

Zonation Patterns of Belizean Offshore Mangrove Forests 41 Years After a Catastrophic Hurricane¹

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ABSTRACT

Mangroves are prone to bearing frequently the full brunt of hurricanes and tropical storms. The extent of destruction and early regeneration are widely studied. The purpose of this study was to add a long-term view of mangrove regeneration and assess the potential effects on mangrove horizontal zonation patterns of catastrophic destruction. Hattie, a category five hurricane, hit the Belizean coast in 1961. It passed directly over the Turneffe Atoll where our study area, Calabash Cay, is located. At four sites on this island, we analyzed mangrove forest structure along transects parallel to the shoreline within zones delineated by species dominance and tree height. We propose an index based on the Simpson index of diversity to express changes in the heterogeneity of the species dominance. Physical–chemical parameters and nutrient availability were also measured. The destruction levels were estimated by analysis of the distribution of diameter at breast heights of the bigger trees in the inland zones. Variations in species dominance among sites and zones could be explained by interactions of various factors. Further, different levels of destruction between the two sides of the island had a significant effect on current patterns of species and structural zonation at Calabash. We conclude that disturbance regime in general should be considered as a factor potentially influencing mangrove horizontal zonation patterns.

Key words: *Avicennia germinans*; Belize; hurricane disturbances; *Laguncularia racemosa*; long-term regeneration; mangrove forest dynamics; *Rhizophora mangle*; species dominance heterogeneity; Turneffe Atoll; zonation patterns.

MANGROVE FORESTS LINE MOST OF THE WORLD'S tropical and subtropical coastlines. In this coastal position, mangroves bear the full brunt of hurricanes and tropical storms, which are a frequent form of disturbance in these latitudes. Tree mortality, tree species resistance, and early forest recovery immediately following hurricane destruction have been widely studied (*e.g.*, Stoddart 1963, Vermeer 1963, Bardsley 1984, Roth 1992, Smith *et al.* 1994, Roth 1997, Imbert *et al.* 1998, Baldwin *et al.* 2001, Sherman & Fahey 2001, Imbert 2002). Rates of hurricane-related mortality in mangrove forests are significantly higher than for any other tropical forests (compared in Baldwin *et al.* 2001; see also Imbert *et al.* 1998). Some recent studies have also analyzed the impacts of these destructions on ecosystem functions such as peat formation (Cahoon *et al.* 2003) or woody debris accumulation (Krauss *et al.* 2005) within the decade following hurricanes. In contrast, few studies have examined long-term recovery patterns (*e.g.*, Smith & Duke 1987). In the studies carried out in the Caribbean, results of species resistance to hurricanes are contradictory. For instance, according to Roth, Smith, and Imbert (Roth 1992, Smith *et al.* 1994, Imbert

et al. 1998, Imbert 2002), *Rhizophora mangle* is the least resistant to hurricane destruction. However, Sherman and Fahey (2001) found that *Avicennia germinans* is the least resistant. Regarding the relative importance of tree size, Roth (1992), Smith *et al.* (1994), and Baldwin *et al.* (2001) found a higher probability of destruction for intermediate and higher size classes. Other studies have shown either an inverse pattern (*e.g.*, Imbert *et al.* 1998), or no difference in damage among size classes (*e.g.*, Sherman & Fahey 2001).

The extent of forest damage depends on the intensity of the hurricane. Category one or two hurricanes on the Saffir–Simpson Hurricane Scale (www.nhc.noaa.gov) should generally inflict less damage than categories three–five. Nevertheless, the percentage of dead trees can also vary depending on site exposure. For example, Imbert (2002) and Sherman and Fahey (2001) found the highest levels of disturbance in zones close to the shoreline (see also *e.g.*, Roth 1992, Imbert *et al.* 1998). Baldwin *et al.* (2001) reported also that the differences in levels of destruction at two sites in Florida depended on their relative position within the path of the eye of Hurricane Andrew. At Turneffe Atoll, Stoddart (1963) described that the mangrove forests on many small windward islands were completely destroyed by Hurricane Hattie, a category five storm

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that struck Belize in October 1961, whereas inside the atoll the vegetation was less damaged.

Delayed mortality is another source of variation in hurricane damage. Some mangrove trees are able to coppice (*e.g.*, *A. germinans* and *Laguncularia racemosa*) and use their prehurricane reserves to create new tissues and foliage (Tomlinson 1986). However, if these trees are severely damaged, they do not live much more than 2 yr after the hurricane (see *e.g.*, Sherman & Fahey 2001). The delayed mortality is not as high in mangroves as in other tropical forests (Imbert *et al.* 1998). Furthermore, mangrove forests appear less resistant but much more resilient than other tropical forests. Imbert *et al.* (1998) suggested that no Caribbean mangrove species are pioneers when compared to rainforests. However, mangrove species apparently present different adaptations for recolonization strategies and wind resistance (Roth 1992), relating the effects of hurricanes to the mangrove dynamics and structure.

To our knowledge, no studies have yet documented the long-term effects of hurricanes on the horizontal zonation patterns of mangrove forests. Such patterns may refer to structural characteristics (structural zonation) or species dominance (species zonation). Structural zonation describes bands parallel to the shore differing in tree density, canopy height, or tree diameters. Species zonation expresses zones successively encountered from offshore to inland with different monospecific composition or particular associations of few tree species. Several hypotheses have been expressed to explain the phenomena driving these patterns: plant succession (Davis 1940), geomorphological factors (Thom 1967), differential dispersal of propagules (Rabinovitz 1978), differential predation on propagules (Smith 1987), interspecific competition (Ball 1980), and species-specific physiological adaptations to gradients (Macnae 1968, for review see Smith 1992). In Belize, differential predation on propagules is not responsible for differences in species zonation (McKee 1995a). McKee (1993) found that physiological adaptations best explain zonation patterns in Belizean mangroves. Together with the species-specific physiological adaptations to gradients of salinity and tidal influence, nutrient availability plays an important role in Caribbean mangrove zonation (Feller *et al.* 2003).

The main objective of this study was to determine whether perturbations such as hurricanes interact with other possible explanatory phenomena mentioned above to have an effect on these horizontal zonation patterns in mangrove ecosystems. The second aim was to document the long-term effects of large-scale destruction on forest structure and to propose some recovery pathway scenarios. The offshore Belizean mangrove islands in Turneffe Atoll provided an ideal location for these investigations since they were previously destroyed by Hurricane Hattie more than 40 yr ago, and the occurrence of only four tree species provides a particular but relatively simple forest system.

METHODS

STUDY AREA AND SITES.—This study was conducted at Calabash Cay (also sometimes referred to as the “Main Calabash Cay” of a “Calabash Cays” group), on the eastern side of Turneffe Atoll,

one of the three Belizean atolls (Fig. 1). It is located approximately 34 km east of the Mesoamerican Barrier Reef and about 50 km from the mainland. Calabash Cay is almost 2 km long and about 1 km at its widest point. It includes an inner lagoon that is linked to the Turneffe lagoon waters by a small creek on the north end of the island (Fig. 1). It is fringed by mangroves on all its inner and outer coasts with the exception of a part of the eastern side. The tidal range is microtidal (average range <30 cm) and is classified as mixed semidiurnal.

The climate is tropical to subtropical, with clearly distinct rainy and dry seasons. The annual rainfall range is below the 2020 mm/yr of Belize city but above 1500 mm (C. Piou, pers. obs.). Average maximum air temperatures vary from 32°C in summer (March–September) to 28°C in winter (October–February). Average minimum temperatures vary with the same monthly pattern from 20–24°C. The climate is influenced by cold fronts (or “Northerns”) coming from North America during the winter months. Between July and November, hurricanes in the Caribbean Region increase the occurrence of heavy rain and strong to catastrophic winds.

On 31 October 1961, Hurricane Hattie, a category five hurricane, hit the Belizean coast. The eye of this hurricane went from east northeast to west southwest over Turneffe Atoll with winds over 260 km/h. The intensity, wind direction, wave action, and storm surge destroyed all of the human habitations and most of the mangrove forests of Calabash Cay. According to Stoddart (1963) who visited Turneffe in 1962, Big Calabash, a small island *ca* 300 m to windward of Calabash Cay, was completely cleared of any mangroves by Hattie. Based on Stoddart's description, a gradient in severity of destruction from east to west was expected for mangrove forest at Calabash Cay. Specifically, Stoddart (1963) described that defoliation of mangrove stands was less severe and regeneration was already occurring in the interior part of Turneffe Atoll by early 1962. Calabash Cay has a large inner lagoon, which is considered a natural shelter by the local population. The wave action and the tidal hurricane surge were weaker inside the inner lagoon than outside. Since the human settlements were destroyed and not rebuilt after Hattie, the regeneration of the mangrove forests of Calabash Cay was not influenced by any anthropogenic activities since 1962. Although tropical storms and lightning strikes could have induced the death of individual trees, no other hurricanes or catastrophic perturbations have affected substantially the Calabash mangroves since Hattie. The gradient of disturbance hypothesized by Stoddart (1963) in a relatively short distance around Calabash makes this area ideal for the main objective of this study.

Four study sites were selected around Calabash along the proposed disturbance gradient. These sites were labeled A–D (Fig. 1). All sites extended from the fringing mangrove forest along the water's edge to the high intertidal margin where buttonwood (*Conocarpus erectus*) thickets dominated adjacent to the upland terrestrial forest. Preliminary surveys were conducted to determine zones within these sites depending on both the apparent structural and the species zonation patterns. Site A was located on the northeast side of Calabash where four zones were defined from the shoreline inland. Site B was located on the northernmost point of Calabash and four zones were defined. Site C was situated on the northwest side of

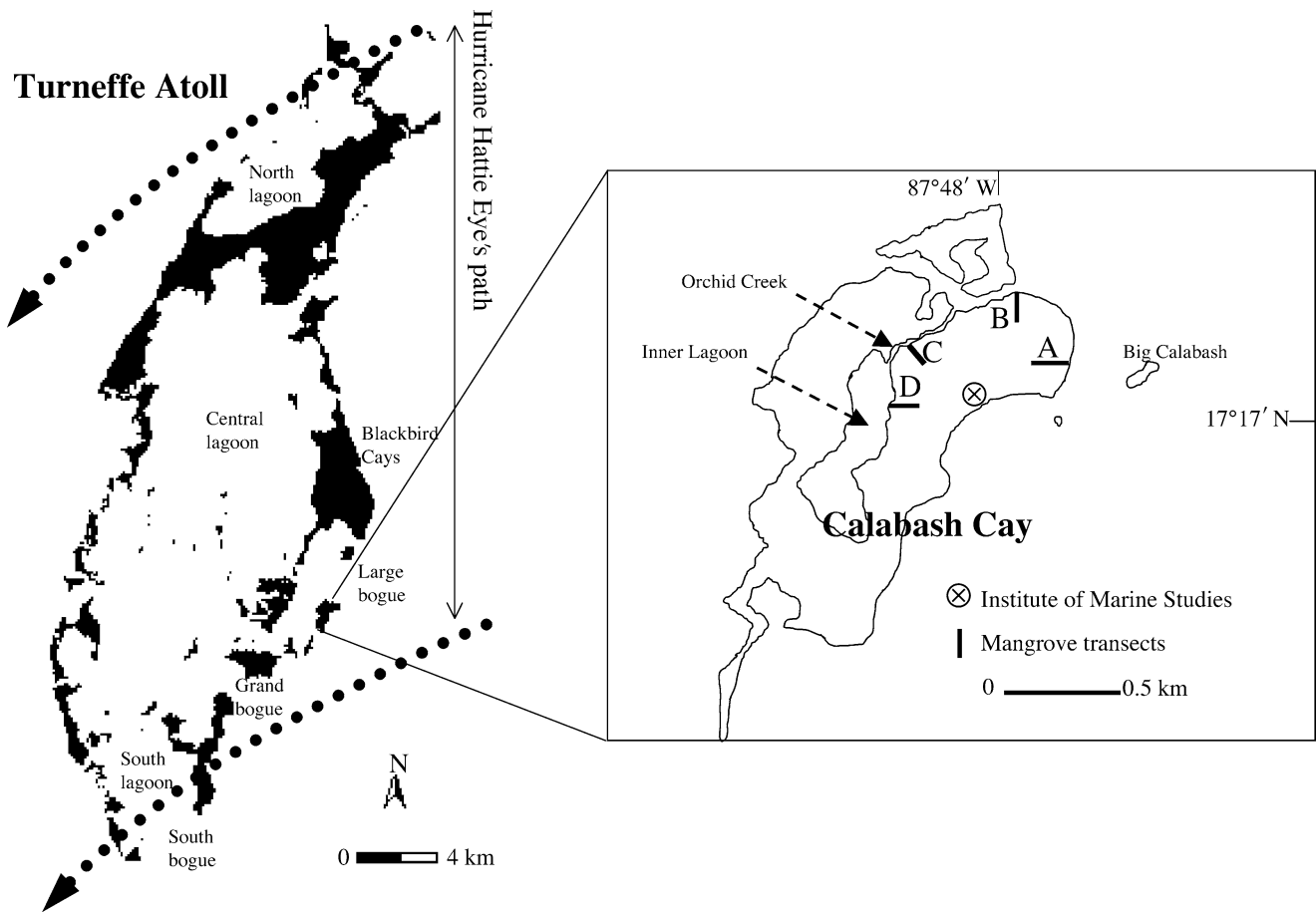


FIGURE 1. Turneffe Atoll with Hurricane Hattie eye's path and Calabash Cay with localization of the sites (modified from Garcia & Holtermann 1998).

Calabash and extended from Orchid Creek to the upland area with six different zones. Site D was located on the east side of the inner lagoon and had three mixed zones.

FOREST MEASUREMENTS.—Mean diameter at breast height (DBH), tree height, density, and species frequencies were measured by the point centered quarter method (PCQM) transects laid within each zone of each site between November 2002 and February 2003. To avoid measuring the same tree twice, the distance between points of the PCQM transects varied between 2 m in the dwarf areas to 12 m in tall basin forests. Each of the PCQM transects consisted of 21 points for a representative measurement of the studied area (Cintrón & Schaeffer-Novelli 1984).

PHYSICAL-CHEMICAL SURVEY.—Porewater salinity and pH were measured with a YSI© 556 Multiprobe System at three different periods: 24–30 November 2002, 6–9 February 2003, and 27 February 2003. Tidal measurements were made 13–22 February 2003. Tide tables and several overnight measurements in a row were used to estimate a February maximum tidal level for each station. A yearly maximum tidal level was computed by extrapolation of these February maximum tidal levels in conjunction with the yearly tide tables. The

slope of the elevation change within each zone was also calculated with the following formula: $slope = \frac{H_3 - H_1}{Dist_{1-3}} \times 100$, where H_1 and H_3 were the relative elevation of the first and last points of each zone, respectively, and $Dist_{1-3}$ was the distance between these two points.

As a measure of site fertility, the nutrient resorption efficiency (RE) and leaf biomass production per unit of nutrient were calculated as an indirect way to determine trends of nutrient availability, as described in Feller *et al.* (1999). Leaves were collected 20–22 February 2003. In each zone where present, four samples of three to five pairs of leaves of *R. mangle* were harvested. A pair composed of a mature leaf and a ready-to-fall senescent leaf from the same twig. Digital images and image analysis software (SigmaScan Pro 4.0) were used to measure leaf area. All samples were oven-dried at 70°C, weighed and ground to pass through a 0.38 mm mesh screen. We measured nitrogen (N) and phosphorus (P) concentrations in the green and senescent leaves, and calculated nutrient RE and biomass production per unit of nutrient invested for each experimental tree. RE was calculated as the percentage of N and P recovered from senescing leaves before leaf fall (Chapin III & Van Cleve 1989): $RE = \frac{N \text{ or } P(\text{mg} \cdot \text{cm}^{-2})_{\text{green leaves}} - N \text{ or } P(\text{mg} \cdot \text{cm}^{-2})_{\text{senescent leaves}}}{N \text{ or } P(\text{mg} \cdot \text{cm}^{-2})_{\text{green leaves}}} \times 100$. Biomass production per unit of nutrient was calculated as the

inverse of the nutrient concentration in senescent leaves (nutrient use efficiency, NUE in g biomass(g N or P)).

INDICATORS OF DESTRUCTION LEVEL.—No direct information was available to estimate differences of mangrove destruction among sites during Hurricane Hattie. Therefore, an indirect measurement was necessary to extrapolate from the standing trees considered older than 41 yr to compare an estimated destruction level among the four sites. From these estimates, a qualitative variable of “complete” or “incomplete destruction” was attributed to each site.

In the most inland mangrove zone, named here hinterland zone, of the four sites, belt transects of 60 m long and 10 m width were established. The hinterland zones were chosen to make certain that the trees measured were in a comparable physical–chemical situation. Within these belt transects, all trees with DBH more than 20 cm were measured. The distribution patterns of these large trees were used to detect extraordinary old or large trees seen as outliers in the right side of the distribution. These outliers were then used as proxies of destruction levels of the four different sites, assuming that they represent the trees older than 41 yr.

In the fringe (*i.e.*, the first zone along the water’s edge) and dwarf zones of site C, a tree aging technique was adapted from Duke and Pinzon (1992) based on leaf scar production to estimate the possible destruction level of this forest. An estimation of leaf scars produced by dwarf *R. mangle* of Turneffe Atoll was 4.1 scars/yr (I.C. Feller, pers. comm.). This number was rounded to 5 to keep an error range and a robust estimate of tree age. Leaf scars were counted from the topmost apical leaves to the bottom of the trees for all stems present in three 1 × 1 m plots. Stems from an individual tree having more than 205 scars were considered to be older than 41 yr. The percentage of trees >41 yr was calculated from these measurements.

DATA ANALYSIS.—The PCQM results were used to calculate an importance value (IV) for each of the four species per zone as described in Cintrón and Schaeffer-Novelli (1984). IV was based on relative density, relative dominance, and relative frequency of each species. Consequently, the sum of the IV of all four species was equal to 300 for each zone. To summarize the IV variation between zones and sites and to consider all species at the same time, we developed an index of species dominance heterogeneity (I_{SDH}) based on the following equation, adapted from the reciprocal index of Simpson (Hill 1973): $I_{SDH} = \frac{300 \times (300-1)}{\sum_{i=1}^q (IV_i \times (IV_i-1))}$, where IV_i is the importance value of the species i and q the number of species. I_{SDH} is comparable to a species diversity index of second order of entropy because it would increase with a higher number of species but give more weight to the evenness in IV. The index was used because it incorporates the relative importance of species in terms of forest structure instead of the number of individuals. Thus dominance change would not only be a question of numbers of individuals, but also of space occupied by each species.

Nonparametric Spearman rank correlation analyses were conducted to investigate the relationships between the physical–chemical factors including the nutrient availability indicators and

the different forest structure variables (excluding I_{SDH}). A factor analysis with principal component extraction and varimax rotation was carried out to group linear correlations among the four nutrient variables. Scores of the two principal factors were used as explanatory variables for further analyses. To investigate the factors influencing the variation of the I_{SDH} , a general linear model analysis using Type V decomposition was used, followed by a general regression model analysis with backward stepwise selection of variables. The following continuous independent variables were considered for both analyses: mean recorded salinity, maximum tidal level, mean pH, slope, and the two synthetic factors of nutrient use and resorption efficiencies. The qualitative variable of destruction was also used as categorical factor in these analyses. The I_{SDH} and slope values were square root ($\arcsin(x/4) + \text{constant}$) transformed to get closer to normality.

RESULTS

FOREST MEASUREMENTS.—The canopy height and DBH at all sites showed general increases from the fringe zone to the hinterland (Fig. 2). However, the resulting structural zonation patterns among sites were different. For example, trees at site C were dwarf over a 60-m wide area followed by a 15-m tall forest whereas trees at site A were relatively homogeneous across the forest. Another main difference among the sites was seen in the species zonation pattern (Fig. 2). As a general pattern, *R. mangle* dominated the fringe zone of all sites. The basin zones were occupied mainly by *A. germinans* in sites B, C, and D. These sites were dominated by *L. racemosa* in the hinterland zones. In contrast, *R. mangle* was dominant in all zones at site A.

Species dominance heterogeneity (I_{SDH}) varied significantly among zones and sites (Fig. 2). Sites C and D were more heterogeneous than sites A and B. The pure dominance of *R. mangle* in zones 1 and 2 of site A was not found in other parts of the island except in the fringe and the first dwarf zone of site C. Also, the only pure area of *A. germinans* was found on site B. An herbaceous species, *Batis maritima*, was found on both sides of the island and in different zone types.

PHYSICAL–CHEMICAL MEASUREMENTS.—The salinity was relatively homogeneous at site A (Table 1). The maximum salinities were measured in *A. germinans* basins at sites B, C, and D. The minimum values were recorded in hinterland zones of all sites. The pH values of sites A and B were neutral at the fringe and hinterland, and slightly lower in the central zones probably linked to anoxic conditions (Table 1). For sites C and D, pH values generally increased toward the hinterland zones. In sites A and B, the first and last zones had higher slope values compared to the central zones, which were almost completely flat. Site D had in general the same pattern, whereas the topography was more varying at site C (Table 1).

Nitrogen-use efficiency (NUE-N) varied slightly, leading to few significant differences among zones and sites (Fig. 3). The highest values occurred in site C, particularly in the dwarf zones. Phosphorus-use efficiency (NUE-P) was also very high in these

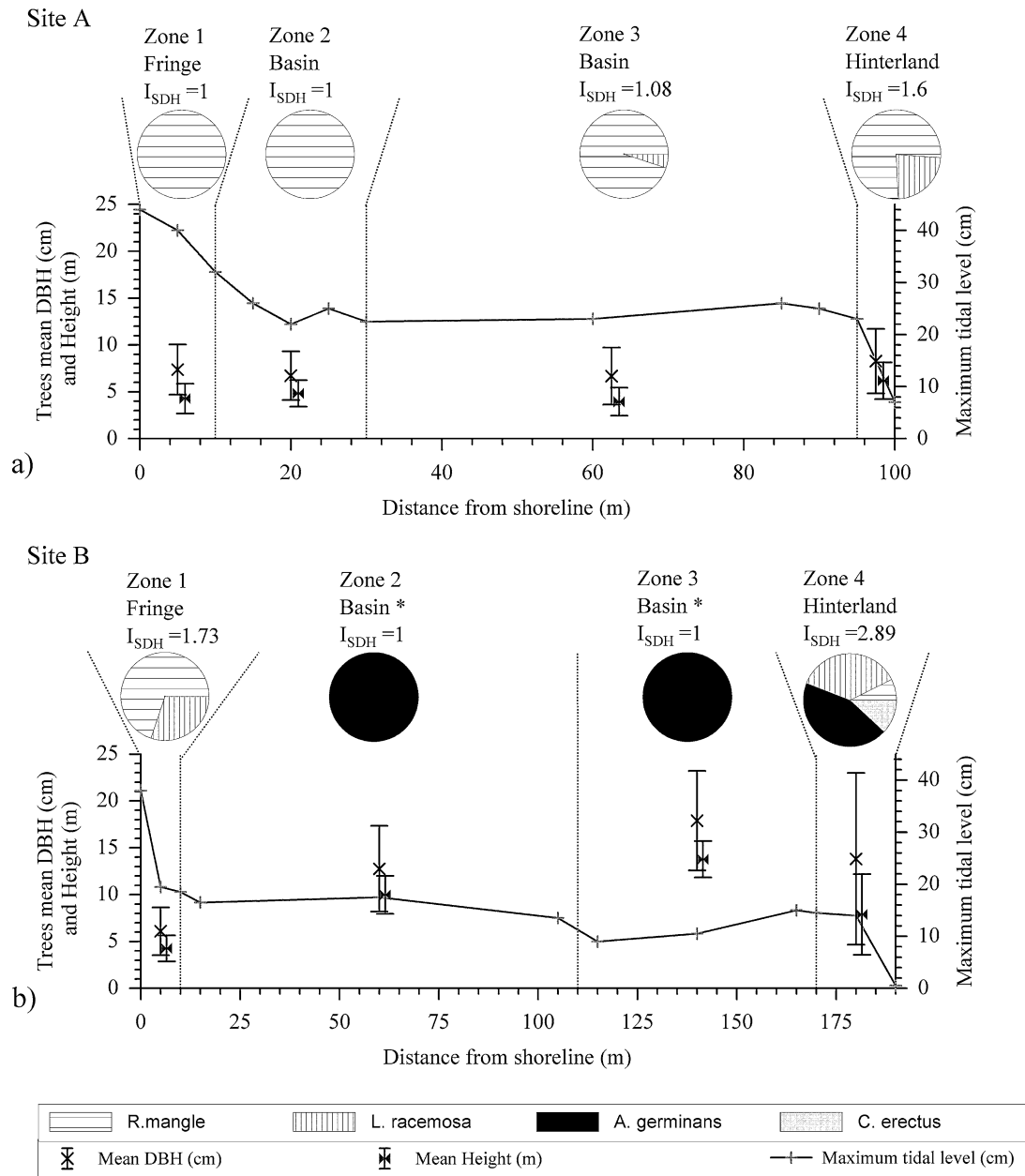


FIGURE 2. Mangrove forest structure of the different sites (A–D respectively). Zones are named according to position and type of structure (*indicate presence of *Batis maritima* on the ground). I_{SDH} values indicate the corresponding Index of species dominance heterogeneity. Pie charts show the species composition. Line graphs show trees mean DBH, mean canopy height per zone (error bars represent standard deviations), and profile of maximum height of tidal level at equinoxes spring high tide (in cm above ground).

dwarf zones of site C. For all sites, NUE-N and NUE-P were generally higher in zone 1 and decreased going landward. There were no significant differences in N-resorption efficiency (RE-N) among the sites (Fig. 4). Similar to patterns of NUE-N and NUE-P, P-resorption efficiency (RE-P) was highest in the dwarf zones and with lowest values in the inland zones at sites B, C, and D (Fig. 4). The variations in NUE and RE among the sites and zones were synthesized with factor analysis (Table 2), which confirms tight correlation of both NUE -N and -P and RE-P.

INDICATORS OF DESTRUCTION LEVEL.—In the belt transects of the hinterland zones of sites A and B, the frequency distribution of DBH of trees >20 cm decreased continuously going toward bigger size classes (Fig. 5). However, in the hinterland zones of sites C and D, the distribution included a few outliers with DBH >55 cm. The largest trees in sites A and B had DBH <37 cm, which together with the continuous decrease, provided evidence that the trees in those sites had grown subsequent to Hurricane Hattie. On the contrary, the frequency distribution of DBH of sites C and D

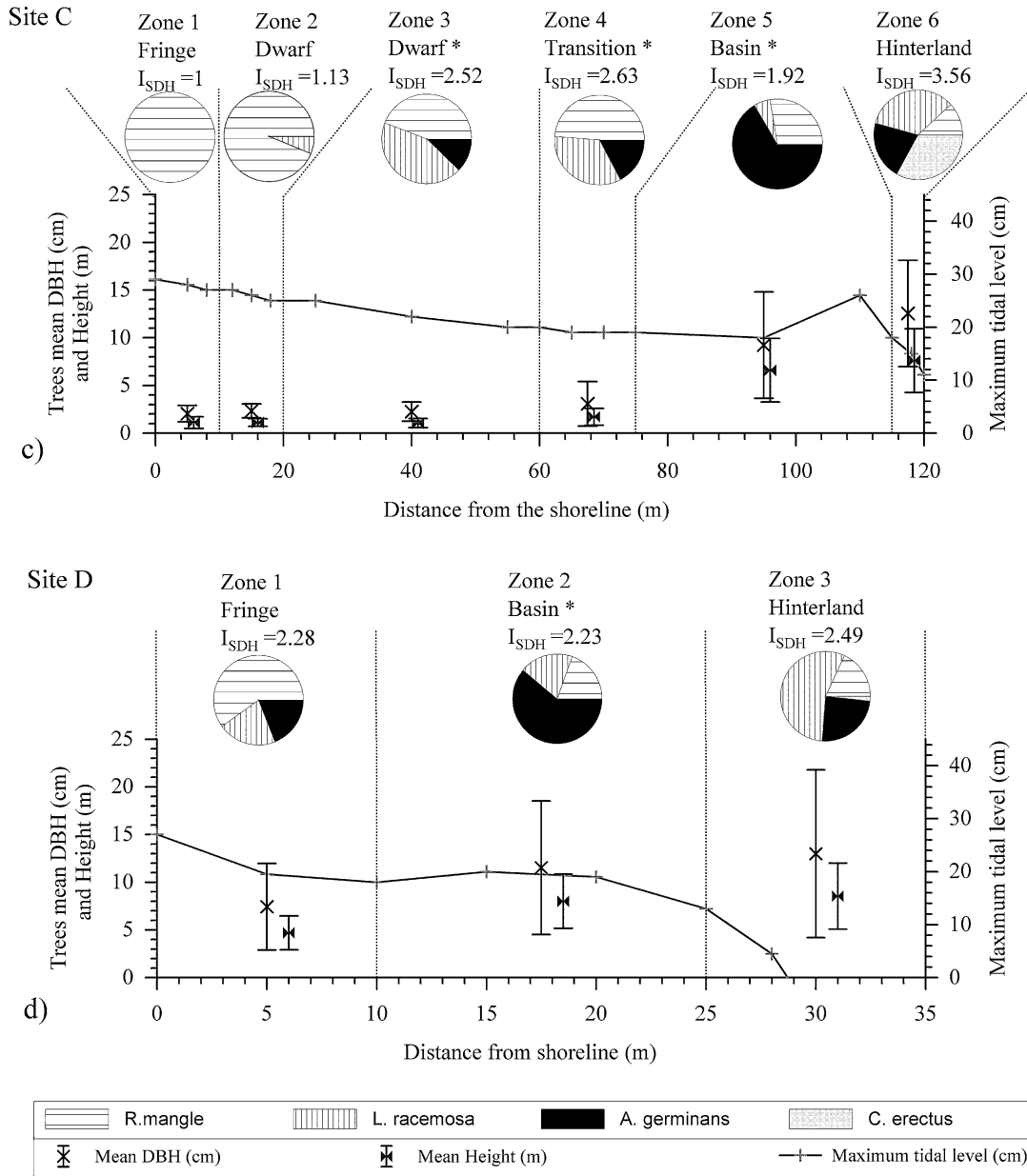


FIGURE 2. *Continued.*

TABLE 1. *Physicochemical measurements results per sites and zones. (Values are mean salinity \pm SD, expressed in practical salinity units (psu); mean pH \pm SD; S = slope of zone ground, in %.)*

Zones	Site A			Site B			Site C			Site D		
	Psu	pH	S	psu	pH	S	psu	pH	S	psu	pH	S
1	37.9 \pm 0.4	6.6 \pm 0.2	1.20	38.9 \pm 0.9	6.7 \pm 0.6	1.95	40.5 \pm 2.7	6.6 \pm 0.1	0.25	40.6 \pm 6.3	6.5 \pm 0.2	0.90
2	36.9 \pm 1.5	6.4 \pm 0.05	0.10	45.1 \pm 8	6.8 \pm 0.3	0.03	44.9 \pm 2.8	6.6 \pm 0.3	0.33	44.7 \pm 6.5	6.9 \pm 0.1	0.70
3	37.7 \pm 2.0	6.4 \pm 0.1	-0.06	46.0 \pm 10.6	6.5 \pm 0.1	-0.12	46.1 \pm 5.0	6.7 \pm 0.2	0.17	21.6 \pm 5.1	7.3 \pm 0.2	2.07
4	37.0 \pm 3.3	7.0 \pm 0.4	1.80	39.6 \pm 10.9	6.9 \pm 0.2	0.70	39.7 \pm 5.1	6.5 \pm 0.1	0.10			
5							42.0 \pm 9.0	6.8 \pm 0.3	-0.20			
6							22.8 \pm 9.1	7.1 \pm 0.1	1.40			

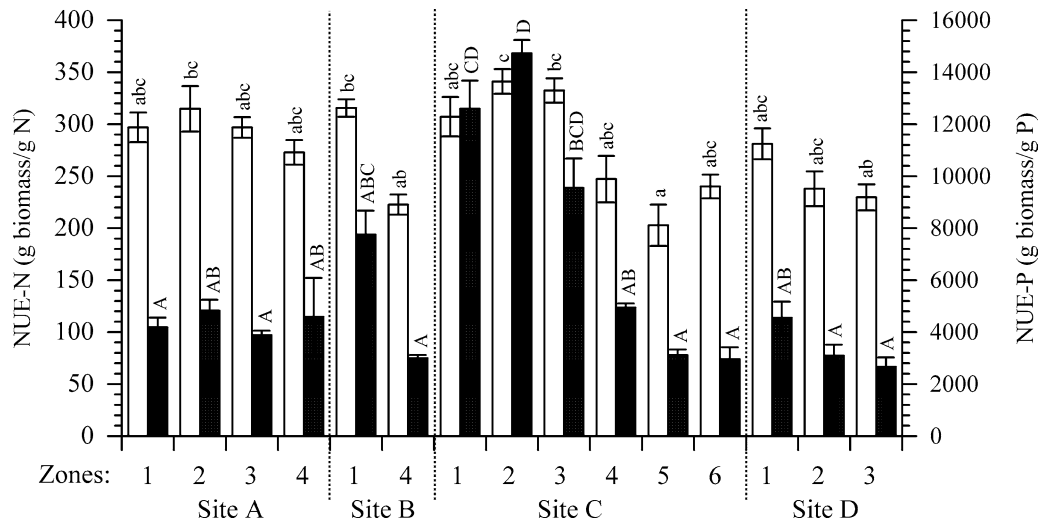


FIGURE 3. *Rhizophora mangle* leaves nutrient use efficiency of nitrogen (white bars) and phosphorus (filled bars) in grams of created leaf biomass/g of N or P (error bars = SE). The x-axis represents the different sites and zone numbers. Letters show the homogeneous groups (*Posthoc* analysis Sheffé test).

was discontinuous between 45 and 55 cm. The few large trees at the end of the distribution survived Hattie and were thus >41 yr old. Additionally, in zones 1 and 2 at site C, more than 61 percent of dwarf trees were >41 yr.

All these observations suggest that Hattie caused complete destruction of the mangrove forest at sites A and B, whereas remnants of the original forests still existed across the forests at sites C and D, indicating incomplete destruction. This information was used to generate a dummy variable of two destruction levels: for sites A and B, 0 = complete destruction during Hattie, for sites C and D, 1 = incomplete destruction during Hattie.

STATISTICAL ANALYSES.—The Spearman correlation analyses showed that the IV of *R. mangle* were negatively correlated to the pH and positively to NUE-N, NUE-P, and RE-P. IVs of *A. germinans* were negatively correlated with NUE-N, NUE-P, and RE-P but positively to the maximum recorded salinity. IVs of *L. racemosa* were negatively correlated with the maximum tidal level and positively to the slope and pH. IVs of *C. erectus* were negatively correlated to the maximum tidal level, the mean salinity, NUE-N, NUE-P, and RE-P but positively to the slope and pH (Spearman correlation test, $P < 0.05$ in all cases). Additionally, NUE-N, NUE-P, and RE-P were negatively correlated with DBH and tree height, and positively

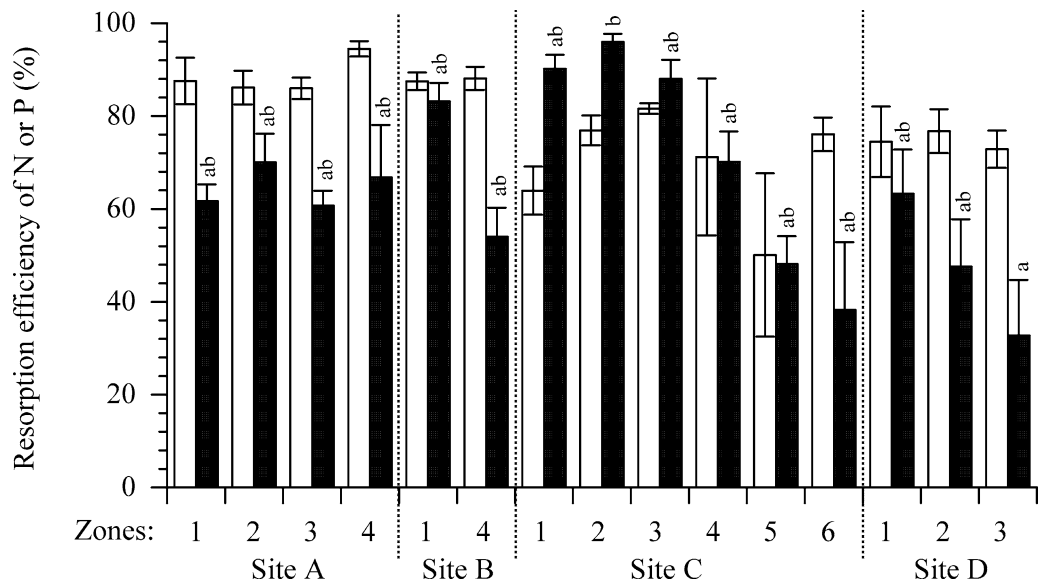


FIGURE 4. *Rhizophora mangle* leaves resorption efficiency of nitrogen (white bars) and phosphorus (filled bars) in percentage (error bars = SE). The x-axis represents the different sites and zone numbers. Letters show the homogeneous groups (*Posthoc* analysis Sheffé test).

TABLE 2. Factor loadings of nutrient use variables factor analysis with principal component extraction method and varimax rotation (marked loadings are >0.70).

	Factor 1	Factor 2
NUE-N	0.738	0.490
NUE-P	0.958	-0.098
RE-N	0.023	0.978
RE-P	0.901	0.153
Eigenvalues	2.273	1.230
Prop. of total var.	0.568	0.307

correlated with tree density (Spearman correlation test, $P < 0.01$ in all cases).

The general linear model constructed with all the variables did not explain significant variations of the index of species dominance heterogeneity (I_{SDH}) (test whole GLM model vs. residual, *Multiple R* = 0.812, $F = 2.483$, $P = 0.102$). However, within this model, the destruction indicator dummy variable had a significant effect on the I_{SDH} (GLM univariate significance; $F = 5.158$, $P = 0.049$). None of the other variables (*i.e.*, salinity, tidal level, pH, slope, and nutrient availability factors) had a significant influence on the I_{SDH} . On the contrary, the general regression model constructed with a backward stepwise selection and selecting the destruction indicator dummy variable and the first factor of nutrient availability indicator (Table 3), explained a significant proportion of the variance of I_{SDH}

(test whole GRM model vs. residual, *Multiple R* = 0.718, $F = 7.450$, $P = 0.006$).

DISCUSSION

Forest measurements results showed clearly different horizontal zonation patterns at Calabash Cay. Firstly, the structural zonation pattern indicated by DBH, tree height, and forest density differed at each site. Correlation analyses suggested that these patterns were related to N-use efficiency, P-use efficiency, and P-resorption efficiency. According to the findings of Feller (1995) and Feller *et al.* (2002, 2003), these values were indicative of nutrient availability. The species zonation patterns were also clearly different from sites to sites. *Rhizophora mangle* was more dominant in low nutrient availability and acidic areas. Similarly, *A. germinans* dominated more in high salinity and high nutrient availability areas, and *L. racemosa* in higher intertidal, steeper, and more neutral-to-basic zones. The restriction of *C. erectus* only in the hinterland zones demonstrated the adaptation of this species to rarely inundated areas (Tomlinson 1986). These trends fit well with other studies in the Caribbean. They suggested that differences in propagules dispersal (Rabinovitz 1978, Jiménez & Sauter 1991), geomorphological factors (Thom 1967), as well as physiological adaptations to gradients across the intertidal zone (Macnae 1968, or *e.g.*, McKee 1995a,b) were interacting factors driving zonation patterns in Calabash Cay.

According to Stoddart (1963), the vegetation of inner parts of Turneffe was less damaged by Hurricane Hattie than the vegetation of outer sites. Both proxies used to indicate destruction levels in

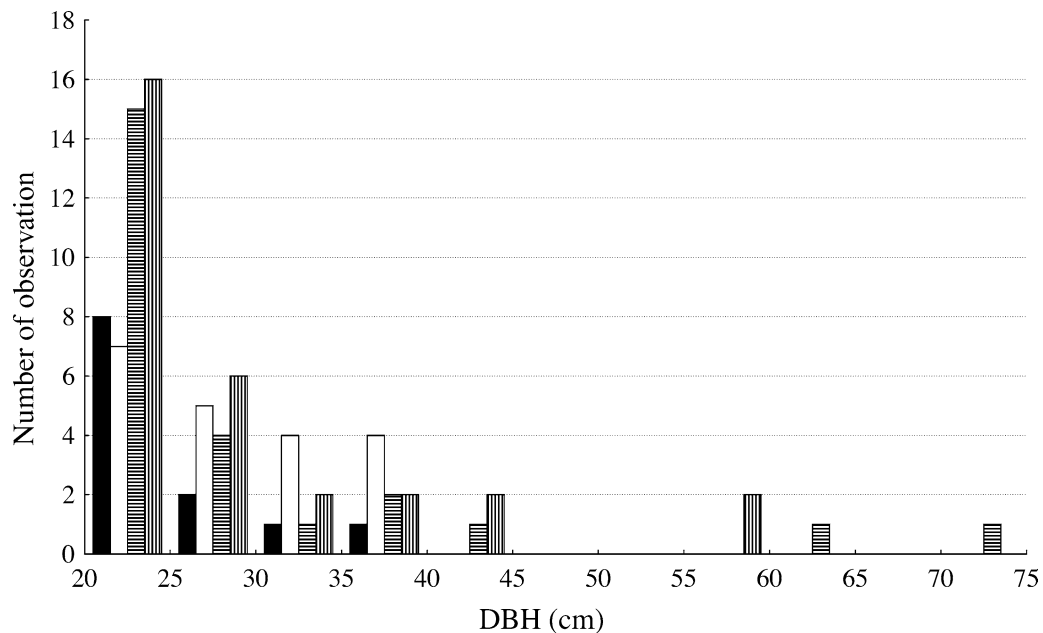


FIGURE 5. Trees DBH class distribution (only DBH >20 cm) in the last zone of each sites (Site A: black filled; Site B: white; Site C: horizontal stripes; and Site D: vertical stripes).

TABLE 3. Univariate tests of significance and summary of parameters of the general regression model with backward stepwise selection of explanatory variables on the I_{SDH} variations (marked factors are significant at $P < 0.05$).

	SS	df	MS	F	P	Parameter	SE
Intercept	0.735	1	0.735	1.515	0.239	-0.208	0.169
Maximum tidal level	Pooled	0					
Mean salinity	Pooled	0					
Mean pH	Pooled	0					
Slope	Pooled	0					
Factor 1 Nutrients	3.934	1	3.934	8.113	0.013	-0.559	0.196
Factor 2 Nutrients	Pooled	0					
Destruction	4.203	1	4.203	8.667	0.011	-0.502	0.170
Error	6.789	14	0.485				

this study supported this observation 41 yr later: the distributions of all trees with DBH >20 cm showed that no old trees (right side outliers) existed in the seaward sites A and B, but some big hollow, remnant trees older than 41yr were found in the inner sites C and D. Secondly, the number of scars indicating the age of dwarf trees also showed incomplete destruction in a sheltered position on the west side of Calabash. The percent of dwarf trees older than 41 yr suggested that the dwarf mangroves of Calabash Cay were the trees that best resisted Hurricane Hattie. These findings were consistent with other observations from the Caribbean (Smith *et al.* 1994, Lugo 1997) and Australia (Bardsley 1984). During Hattie, the high water level due to the storm surge would have covered these small individuals, preventing them from being blown down by strong winds. If these trees had been exposed to wave action, it is likely that they would have been killed as the fringing zones of most hurricane-destroyed sites (*e.g.*, Imbert 2002). Thus, the survivability of the dwarf trees makes them potential sources of propagules for recolonization processes after large perturbations.

The index of species dominance heterogeneity (I_{SDH}) showed differences among zones and sites. One of the general trends for each site was that the hinterland zone had the maximum I_{SDH} value. This trend resulted from the higher possibility of finding pure *R. mangle* or *A. germinans* stands in the lower intertidal zones than in the hinterland zones where *L. racemosa* was frequently mixed with *C. erectus*. Besides these intrasite variations, the I_{SDH} at the east side of the island (*i.e.*, the exposed part that sustained the most damage from Hattie) was more homogeneous than the west side (sheltered part). Our statistical results with the GLM model showed the importance of the destruction indicator to these forest heterogeneity differences. The GRM model also included the factors indicating nutrient availability, which could be related to two aspects of forest heterogeneity. First, P-use efficiency and resorption efficiency increased from the fringe to the upper zones, as did the I_{SDH} . Second, N-use efficiency was highest at sites where *R. mangle* dominated, leading to a low I_{SDH} . These relationships supported the hypothesis that nutrient availability was important to species dominance. Yet, only the model including both the nutrient availability and the de-

struction indicator explained the differences of forest heterogeneity between the two sides of Calabash. These results suggested that forest dynamics at Calabash were influenced by the remnant forest that survived Hattie. A possible scenario was that the surviving *A. germinans* and *L. racemosa*, as well as the dwarf *R. mangle* trees on the western side of the island served as a reservoir for propagules on the nearby areas. In combination with external propagules, this could have resulted in a relatively rapid recolonization of Calabash. Succession modified by the presence of the larger trees might have increased the spatial patchiness by competition effects. We observed that some *R. mangle* trees developed as an understory in *A. germinans* basins at the sheltered sites, which indicated that this complex phenomenon was not finished yet. *Rhizophora mangle* may eventually outcompete the two other species in some zones. In contrast, on the eastern sites, succession and competition probably happened according to the species characteristics to abiotic conditions. This would have led to more homogeneous zones with clearer partitioning of the species along the intertidal. The example of Calabash Cay having the most heterogeneous sites on the least-destroyed sites except for the dwarf areas was contradictory to what Baldwin *et al.* (2001) predicted for Biscayne Bay (Florida); however, their observations of the regeneration of mangrove sites were only 7 yr after Hurricane Andrew, and illustrated the influence of several herbaceous species on the early regeneration pathways. The herbaceous species present in Calabash Cay were found in both heterogeneous and homogeneous forests. Our study was consistent with Imbert (2002), who found that the number of surviving trees influenced the recovery pathways and succession. All these studies showed that remnant vegetation plays an important role for the recovery of mangrove forests after hurricane destruction.

To conclude, this study suggests that disturbance intensity can influence the recovery pathways and succession in mangrove forests. Detailed quantitative data on forest structure before and after disturbance, following the regeneration processes would provide stronger evidence of this relationship. The example of Calabash Cay mangroves showed that the perturbation regime should be considered when interpreting horizontal zonation patterns of mangrove forests.

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