.

CONCLUSIONS

Our findings support several conclusions regarding the response of neotropical mangrove forests located in the middle to lower intertidal zone to hurricanes. The results of our study pertain primarily to fringe forests and may not reflect hurricane effects in mangrove forests having a different hydrologic regime (e.g., in higher regions of the intertidal zone or in impounded areas where regular tidal flushing does not occur).

- (1) *Rhizophora mangle* may experience higher rates of hurricane-related mortality than *A. germinans* or *L. racemosa*. Observed mortality rates due to Hurricane Andrew were 85.1% for *R. mangle*, 65.0% for *A. germinans*, and 59.5% for *L. racemosa*. The inability of *R. mangle* to resprout epicormically may be the main reason for its lower survival.
- (2) Larger trees are more likely to be killed in a hurricane than smaller trees. We found a significant non-linear relationship between tree size and mortality for *L. racemosa* and *R. mangle*.
- (3) Despite its higher mortality, *R. mangle* may experience less severe structural damage than *A. germinans* and *L. racemosa*. Lower percentages of *R. mangle* trees snapped than did *A. germinans* and *L. racemosa* trees. This may be due in part to the generally smaller

size of *R. mangle*, although aerial roots may reduce the susceptibility of *R. mangle* to trunk snap or tip-up.

- (4) In the middle to lower intertidal zone where *R. mangle* is dominant, reestablishment of the population of *R. mangle* will be primarily from seedlings, many of them advance recruits. We observed high densities of *R. mangle* seedlings that were released following opening of the canopy by Hurricane Andrew and grew rapidly during 1993. Recruitment of new adult genets of *A. germinans* and *L. racemosa* following the hurricane may occur infrequently, and epicormic resprouting appears to be the main regeneration mechanism for these species. Similar patterns of regeneration appear to have occurred in mangrove forests impacted by Hurricane Betsy in 1965.

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RESUMEN

Se evaluó el daño causado por el huracán Andrew, ocurrido el 24 de agosto de 1992, en dos sitios en los manglares de la bahía Biscayne en el sur de Florida. También se relevaron dos sitios, no afectados por el huracán Andrew, que fueron afectados por un huracán por última vez en 1965. Se encontraron diferencias entre las especies *Avicennia germinans* (L.) Stearn (mangle negro), *Laguncularia racemosa* Gaertn.f. (mangle blanco) y *Rhizophora mangle* L. (mangle rojo) en el daño y la mortalidad asociados con los huracanes, y en los mecanismos de regeneración luego de un huracán. La mortalidad asociada con el huracán Andrew fue máxima en *R. mangle* (85.1%), y menor en *A. germinans* (65.0%) y *L. racemosa* (59.5%). Estos niveles de mortalidad son mucho más altos que los observados en otras comunidades vegetales del sur de Florida. Probablemente la mayor supervivencia de *A. germinans* y *L. racemosa* se deba a que estas especies tienen capacidad para emitir brotes epicórmicos; capacidad que no fue observada en *R. mangle*. La mortalidad y la frecuencia de daño severo (tronco partido o descalzado) observados como consecuencia del huracán fueron mayores en los árboles grandes que los árboles pequeños. El daño a *R. mangle* fue proporcionalmente menor que el daño a *A. germinans* y a *L. racemosa*. La recuperación de *R. mangle* estaría ocurriendo principalmente a partir de establecimiento de plántulas, y la regeneración de *A. germinans* y de *L. racemosa* estaría ocurriendo a partir de brotes epicórmicos. Aparentemente, el proceso de regeneración ocurrido en los sitios afectados por el huracán Betsy en 1965 habría tenido características similares al observado en los sitios afectados por el huracán Andrew.