

Early post-hurricane stand development in Fringe mangrove forests of contrasting productivity

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Abstract

We examined the immediate effects of a hurricane (Hurricane Andrew, August 1992) in a coastal landscape in sub-tropical Florida, and then monitored stand recovery in Fringe mangrove sites of different productive capacity for 9 years after the disturbance. Structural impacts of the hurricane were confined almost entirely to forests within 200–300 m of the coast. Mortality and damage were concentrated on canopy individuals. Following the hurricane, rapid canopy recovery and the early onset of competition among Fringe forest stems, as evidenced by relatively high mortality of smaller individuals, magnified the initial dominance of hurricane survivors and early-established seedlings over later cohorts, and limited recruitment to the brief period prior to canopy closure. Changes in the relative abundance of the two dominant mangrove species following disturbance varied strongly along the productivity gradient. The shade-tolerant *Rhizophora mangle* L. generally became the overwhelming canopy dominant in the competitive environment of the recovering Coastal Fringe forest following hurricane, but the shade-intolerant *Laguncularia racemosa* (L.) C.F. Gaertn was better represented in less productive Interior Fringe sites, where canopy closure was delayed. Site productivity is an important determinant of the success of mangrove species during post-hurricane stand development, and consequently of the zonation of communities in the coastal landscape.

Introduction

New World mangrove forests are disturbed frequently, especially in the Caribbean basin and adjacent areas. Many of the disturbances in the region are severe enough to return affected forests to an early stage of stand development. Consequently, the area of mangrove forest in the brief recruitment and thinning stages of development may be large compared to acreage in mature or old growth stages (Oliver 1981; Lugo et al. 1983; Putz

and Chan 1986; Boucher et al. 1990; Oliver and Larson 1990; Yih et al. 1991). In these youthful landscapes, shaped by a multi-scalar suite of perturbations, the capacity to survive the direct effects of disturbance, and/or to become established, grow rapidly, and compete successfully with neighbors during the post-impact period should have important repercussions at the population level and above.

Of course, response to disturbance is not a fixed and generalizable character of a species or

community type. Instead, it varies with a host of factors, especially the nature of the disturbance, the quality or productivity of the site, and the developmental stage or structure of the impacted community (Denslow 1980; Attiwill 1994; Vandermeer et al. 2000; Grime 2001). This is especially true in mangrove landscapes, where disturbance regime, site quality, and community structure are often arranged predictably along a complex gradient with distance to the coast (Ross et al. 2002).

In Oliver and Larson's (1990) well-known model of forest development, the recovery period after disturbance may include a Stand Initiation Phase, in which resources are plentiful and competition is minimal, followed by a Stem Exclusion Phase, in which competition begins to drive stand development patterns, resulting in differentiation among individuals. In mixed-species stands, the differentiation process is the arena in which species become arranged into their characteristic structural niches in the developing forest canopy. Vandermeer et al. (1996) directly addressed competitive dominance among species in the recovering forest. They suggested that disturbance may interrupt the competitive process in a community so that the development of competitive dominance is retarded, resulting in an enrichment of species diversity. However, once the community enters into the Stem Exclusion phase, both intra- and inter-specific competition increases, altering the species' trajectories established during the earliest stages of recovery (Oliver and Larson 1990), perhaps with varying effects on shade tolerant and intolerant species. The differentiation process that underlies these changes is also likely to be sensitive to site productivity. Differentiation frequently occurs more slowly or not at all on very unproductive sites (Oliver and Larson 1990), though Sheil and Burslem (2003) argue that in some cases fertile site conditions may inhibit competitive exclusion, i.e., the process by which increasing dominance by one or more species drives others to local extinction.

In Florida, mangrove communities are most extensive in the southern tip of the peninsula, where they occur in an assortment of geomorphologic settings. Fringe, riverine, overwash, basin, and dwarf mangrove forests, spanning a wide range in structure and productivity (Craighead 1971; Lugo and Snedaker 1974; Pool et al. 1977; Olmsted et al. 1981; Gilmore and Snedaker 1993;

Odum and McIvor 1990), are all common in the region. South Florida mangrove forests are affected by at least four major types of natural disturbance: (1) hurricanes or tropical storms in which the principal damaging agent is wind (Alexander 1967; Doyle et al. 1995; Ross et al. 2000; Baldwin et al. 2001), (2) hurricanes accompanied by a storm surge that deposits massive volumes of marine sediment (Craighead and Gilbert 1962), (3) lightning strikes (Smith et al. 1994), and (4) freeze events (Lugo and Patterson-Zucca 1977; Olmsted et al. 1993). These disturbance types differ in severity and spatial scale, and possibly in the communities they are most likely to affect along the coastal gradient.

Three tree species are found in varying abundance throughout the extensive South Florida mangrove forest: *Rhizophora mangle* L. (red mangrove), *Laguncularia racemosa* (L.) C.F. Gaertn. (white mangrove), and *Avicennia germinans* (L.) Stearn. (black mangrove). A fourth species, *Conocarpus erectus* L. (buttonwood) is also locally important. Among these species, *R. mangle* is considered to be the most shade tolerant (Wadsworth 1959; Rabinowitz 1978; Ball 1980), and is typically the most abundant adjacent to the coast, with *A. germinans* and then *L. racemosa* and *C. erectus* reaching their highest concentrations further inland (Davis 1940). A parallel sequence in site productivity is often observed, with relatively productive forests closest to the coast and forests of lower productivity toward the interior (Ross et al. 2001).

In this paper, we explore community dynamics following the passage of Hurricane Andrew, a violent windstorm that was unaccompanied by significant sediment deposition within the study area. Within the context of the broader coastal landscape, we focus particularly on stand responses within the Fringe forests, i.e., tall forests within the zone subject to regular tidal flooding events. We describe stand dynamics during the early stages of recovery, i.e., up to nine years post-hurricane, in several Fringe forest locations, including a set of sites adjacent to the coast and a second group further inland. Our objective was to explore the differentiation process among mangrove species and size classes across this gradient of proximity to the coast, which in our study area also represented a gradient in site productivity. In accordance with the Oliver and Larson (1990) view of the early stages of succession as a period char-

acterized by gradually increasing dominance by large, early-established individuals over smaller ones, we expected that (a) seedling establishment would decline from an early peak, especially among shade intolerant species, (b) mortality and growth of shade intolerant species would exhibit considerable size-dependence over the study period, and (c) species- and size-dependence in seedling establishment, mortality, and growth would be most strongly expressed on the more productive sites nearest to the coast. More generally, we expected that patterns of recovery following Hurricane Andrew would provide important background regarding the role of disturbance in the distribution of mangrove species with respect to the coast.

Methods

Study area

The study was conducted in mangrove wetlands within the Biscayne Coastal Wetlands (BCW) complex, along the mainland (western) shore of Biscayne Bay in Biscayne National Park (Figure 1). Bounded on the south, west, and north by large canals, it comprised five hydrologically independent blocks of 25–30 ha, separated by east-west oriented drainage ditches or small canals. We report here on data collected in 1993–2001 in Blocks 1, 2 and 4 from the south. Blocks 1 and 4 served as Treatment and Control units, respectively, for an experimental re-diversion of fresh water into the mangrove swamp from the L-31E canal, which bounds the area on the west. Initiated in August 1997, the treatment elicited significant effects on the physical environment and Dwarf mangrove communities within about 200 m of the delivery structure, but impacts outside of that zone were negligible (Ross et al. 2003). In this paper, we focus on stand dynamics in Fringe forests well beyond the influence of the treatment.

Mangroves in BCW exhibit a distinct zonation in structure. Areas closest to the coast support tall forests that may exceed 20 m in height at maturity. Further inland, forest stature decreases, finally becoming reduced to low scrub vegetation less than 1.5 m tall in extensive areas several hundreds of meters or more from shore. The end members along this gradient may be characterized as Fringe

and Dwarf forest, respectively, in the classification system of Lugo and Snedaker (1974). As described for other South Florida locations (Craighead 1971; Lugo and Snedaker 1974; Pool et al. 1977; Olmsted et al. 1981; Odum and McIvor 1990), Dwarf forests in the study area are associated with shallow topographic basins. Between the Fringe and Dwarf forests, a variably broad Transitional forest of intermediate height may be recognized (Ross et al. 2003). Moreover, the Fringe forest may be divided into Coastal and Interior sub-units based on differences in species composition and site growth potential. In the BCW study area, the Coastal Fringe forest was dominated by *R. mangle*, and supported a substantially higher canopy than the Interior Fringe forest. The latter comprised a more heterogeneous species assemblage, with *L. racemosa* co-dominant with *R. mangle*, and *A. germinans* locally abundant.

The vegetation pattern in the BCW study area reflects a strong coast-to-interior gradient of diminishing aboveground productivity, with annual production in Fringe forest exceeding that of Dwarf forest by more than three times (Ross et al. 2001). Fringe forests occur on organic soils (Lauderhill mucks) of 60 cm depth or more (USDA NRCS 1996). They are tidally inundated and drained twice daily (typical amplitude 0.2–0.3 m) throughout most of the year. Dwarf forests grow on calcareous soils (Perrine marls; USDA NRCS 1996) that are typically thinner than the sediments that underlie the Fringe forests. Flooding is less regular than in the Fringe forest, but once inundated by tides or heavy rains, the surface may remain under water for many days. These physical conditions result in a relative deficiency of phosphorus in the Dwarf forest, as reflected by high leaf nitrogen:phosphorus (N/P) ratio and sediment alkaline phosphatase activity (Ross et al. 2003).

The landscape of the BCW study area is in a transitional state. Teas et al. (1976) documented the encroachment of mangrove vegetation into fresh water wetlands in southern Biscayne Bay, dating back to the earliest coastal survey in 1765. With the rapid expansion of the south Florida population after 1900, a complex drainage network was established to promote agriculture while controlling mosquitoes. By 1960, salt-water intrusion had become a serious problem, necessitating the establishment of the N-S-trending L-31E levee and canal, with water control structures at its

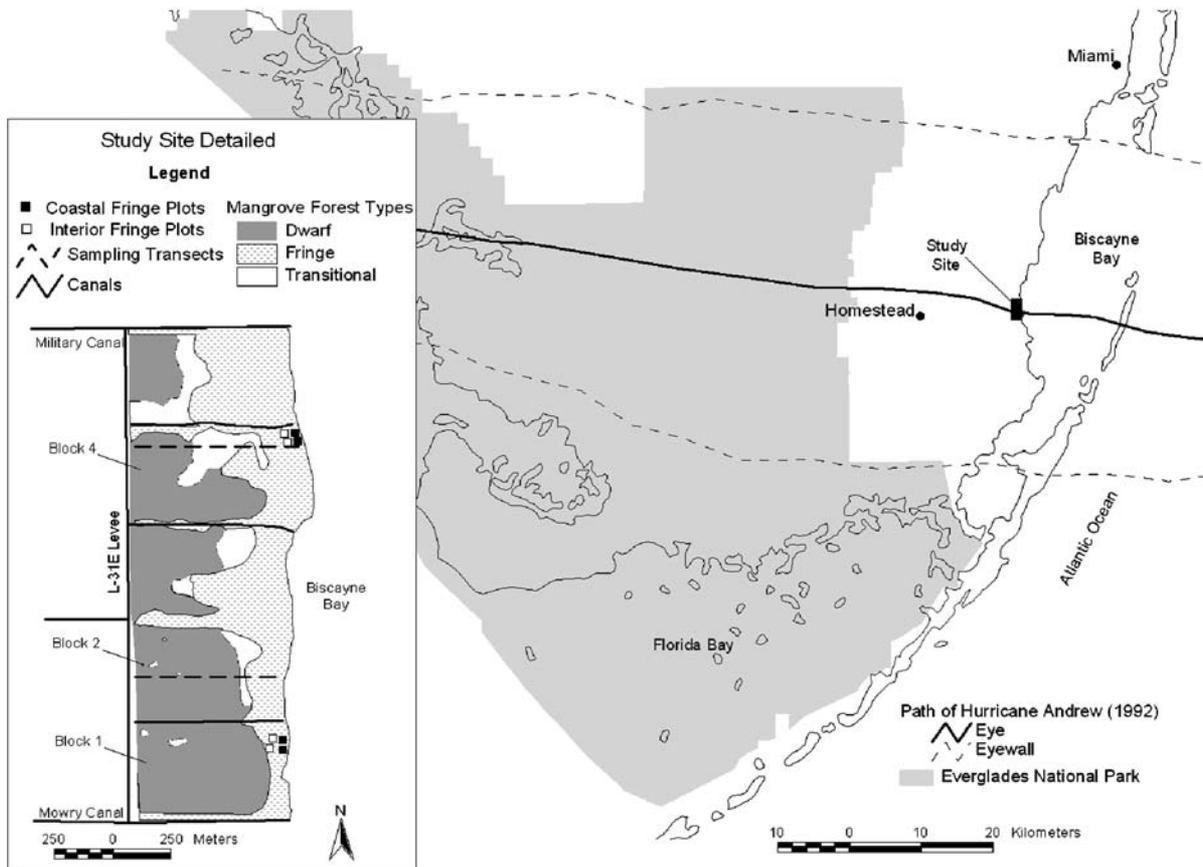


Figure 1. Plot and transect layout within study area in southwestern Biscayne Bay, Florida, USA.

intersections with the major E-W canals. In conjunction with the recent acceleration of sea level rise in the region (Wanless et al. 1994), these drainage activities contributed to the transgression of mangroves into the fresh water marshes. Thus, over a period of a few decades, a thin strip of fringing mangrove forest widened in many southern Biscayne Bay locations to hundreds of meters in width, and the graminoid communities immediately inland were supplanted by dwarf mangrove forest (Egler 1952; Teas et al. 1976; Ross et al. 2000).

All of the disturbance types common to Caribbean mangrove forests have affected the BCW study area. Lightning periodically creates small gaps in the Fringe forests, and freezes are common in the Dwarf mangroves. A severe freeze on December 24–25, 1989, when temperatures reached -4°C at a National Weather Service station about 6 km west of our sites (Degner et al. 2002), caused severe damage in Dwarf forests south of the study area (Olmsted et al. 1993), but

probably did not elicit significant impacts in associated Fringe forests (Ross et al. 2003). In 1926, 1946, and 1965, hurricanes of Category 3 or higher passed within 50 km of the study area. On August 24, 1992, the eye of Hurricane Andrew passed directly over the site (Figure 1). This extremely compact Category 5 hurricane produced sustained winds estimated at ca. 60 m s^{-1} (Powell and Houston 1996), but precipitation was generally $<7\text{ cm}$. Maximum storm surges in Biscayne Bay were about 5.2 m, declining sharply north and south of their peak, ca 15 km north of the study area; within the study area itself, the storm surge was estimated at 2.0–2.6 m above sea level (NOAA, Miami Herald 1993).

Transect sampling

To assess forest structure across the coastal landscape after Hurricane Andrew, we sampled vege-

tation along two transects in June 1993. The transects bisected Blocks 2 and 4, extending from the foot of the L-31E canal levee to the shore of Biscayne Bay, a distance of 620 and 700 m, respectively. We established sampling stations at 20-m intervals along each transect, and a distance-based point-centered-quarter (PCQ) method was employed to describe the structure and composition of the forest (Cottam and Curtis 1956). In four quadrants at each station, we located the closest living stem of *R. mangle*, *L. racemosa*, *A. germinans*, and *C. erectus* in three size classes – Category I, ≤ 60 cm height; Category II, 60–250 cm height; and Category III (trees), ≥ 250 cm height – as well as the nearest hurricane-killed stem > 2.5 cm DBH, to a maximum distance of 5 m. For live trees, we recorded the height, DBH (or basal diameter), and distance from the plot center. For hurricane-killed trees, we recorded the distance from tree base to plot center, DBH, and pre-hurricane height, based on the length of the uprooted, broken, or standing stem. For uprooted trees, we also recorded the orientation of the fallen stem.

We summarized PCQ data as follows: for each station, each species' density was calculated in all three size classes, based on mean point-plant distance in four quadrants. If a species/size class was not present within 5 m of the point in any quadrant, we assigned it a density of 0. If it was present in at least one quadrant, we assigned it a distance of 10 m in the quadrant(s) in which it was absent. We calculated point estimates of basal area (BA) of each species by multiplying the density estimate for each category by the average BA for sampled stems.

We repeated the initial survey at 17 Fringe forest stations in February 1996 and at all stations in January–February 2002. To express trends in species abundance, we calculated the relative density (species percent of total density of all individuals) of the two dominant species, *R. mangle* and *L. racemosa*, during the course of the study.

Annual census plots

Point quarter sampling is an effective method of describing stand structure over large areas, but population processes (establishment, growth, and mortality) are addressed most effectively through periodic observation of tagged, mapped individuals within fixed plots. In conjunction with the

freshwater re-diversion pilot project alluded to earlier, we selected eight plot locations in the Fringe forest of Blocks 1 and 4 through a stratified random sampling process (Figure 1). Two groups, Coastal and Interior, were distinguished among these plots, with both groups including two representatives from each block. Coastal Fringe plots were within 60 m of the coast, while Interior plots were 100–150 m inland.

Plots were rectangular, with a width of 0.5 m and length that varied from 6 to 10 m, depending on initial stem density. During the first census in April–July 1995 and subsequent annual surveys in November/December of the next 6 years, each newly encountered, lignified individual that had produced a minimum of two pairs of leaves was labeled with an aluminum tag and added to the database. Over the course of the study, we monitored the growth and survival of 1024 individuals (Coastal Fringe forest, 284 individuals in 20 m² total plot area; Interior Fringe forest, 740 individuals in 18 m²). The following information was recorded annually for each individual: status (live/dead), crown center and stem base coordinates within plot (± 5 cm), height at crown base, total height, crown length and width, basal diameter, and diameter at 1.4 m above the ground (DBH: stems > 200 cm only).

Stand structure, seedling establishment, mortality, and height growth were summarized by forest type and species. Total aboveground biomass was estimated by applying equations developed for the BCW study area by Ross et al. (2001) to structural data for each plot. Because the data were highly skewed, a non-parametric test statistic (Mann–Whitney *U*) was used to compare Coastal and Interior Fringe forest biomass on several dates. To address possible competitive impacts of large individuals on smaller ones, we used logistic regression to quantify the relationships between the size of individuals at the beginning of a period and their likelihood of survival through it. To assess the effects of site, species, and size class on height growth during recovery, we applied analysis of variance, followed where appropriate by multiple comparison tests (Tukey's test), to data from 1995 to 2001.

Results

PCQ survey estimates of maximum canopy height prior to the hurricane provide a broad view of the

mangrove structural gradient along both E-W, canal-to-bay transects (Figure 2). In 1992, vegetation zonation in Block 2 consisted of a relatively broad (360 m) Dwarf forest, a narrow (60 m) Transition forest, and a Fringe forest zone about 200 m in width and ranging up to 19 m in height. The Dwarf forest was considerably less extensive in Block 4, and the height gradient from there to the tall Fringe forest was much less abrupt. In Block 4, the Coastal Fringe zone was distinguishable as a band of taller forest about 60 m wide, but in Block 2 the structural distinction between Coastal and Interior Fringe forest was not as well defined.

The high winds associated with the Hurricane Andrew's leading edge broke and uprooted the tall trees of the Fringe forest, leaving them in towering piles with crowns oriented toward the southeast. Immediately to the west, observed mortality in the shorter and denser Transition forest was less than 5%. Similarly, a visual reconnaissance of the Dwarf forest immediately after the hurricane suggested that storm-related mortality there was negligible. Wrack deposits were locally significant, but even defoliation appeared minimal. We therefore confine further consideration of hurricane response to the Fringe forest, where the storm's impacts were dramatic.

The Fringe forest canopy comprised about 4000 trees ha^{-1} > 2.5 m in height prior to the hurricane, with a basal area of $29.8 \text{ m}^2 \text{ ha}^{-1}$ (Table 1). On a density basis, *R. mangle* was the most abundant tree, but *L. racemosa* was dominant in the large size classes (>15 cm DBH). *A. germinans* was present as scattered large individuals. The passage of Hurricane Andrew resulted in tree mortality of 94% (density basis, stems >2.5 cm DBH). Though all species were hard hit, disproportionately high mortality in *R. mangle* resulted in a large decrease in its relative density, and an increase in that of *L. racemosa* (Table 1). Along with a patchily distributed set of mangrove seedlings (predominantly *R. mangle*, at about 15,000 stems ha^{-1}), the few surviving trees provided little cover for the exposed forest floor. Periodic observations over the next year or so indicated that, except in isolated microsites along some drainages, open conditions continued to prevail.

By 1996, however, the lower strata of the Fringe forest was already densely occupied, with *L. racemosa* most abundant among the seedling class but sharing dominance with *R. mangle* among saplings (Table 1). The period between 1996 and our final survey was one of continuing development of the Fringe forest canopy and

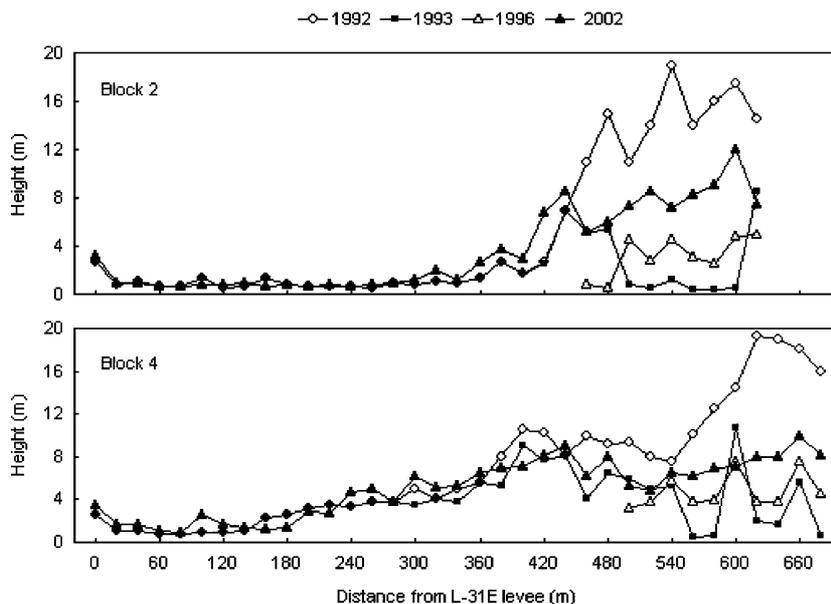


Figure 2. Estimated forest canopy heights along two E-W transects before Hurricane Andrew (1992) and three times thereafter (1993, 1996 and 2002).

Table 1. Size structure of tree species in the Fringe forest, based on PCQ data from 17 points sampled in 1993, 1996, and 2002.

Species	Life form	Year			
		1992	1993	1996	2002
<i>Avicennia germinans</i>	Seedlings	?	140	5000	1060
	Saplings	?	0	293	186
	2.6–5.0 cm	0	0	53	96
	5.1–10.0 cm	0	0	11	124
	10.1–15.0 cm	0	0	0	0
	15.1–20.0 cm	8	0	0	0
	>20.0 cm	9	0	0	0
<i>Laguncularia racemosa</i>	Seedlings	?	720	208,000	2,160
	Saplings	?	0	2050	2020
	2.6–5.0 cm	422	82	581	1450
	5.1–10.0 cm	496	97	148	1800
	10.1–15.0 cm	21	0	0	9
	15.1–20.0 cm	365	0	0	0
	>20.0 cm	271	17	0	9
<i>Rhizophora mangle</i>	Seedlings	?	14,360	94,670	29,340
	Saplings	?	24	14,700	8800
	2.6–5.0 cm	1620	42	94	4440
	5.1–10.0 cm	789	0	576	519
	10.1–15.0 cm	16	0	0	0
	15.1–20.0 cm	9	0	0	0
	>20.0 cm	18	0	0	0
<i>R. mangle</i> rel. density	≥2.6 cm	60.6	17.6	45.8	58.7
<i>L. racemosa</i> rel. density	≥2.6 cm	38.9	82.4	49.8	38.7
Tot. Bas. Area (m ² ha ⁻¹)		29.8	1.6	6.7	29.5

Estimated densities are individuals per hectare.

declining seedling density. By 2002, *R. mangle* once again showed the highest densities of the three mangrove species, in both the understory and tree layers, and tree composition was much as it had been prior to the hurricane. At 29.5 m² ha⁻¹, basal area was equal to that in the pre-hurricane forest, though it was concentrated among almost 9000 stems per hectare of pole size (<10 cm DBH).

The census plot data provide detail on the changes outlined above, especially with regard to the dynamics of Coastal and Interior forests. Mean (±S.E.) biomass across the four replicate sites per type in 1995 were 27 (range 16–47) and 9 (range 6–13) Mg ha⁻¹ in Coastal and Interior Fringe, respectively. Six years later, total above-ground biomass remained much higher in Coastal than Interior sites [150 (range 76–341) and 62 (range 38–75) Mg ha⁻¹, respectively]. A non-parametric test indicated that both initial and final biomass differed between the two Forest types (Mann–Whitney $U = 0.00$, $p = .020$).

Dominant trees in the Coastal Fringe were already larger than those in the Interior Fringe within 3 years of the hurricane (1995), and by 2001, maximum tree heights reached 8–9 m in the Coastal Fringe compared to 5–6 m in the Interior Fringe (Figure 3). With rapid canopy development in the Coastal Fringe forest, a gap in the size distribution among seedlings and small saplings developed by the end of the study period. The gap was apparently created by winnowing out of slow-growing individuals among a large group of *L. racemosa* seedlings established early in the monitoring period. In this forest, *R. mangle* remained nearly monospecific in the canopy throughout the period, and had become so in the understory by 2001 (Table 2). The slower developing Interior Forest differed in several ways. Instead of decreasing, seedling density in these plots was higher in 2001 than 1995 (Figure 3). Moreover, the Interior forest was a mixed-species assemblage, with *L. racemosa* sharing dominance with *R. mangle* in the canopy layer. In this forest,

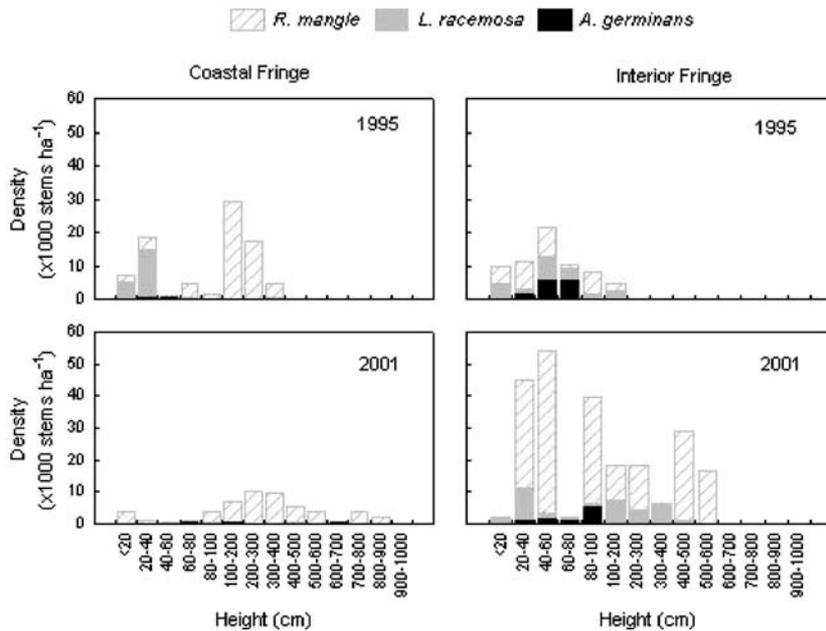


Figure 3. Height profiles of Coastal and Interior Fringe forests in 1995 and 2001. Data are from four census plots per forest type (see Figure 1).

the proportional representation of *L. racemosa* in the larger size classes (>1 m tall) increased over the period, while *R. mangle*'s representation increased in the seedling categories (Table 2).

The demography of seedlings established in 1996–2001 (Figure 4) is helpful in understanding some of the structural variation summarized in Figure 3. *L. racemosa* establishment declined sharply from a peak in 1996 in both Fringe forests, with seedling input higher in the Interior forest throughout the period. Mortality among *L. racemosa* seedlings was high in both forests, such that only in the Interior forest did any representatives of the large 1996 cohort survive through 2001. *R. mangle* seedling dynamics followed a different course, with low but generally increasing levels of

establishment from the beginning to the end of the period, and mortality relatively low throughout. Cumulative establishment of both *R. mangle* and *L. racemosa* were higher in the Interior than the Coastal forest. Overall, these seedling dynamics contributed to a sharp increase in the relative density of *R. mangle*, and a corresponding decrease in that of *L. racemosa* in the <1 m size class by 2001 (Table 2).

Logistic regression indicated that the effect of the site-by-height interaction on *R. mangle* survival was highly significant (Wald statistic = 18.36, $p < .001$) (Figure 5). The effect of height was therefore analyzed separately by site, and it proved significant in both cases (Chi-square of 1-factor model: 68.66 and 75.62 in Coastal and

Table 2. Relative densities of *R. mangle* and *L. racemosa* in two Fringe forest types, by height class and year.

Forest	Species	1995		2001	
		<1 m	≥ 1 m	<1 m	≥ 1 m
Coastal fringe	<i>R. mangle</i>	35.4	99.0	90.0	96.4
	<i>L. racemosa</i>	61.5	1.0	5.0	1.2
Interior fringe	<i>R. mangle</i>	50.8	87.2	82.3	65.4
	<i>L. racemosa</i>	45.2	12.8	13.9	34.6

Data for *A. germinans*, a minor component in these forests, are not shown.

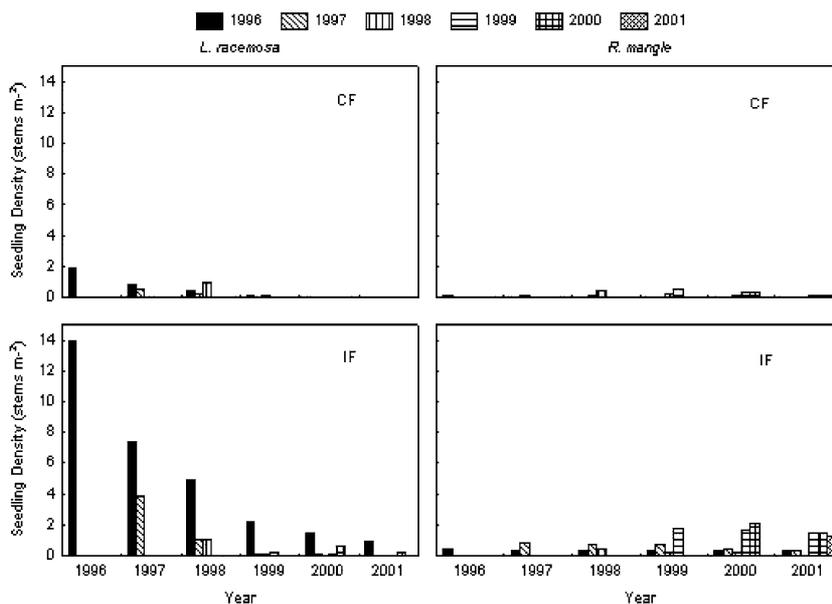


Figure 4. Mean seedling densities of *R. mangle* and *L. racemosa* cohorts established in 1996–2001 in Coastal (CF) and Interior Fringe (IF) forest plots.

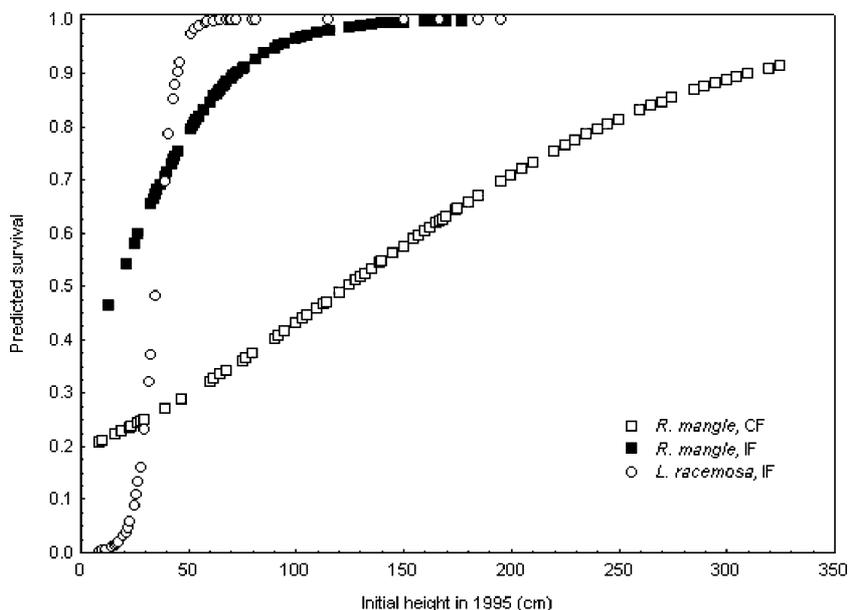


Figure 5. Logistic regression functions of *R. mangle* and *L. racemosa* survival with respect to height in two Fringe forest types (Coastal: CF & Interior: IF), 1995–2001. *L. racemosa* was too sparse in Coastal Fringe to model.

Interior sites, respectively; $p < .001$ for both sites). *R. mangle* survival increased with initial height in both forests, but at a different rate; for instance, 50% probability of survival was reached at 35 cm

height in the Interior forest, but not until 140 cm in the Coastal forest (Figure 5). Survival analysis for *R. mangle* and *L. racemosa* in the Interior Forest, where both species were well represented,

also indicated a significant species-by-height interaction effect, so the two species were analyzed separately. The effect of height on the survival of each species proved to be significant (Chi-square: 14.06 for *R. mangle*, 57.71 for *L. racemosa*; $p < .001$ for both), with survival of both species increasing with initial size. However, the two species curves crossed at about 40 cm, such that small *R. mangle* had a better chance of survival, but at larger sizes, *L. racemosa* was slightly more persistent (Figure 5).

Analysis of the full factorial model for height growth in the Fringe forest was not possible because too few stems survived the monitoring period in several categories. Two-way ANOVA revealed no evidence of significant ($p < .01$) species or size effects within the Interior Fringe forest on height growth, nor of site or size effects within the *R. mangle* population. *R. mangle* did exhibit a non-significant trend of increasing growth with greater initial height in both sites, and one-way ANOVA indicated that large *R. mangle* stems grew faster in the Coastal than Interior Fringe forest (Table 3).

Discussion

We used annual census data from 1995 to 2001 (Years 3–9 following Hurricane Andrew) to examine post-hurricane community dynamics in mangrove forests that occupy adjacent positions along a much longer coastal gradient in hydrology, soils, productivity, and vegetation composition. We concentrated our attention on Coastal and Interior Fringe forests at the seaward end of the gradient because more inland locations were unaffected by the hurricane. Dwarf and Transitional forests may be more vulnerable to other types of disturbance, especially freeze events that

periodically affect south Florida (Olmsted et al. 1993; Ross et al. 2003). The lack of hurricane damage in the BCW Dwarf forest (Figure 2) may be a result of storm tide levels that were high enough to completely immerse the low vegetation in this community during the period of strongest winds. Craighead (1971) observed that high tides protected mangrove individuals less than 2 m tall from the complete defoliation experienced by larger trees during Hurricane Donna (1960). While it was not possible to examine recovery across the entire coastal gradient after Hurricane Andrew, differences in stand development patterns within the Fringe forest suggest that post-disturbance processes may play a role in the frequently observed zonation of mangrove species assemblages with distance to the coast.

Direct impacts of the hurricane

Though it did not remove all legacies of the communities it impacted, the rapid passage of Hurricane Andrew through the BCW study area largely marked the end of the developmental sequence of one Fringe mangrove forest and the beginning of the next. At 94% mortality, the few survivors of the hurricane were small trees or sprouts of large ones, distributed in a seemingly random pattern throughout the area. The vulnerability of large trees to windstorms has been reported for other mangrove forests (Baldwin et al. 1995; Imbert et al. 1996; McCoy et al. 1996), but the high overall level of mortality was atypical. Survival in the forests we studied was lower than in any of the mangrove studies reviewed by Everham and Brokaw (1996). This is likely a result of the sheer force of the maximum winds, which exceeded 60 m s^{-1} at BCW (Powell and Houston 1996).

Table 3. Mean annual height growth (in cm) in the Coastal (CF) and Interior (IF) Fringe forest, 1995–2001.

Species	Plot	Height in 1995	
		<1 m	≥1 m
<i>R. mangle</i>	IF	19.3 ^{a,x}	29.5 ^{a,x}
	CF	29.4 ^{a,x}	42.3 ^{b,x}
<i>L. racemosa</i>	IF	29.6 ^x	30.6 ^x

Data are from individuals that survived the period without dying back (losing more than 10 cm in height). Means within a species followed by the same superscript do not differ ($p < .01$). “a” and “b” superscripts apply to intra-specific comparisons between plots within a height class, and “x” and “y” superscripts to within-plot comparisons. *L. racemosa* individuals in CF were too few for analysis.

Smith et al. (1994) reported that mortality due to Hurricane Andrew in mangrove forests on the west side of the Florida peninsula ranged downward from a peak of >75%.

Stand development following hurricanes

Our analyses of mangrove forest dynamics after Hurricane Andrew focused on the transition between the Oliver and Larson's (1990) Stand Initiation and Stem Exclusion phases. Specifically, we wished to know whether the rate of approach toward this transition varied with proximity to the coast, and whether mangrove species responded differently to such variation. The transition between the two phases occurs when large individuals begin to interfere with the establishment, survival, or growth of smaller ones. We reasoned that a marked decline in seedling establishment during the early stages of stand development might signify such interference, through light limitation and/or root competition from large individuals as they become assembled in the upper strata of the forest. Likewise, we reasoned that positive associations between the size of mangrove individuals early in the recovery sequence and the survival and/or growth of these individuals over the next 6 years might provide further indication of progress through the stand development process.

Patterns of seedling establishment and stem survival observed during 1995–2001 (Figures 4–5, Tables 2–3) indicated (1) that the Stem Exclusion phase of development was well advanced in both BCW Fringe forests by Year 9 after Hurricane Andrew, and (2) that interference effects of larger individuals on smaller ones were fixed more rapidly and/or definitively in the Coastal Fringe than the Interior Fringe forest. The advent of self-thinning so early during mangrove stand development is likely a result of their high productivity. At $26.1 \text{ Mg ha}^{-1} \text{ yr}^{-1}$, mean above-ground production for all BCW Fringe forests during 1996–1997 is among the highest reported for mangrove forests anywhere (Ross et al. 2001). Within these forests, those closest to the coast developed most quickly, reaching effective canopy closure within 5–6 years of Hurricane Andrew (Ross personal observation), and attaining a mean biomass of 150 Mg ha^{-1} within 9 years. South Florida mangrove forests are reported to reach

structural maturity within 20–25 years (Lugo and Snedaker 1974), though only a few exceed 200 Mg ha^{-1} in total aboveground biomass (Simard et al. in review). Based on these estimates, it seems likely that the self-thinning process that we observed during the early stages of stand development plays an important role in limiting the accumulation of biomass beyond some site-specific limit.

The swift establishment of a size-related hierarchy in plant performance may affect forest composition as well as structure, depending on species' responses to it. Our data indicate that the dominant species in the BCW study area indeed differ in their responses. *A. germinans* and *C. erectus* were not abundant enough in our plots to form any conclusions, but *L. racemosa* was clearly sensitive to the competitive post-hurricane environment. We found that even in the Interior Fringe, where stand development was relatively slow, *L. racemosa* seedlings needed to be much larger than those of *R. mangle* by Year 3 to have an equal chance of survival to the end of the study (Figure 5). Similarly, successful *L. racemosa* seedling recruitment was virtually nil beyond Year 3, while *R. mangle* seedlings continued to become established in low numbers throughout the study period (Figure 4). *R. mangle* seedling populations were already substantial 10 months after Hurricane Andrew, probably because they were present as advance regeneration in the pre-hurricane understory (Table 1; see also Baldwin et al. 2001). These relicts of the original forest apparently comprised many of the stems that dominated the Fringe forests 10 years later.

The ecological niches of *R. mangle* and *L. racemosa* have been studied in a number of settings (Wadsworth 1959; Rabinowitz 1978; Ball 1980; Roth 1992; Chen and Twilley 1998; Sherman et al. 2000). When these species grow in mixture, as they often do, *R. mangle* frequently exhibits the highest shoot cover, sapling density, and leaf area, while the tallest stems are more often *L. racemosa*. On the basis of such structural considerations, Ball (1980) argued that *R. mangle*'s shade tolerance was greater than that of *L. racemosa*, allowing it to eventually dominate stands in which the two species occurred together. Wadsworth (1959) also considered *L. racemosa* to be shade intolerant in comparison to other mangroves, and Rabinowitz (1978) found that *L. racemosa* seedlings were less

persistent than those of *R. mangle* under low light conditions in Panama. Daniel et al. (1979) defines 'tolerance' as the relative capacity of a tree species to compete under low light and high root competition, recognized most reliably by the condition of its reproduction under varying canopy conditions. In our study, we addressed a similarly diffuse response to competition from above, but one that applied specifically to the dynamics of small or late-arriving individuals during the period of reorganization following disturbance. The long-term implications of species responses during this early stage of stand development may depend on the disturbance regime that follows, as described below.

Disturbance and coastal vegetation pattern

Stand-replacing hurricanes are a fundamental, evolutionarily significant fact of life for mangrove forests fringing the Caribbean Sea and adjacent waters within a band $\sim 15\text{--}27^\circ$ N latitude. Return intervals for major hurricanes in this region are 20–30 years (Lugo and Snedaker 1974; Odum et al. 1982; Ross et al. 2002), which is far less than the maximum life span of the major mangrove tree species. Gap-producing disturbances such as lightning strikes are also common events in Caribbean Fringe forests, but probably recur less frequently than hurricanes due to the small area affected per event (Smith 1992; Whelan 2005). Working in mangrove forests in the Dominican Republic, Sherman et al. (2000) calculated a formation rate for lightning gaps of 0.23% year⁻¹, which equates to once every 435 years. Nevertheless, colonizers of lightning gaps in southwest Florida survived well following Hurricane Andrew, and subsequently served as important sources of recruitment into the recovering forest (Smith et al. 1994). Moreover, gap dynamics are apt to be especially important in Caribbean mangrove ecosystems in which hurricanes are less common than in south Florida, e.g., along the northern coast of South America. Because mangrove recruits are notably scarce or short-lived under full canopy (Rabinowitz 1978; Janzen 1985; Smith 1992), one may surmise that the distribution of communities in the landscape is a consequence of stand dynamics in the short aftermath of these two very different scales of disturbance, when the

competitive process in the community are suddenly reset (Vandermeer et al. 2000).

The strong zonation in vegetation composition evident in many mangrove landscapes has long challenged the imagination of coastal ecologists (Davis 1940; Egler 1952; Thom 1967; Rabinowitz 1978; Ball 1980; Smith 1987; Ellison and Farnsworth 1993). Zonal vegetation patterning is evident even within the coastal forest of the exceedingly flat south Florida mainland, though the monospecific zonation described by Davis (1940) is frequently ill-defined. More often, *Rhizophora*-dominated communities closest to shore give way to a mixed species forest immediately inland, in a pattern similar to the Belizean mangal studied by Ellison and Farnsworth (1993). Typically, the spatial change in species composition proceeding away from the coast is accompanied by a decrease in forest stature and productivity (Lugo and Snedaker 1974; Twilley 1998; Ross et al. 2001), which may be associated with reduced nutrient availability (Boto and Wellington 1983; Feller et al. 1999).

The demographic patterns we observed following Hurricane Andrew suggest this possibility: that the spatial patterns in composition in the south Florida coastal landscape may be functionally related to the parallel gradient in productivity, through species-specific responses to different levels of competition during the early years after hurricanes. According to this line of reasoning, the post-hurricane environment in the very productive Coastal Fringe sites places an especially high premium on establishing early and maintaining a favorable position in the size hierarchy. *R. mangle* is well-suited in these regards, by virtue of its capacity to maintain a cohort of small, short-lived advance regeneration in the pre-hurricane forest, poised to grow rapidly upon canopy removal (Rabinowitz 1978; Baldwin et al. 2001), and its relative insensitivity to interference from larger individuals during the recovery period (Figure 5). Lacking these characteristics, *L. racemosa* is restricted to the less productive Interior Fringe sites, where the more leisurely rate of post-hurricane recovery provides its small seedlings a broader window in which to become firmly established, and eventually to form part of a mixed species stand. The development of a mixed community in the Interior Fringe forest is consistent with the view that low productivity retards the expression

of competitive dominance following disturbance, thereby allowing the maintenance of high species diversity within the same functional group (Huston 1999).

The above interpretation emphasizes generalized species responses to competition, rather than to other stresses (salinity, anoxia, sulfide levels, etc.) or processes (e.g., dispersal, predation) that may vary across the post-disturbance coastal gradient. The justification for this view lies in the size-related mortality patterns that developed early in recovery at BCW, indicating strong density-dependent effects. Clearly, elaboration of the roles of disturbance and productivity on species distribution in mangrove-dominated landscapes will require that the census approach utilized here be supplemented by experimental approaches, for which there are many good examples in the coastal wetland literature (e.g., Rabinowitz 1978; Silander and Antonovics 1982; Smith 1987; Bertness 1991; Ellison and Farnsworth 1993).

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