Biological Sciences

SPATIAL PATTERNS OF REGENERATION AFTER HURRICANE ANDREW IN TWO SOUTH FLORIDA FRINGE MANGROVE FORESTS

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ABSTRACT: *We examined spatial patterns of regeneration in two fringing mangrove forests along Biscayne Bay, Florida, five years after Hurricane Andrew. We quantified the intra- and interspecific spatial dispersion of* Avicennia germinans *(L.) Stearn (black mangrove),* Laguncularia racemosa Gaertn.f. *(white mangrove) and* Rhizophora mangle L. *(red mangrove) within plots affected by the northern eyewall (Cutler Canal, higher maximum winds and storm tide) and by the eye (Mowry Canal, lower maximum winds and storm tide) of the hurricane. We used point-to-plant and plant-to-plant distances to calculate dispersion indices for surviving trees and saplings of each species. Trees and saplings of all species were strongly aggregated at both sites. However, saplings of all species were hyperdispersed from hurricane-surviving trees and heterospecific saplings. This pattern tended to be stronger at Mowry Canal than Cutler Canal. Furthermore, aggregates of saplings at Mowry Canal tended to be monospecific, whereas more local mixing of species occurred at Cutler Canal. We hypothesize that greater storm intensity and higher mortality of* Rhizophora *advance recruits at Cutler Canal may have contributed to these differences in regeneration. Our results suggest that local variation in hurricane effects may be important to spatial patterns in south Florida fringing mangrove forests.*

Key Words: Avicennia germinans, Florida, hurricanes, *Laguncularia racemosa*, mangal, nearest-neighbor analyses, *Rhizophora mangle*, spatial pattern, tropical cyclones

SPATIAL patterns in mangrove forests have been of interest for decades (see reviews in Snedaker, 1982; Smith, 1992). These forests have been repeatedly described as consisting of monospecific zones in which the dominant species change with elevation and distance to the shoreline (e.g., Chapman, 1944; Snedaker, 1982). However, more recent studies have indicated that, in some areas, mangrove species tend to overlap locally (Bunt et al., 1982; Ellison et al., 2000). This pattern may occur primarily in hurricane-frequented regions, where repeated canopy openings provide opportunities for seedling establishment and local mixing of species (Roth, 1992; Baldwin et al., 1995; 2001; Piou et al., 2006).

The spatial dispersion of hurricane-surviving mangroves may be important to patterns of regeneration and recovery following hurricanes. High winds and

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tides associated with hurricanes damage and kill mangroves (Roth, 1992; Baldwin et al., 1995; McCoy et al., 1996; Sherman et al., 2001; Cahoon et al., 2003) as well as alter substrate conditions (Cahoon et al., 2003). Surviving trees and saplings may affect establishment and growth of new recruits positively by providing seed sources, but negatively by occupying space potentially available for colonization (Baldwin et al., 2001). Furthermore, local differences in storm intensity may result in differences among sites in the number of survivors and alteration of substrates. Thus, immediate post-hurricane landscapes may contain patches of surviving trees, surviving saplings, and areas of bare soil (Baldwin et al., 1995; 2001). The frequency and dispersion of these patches in the post-hurricane landscape may influence future patterns of regeneration.

We quantified spatial dispersion of trees and saplings in two fringe mangrove forests along Biscayne Bay, Florida, five years after Hurricane Andrew. The category 5 storm passed south of Miami on 24 August 1992 and felled or damaged more than 75% of trees in these forests (Smith et al., 1994). Local variation in storm intensity occurred such that areas under the northern eyewall sustained higher wind speeds and storm tides than areas near the eye of the storm (Wakimoto and Black, 1994; Powell and Houston, 1996). In one site beneath the path of the northern eyewall and one site beneath the path of the eye, we examined tree and sapling spatial patterns hierarchically. We used point-to-plant and plant-to-plant distances to address three questions related to spatial dispersion of trees and saplings (Pielou, 1977): (1) Are trees and saplings aggregated into clumps? (2) Are saplings located farther from trees than would be expected by random dispersion? (3) Do sapling dispersion patterns relative to conspecifics differ from those relative to heterospecifics?

METHODS—*Study sites*—We studied fringe mangrove forests at two sites along the west coast of Biscayne Bay, Dade County, Florida. The northern site, Cutler Canal (25° 37′ N, 80° 21′ W), is located on the Charles Deering Estate, a metro-Dade County preserve. Mowry Canal is located ~18 km to the south in Biscayne National Park (25° 28′ N, 80° 21′ W). Both sites are in the lower to middle intertidal zone and have no natural or human-made structures that impair drainage after inundation. Prior to Hurricane Andrew, both sites contained 15-m tall mixed stands of *Avicennia germinans* (L.) Stearn (black mangrove), *Laguncularia racemosa* (L.) Gaertn.f. (white mangrove), and *Rhizophora mangle* L. (red mangrove) (Baldwin et al., 1995).

Hurricane Andrew passed directly over both sites, but wind speeds and storm tides were higher at Cutler Canal. The northern eyewall of the hurricane passed directly over Cutler Canal. Maximum wind speeds were estimated as 238 km/h offshore and 223 km/h just inland, with gusts possibly >280 km/hr (Wakimoto and Black, 1994; Powell and Houston, 1996). Maximum recorded storm tides of 5.2 m occurred near Cutler Canal. The eye of the hurricane passed directly over Mowry Canal. Wind speeds and storm surge levels associated with the eye of the storm were lower than those recorded in the northern eyewall. Sustained winds were estimated as 198 km/h; storm tide estimates were 2.1–2.8 m (Powell and Houston, 1996).

Hurricane Andrew altered community structure at both sites. At the time of the hurricane in 1992, Cutler and Mowry Canals contained the same mangrove species, but in different relative abundances. *Rhizophora* trees were most abundant at Cutler Canal, while *Laguncularia* trees were most abundant at Mowry Canal (Baldwin et al., 1995). *Rhizophora* seedlings dominated the understory at both sites, while few seedlings of *Avicennia* or *Laguncularia* were present (Baldwin et al., 1995). Hurricane-induced mortality was highest for *Rhizophora* trees (Baldwin et al., 1995), primarily because both *Laguncularia* and *Avicennia* resprouted epicormically following the storm

(Baldwin et al., 2001). *Rhizophora* seedling survival was higher at Mowry Canal where storm surge was lower (Baldwin et al., 1995; 2001). Few seedlings of *Avicennia* or *Laguncularia* were present immediately after the hurricane, but within two years propagules of both species had germinated at the sites (Baldwin et al., 1995). By the time of our study in 1997, hurricane-surviving trees of *Laguncularia* and *Avicennia* had produced large spreading bases of sprouts 2–4 m in length. In addition, *Rhizophora* saplings, which had been seedlings at the time of the hurricane, averaged 2–3 m height, and were abundant at both sites. Saplings of *Avicennia* and *Laguncularia*, all of which germinated after the hurricane, typically were 1.5–3 m tall at both sites.

Experimental design and sampling—We quantified spatial dispersion of mangrove trees and saplings within pairs of plots at Cutler and Mowry Canals. We relocated the 50 × 10 m transects (two per site) established by Baldwin and co-workers (1995) and expanded each to create 50 × 50 m plots (subdivided into 10 × 10 m subplots). The eastern edge of each plot was located 5–10 m from the shore. In each plot, we defined trees as stems ≥ 2.5 cm diameter at breast height (dbh) that had survived the hurricane. Saplings were stems < 2.5 cm dbh but ≥ 1 m height. Saplings were either seedlings or small saplings at the time of the hurricane or had established after the hurricane. Mangroves < 1 m tall were not included in this study. We used these plots to obtain the distance measurements detailed below as well as estimates of mangrove density.

We measured a series of point-to-plant and plant-to-plant distances to address questions related to spatial dispersion of trees and saplings. First, in each plot, we measured the distances from 20 randomly-located points to the nearest neighbor tree and the nearest neighbor sapling, regardless of species, to assess whether trees and saplings were clumped, randomly dispersed, or hyperdispersed. We restricted random points to the inner 30 × 30 m of the plot to minimize edge effects. Second, we randomly selected in each plot 20 hurricane-surviving trees, regardless of species, and measured the distance to the nearest sapling of any species to determine whether saplings were located farther from trees than would be expected by random dispersion. We restricted randomly-selected trees to the inner 30 × 30 m plot. Third, we measured the distance from randomly-selected saplings (ca. 24 per site) to the 20 nearest neighbor sapling of each species to assess whether sapling dispersion patterns of saplings differ among conspecifics and heterospecifics.

Statistical analyses—We tested dispersion patterns for significant departure from random expectation using an index (α) described by Pielou (Pielou, 1959; 1977). Pielou's index (α) is equal to $\pi D \overline{\omega}_i$, where D is the independently determined density of the population and $\overline{\omega}_i$ equals the mean of the squares of the distances from either points to plants or plants to plants. The expected value, $E(\pi D \overline{\omega}_i)$, equals (n-1)/n, where n is the number of points or plants from which distances are measured. In a random population $2n\alpha$ follows a χ^2 distribution with 2n degrees of freedom. When analyzing point-to-plant distances, a value of α significantly greater than $E(\pi D \overline{\omega}_i)$ suggests that the plants are aggregated, whereas a value significantly less than $E(\pi D \overline{\omega}_i)$ suggests hyperdispersion. The interpretation is reversed for plant-to-plant measurements.

We selected Pielou's dispersion index because it can be used with both point-plant and plant-plant distances, allowing characterization of dispersion pattern at two scales. For example, if plants were aggregated within the plot but randomly dispersed within clumps, point-plant distances would indicate the aggregated pattern, and plant-plant distances would indicate a random within-clump pattern. We did not use Ripley's K (Ripley, 1981) because we did not have both trees and saplings mapped in plots.

We analyzed distances from random saplings of each species to the 20 nearest neighbor *Rhizophora* saplings to determine if clumps of *Avicennia* and *Laguncularia* tended to be spatially separate from clumps of *Rhizophora*. A bootstrapping technique (Efron and Tibshirani, 1993) was used to calculate 95% confidence intervals for the distribution of distances from randomly selected saplings of each species to 20 nearest neighbor saplings. Each bootstrapped confidence interval was the result of 2000 iterations for distance data to each neighbor. All bootstrapping procedures were conducted using S-Plus 5 for Unix (S-Plus, 1998).

TABLE 1.   Dispersion of mangrove trees five years after Hurricane Andrew. Alpha is Pielou's dispersion index (α) based on tree density and mean distances from N random points to nearest-neighboring trees. Dispersion patterns (DP) indicated as aggregated (A) or hyperdispersed (H) are those significantly different from random (R). Significance levels = *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

| | | | | By Species | | | | | |
| | | | | Alpha | | | DP | | |
Site	N	Alpha	DP	*Avicennia*	*Laguncularia*	*Rhizophora*	*Avicennia*	*Laguncularia*	*Rhizophora*
Cutler	40	1.68	A***	4.58	4.11	1.38	A***	A***	A*
Mowry	40	1.85	A***	2.33	1.61	1.79	A***	A**	A***

RESULTS—Within the two 50 × 50-m plots at each site, a total of 469 hurricane-surviving trees were present at Mowry Canal and 224 at Cutler Canal. On average, fewer than 10 trees were present in 10 × 10-m subplots at both sites. Tree density was locally variable, however, and ranged from 0 to 67 trees among 10 × 10-m subplots. Saplings were abundant at both sites. On average 100–150 saplings were found in 10 × 10-m subplots in plots at each site. Densities within subplots at each site ranged from 34 to 194 saplings per 100 m^2. At Mowry Canal, *Rhizophora* was about eight times more abundant than *Laguncularia* and more than an order of magnitude more common than *Avicennia*.

Both trees and saplings were aggregated into clumps five years after the hurricane. Dispersion indices based on random point to tree distances indicated this pattern was consistent across both sites for all species (Table 1). Similarly, random point-to-sapling dispersion indices suggested that saplings, as a group, were strongly aggregated at both sites (Cutler $\alpha = 6.12$, $P < 0.001$; Mowry $\alpha = 3.06$, $P < 0.001$).

Random tree-to-sapling indices suggested that saplings, regardless of species, were located farther from surviving trees than would be expected by random dispersion (Table 2). This pattern of hyperdispersion was consistent across sites and species, but was particularly pronounced for *Laguncularia* saplings at both sites.

Within clumps, dispersion patterns of saplings differed between conspecifics and heterospecifics. For each species, saplings were either randomly dispersed or aggregated relative to conspecifics (Table 3). Conversely, saplings were almost always hyperdispersed relative to heterospecific saplings (Table 3). Only *Avicennia* saplings at Cutler Canal were randomly dispersed relative to *Laguncularia* saplings. Furthermore, the degree of hyperdispersion tended be greater (i.e. had larger α values) at Mowry Canal than at Cutler Canal (Table 3).

Clumps of saplings tended to contain more species at Cutler Canal than at Mowry Canal. Bootstrapped confidence intervals for distances from randomly selected saplings of each species to nearest neighbor *Rhizophora* saplings overlapped more at Cutler Canal than at Mowry Canal (Fig. 1). At Mowry

TABLE 2. Dispersion of mangrove saplings relative to trees five years after Hurricane Andrew. Alpha is Pielou's dispersion index (α) based on sapling density and mean distances from N trees to the nearest-neighbor sapling. Dispersion patterns (DP) indicated as aggregated (A) or hyperdispersed (H) are those significantly different from random (R). Significance levels = *$P <$ 0.05; **$P < 0.01$; ***$P < 0.001$.

| | | Any Species | | By Species | | | | | |
| | | | | Alpha | | | DP | | |
Site	N	Alpha	DP	Avicennia	Laguncularia	Rhizophora	Avicennia	Laguncularia	Rhizophora
Cutler	38	12.17	H***	3.53	11.99	6.03	H***	H***	H***
Mowry	40	3.42	H***	6.48	32.96	1.54	H***	H***	H***

Canal, the 20 nearest neighbor *Rhizophora* saplings were always closest to conspecific saplings (<2 m) and farthest from randomly selected *Laguncularia* saplings. Distances from *Rhizophora* neighbors to *Avicennia* saplings were always intermediate (Fig. 1). At Cutler Canal, *Rhizophora* saplings again tended to be closer to conspecifics than sapling *Avicennia* or *Laguncularia*, but the confidence intervals overlapped. This pattern suggests that sapling species tended to be more separated spatially at Mowry Canal than at Cutler Canal.

DISCUSSION—Non-random dispersion patterns were frequent in the mangrove forests in our study. Five years after Hurricane Andrew, both trees and saplings were strongly aggregated into clumps. Similar patterns of aggregation are also frequent in more diverse temperate (Aldrich et al., 2003) and tropical forests (Condit et al., 2000). Conversely, saplings tended to be hyperdispersed from hurricane-surviving trees and heterospecific saplings. Non-random spatial patterns in fringe mangrove forests may result from the interaction of a number of factors including: local edaphic conditions, limited

TABLE 3. Dispersion of mangrove saplings relative to other saplings five years after Hurricane Andrew. Alpha is Pielou's dispersion index (α) based on density and mean distances from N randomly selected saplings to nearest conspecific saplings (main diagonal) or heterospecific saplings. Dispersion patterns (DP) indicated as aggregated (A) or hyperdispersed (H) are those significantly different from random (R). Significance levels = *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

| | | | Alpha | | | DP | | |
Site	Species	N	Avicennia	Laguncularia	Rhizophora	Avicennia	Laguncularia	Rhizophora
Cutler								
	Avicennia	24	<u>1.21</u>	2.23	1.81	<u>R</u>	H***	H**
	Laguncularia	23	0.68	<u>1.14</u>	3.13	R	<u>R</u>	H***
	Rhizophora	23	1.71	4.82	<u>1.24</u>	H***	<u>H</u>***	<u>R</u>
Mowry								
	Avicennia	24	<u>1.11</u>	3.42	1.67	<u>R</u>	H***	H**
	Laguncularia	24	5.71	<u>0.28</u>	12.27	<u>H</u>***	<u>A</u>***	H***
	Rhizophora	24	2.64	2.69	<u>0.59</u>	H***	<u>H</u>***	<u>A</u>*
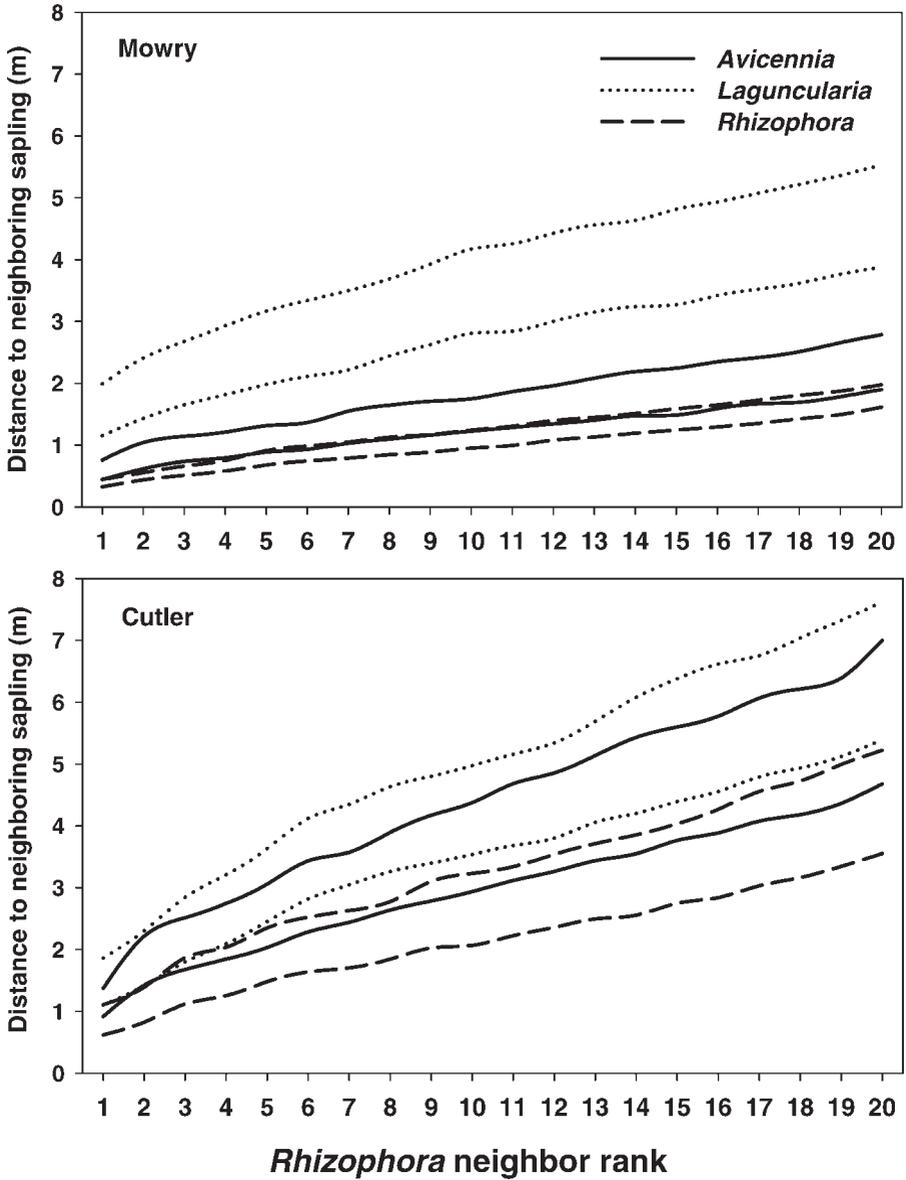
Fig. 1.   Upper and lower 95% confidence intervals of the distributions of mean distances from randomly selected saplings of each species to the 20 nearest neighboring *Rhizophora* saplings at Cutler and Mowry Canals, Florida. Overlapping 95% confidence intervals indicate more local mixing of species.

dispersal, as well as past disturbances that result in localized canopy gaps (Smith et al., 1994; Sherman et al., 2000). Our data suggest that hurricanes also contribute to these spatial patterns by producing local variation in the density and location of hurricane-surviving trees and saplings. These results are

consistent with other studies (Baldwin et al., 2001; Piou et al., 2006) that have suggested the importance of hurricane survivors to post-hurricane forest structure and regeneration patterns.

At the time of our study, the mangrove forests at Mowry and Cutler Canals tended to consist of clumps of hurricane-surviving trees, hurricane-surviving saplings (*Rhizophora* that were seedlings at the time of the hurricane), and colonizing saplings (*Avicennia* and *Laguncularia* that established after the hurricane). Hurricane-surviving trees occurred in localized areas, perhaps those of less intense winds or lower tidal surge (Baldwin et al., 2001). Few saplings occurred in these areas; hence, saplings were found farther away from surviving trees than expected by chance. By five years after the hurricane, dense monospecific patches of *Rhizophora* saplings (ca. 3–4-m height) occurred in areas where understory seedlings had survived the storm (Baldwin et al., 2001). These areas tended to be located away from surviving canopy trees. Canopy trees in these areas may have been killed by the hurricane or were absent due to lightning-induced mortality occurring before the hurricane (Smith et al., 1994). Clumps of colonizing saplings of *Avicennia* or *Laguncularia* occurred in areas away from trees or *Rhizophora* saplings. These bare areas may have been produced by storm surge deposition of fallen trees or scouring from temporary channels during the hurricane.

The number and location of *Rhizophora* seedlings surviving the hurricane may account for differences in the intensity of aggregation and local mixing of saplings at our sites. *Rhizophora* seedlings are capable of survival and growth under low light conditions, while seedlings of *Avicennia* and *Laguncularia* are shade intolerant (Rabinowitz, 1978). Thus *Rhizophora* seedlings can cover the understory of closed canopy mangrove forests during periods between hurricanes (Baldwin et al., 1995; 2001; Sherman et al., 2000). At Mowry Canal, where storm winds and tides were less intense, large numbers of *Rhizophora* seedlings survived the hurricane (Baldwin et al., 1995) and subsequently formed dense sapling clumps that tended to be separated from saplings of other species. In contrast, at Cutler Canal, which experienced the highest winds and tides produced by the storm, *Rhizophora* seedling mortality was higher (Baldwin et al., 1995) and post-hurricane clumps were less dense with more mixing of species. Openings free of *Rhizophora* seedlings at Cutler Canal appeared to provide regeneration sites for *Avicennia* and *Laguncularia* following the hurricane. While local environmental factors certainly contribute to differences in spatial patterns among mangrove forests, Baldwin and co-workers (2001) found only small absolute differences in redox potential and salinity between the two sites used in this study. Our results support those of Baldwin and co-workers (2001) that the fate of *Rhizophora* seedlings during the hurricane was an important determinant of patterns to post-hurricane regeneration.

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