

Small-scale disturbance and regeneration dynamics in a neotropical mangrove forest

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Summary

1 Mangrove forests are affected by a variety of natural disturbances that differ in scale, intensity and frequency. Small canopy gaps, although common, have not been well studied. We examined the role of lightning-created canopy gaps in the dynamics of a 47-km² intertidal mangrove community in the Dominican Republic, by quantifying the spatial patterns of overstorey tree distributions, spatial and temporal patterns of gap formation, and tree regeneration in gaps and beneath the closed forest. We hypothesized that regeneration in these gaps would maintain and reinforce species' distribution patterns across the intertidal gradient in this mangrove ecosystem.

2 All 52 gaps surveyed in the field were nearly circular canopy openings created by lightning. Expanded gap size indicated an average diameter of 30.4 m. The total area of forest in the gap-phase is currently 1.9%, with an annual formation rate of 0.23% year⁻¹. Canopy turnover was calculated to range from 421 to 842 years; however, gaps were not randomly distributed across the mangrove forest and canopy turnover in the most gap-prone areas ranged from 194 to 386 years.

3 Seedling density was not different under gaps and under the forest canopy, but sapling density and sapling growth rates of three species were significantly greater in canopy gaps. The annual mortality rate of *Rhizophora mangle* (9%) in canopy gaps was significantly lower than either *Laguncularia racemosa* (32%) or *Avicennia germinans* (56%). Gap regeneration was dominated by *R. mangle* throughout the forest.

4 The results of this study do not support our initial hypothesis but suggest that the distribution and abundance of *R. mangle* will increase throughout the forest over time, given the present disturbance regime. Field observations indicated that the peat mat collapses in lightning-created gaps following their formation, resulting in increased levels of standing water. We suggest the successful regeneration of *R. mangle* is favoured in these gaps because of its greater tolerance to flooding conditions.

Keywords: canopy gaps, community dynamics, disturbance, mangroves, regeneration

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Introduction

Mangrove forests dominate protected coastal areas in the tropics and subtropics. These forest communities are often characterized by distinct zonation patterns of constituent species across the intertidal

gradient. For example, in the Caribbean the red mangrove, *Rhizophora mangle* L. (Rhizophoraceae), typically occupies the lower intertidal zones, whereas the black mangrove, *Avicennia germinans* (L.) Stearn (Avicenniaceae), and white mangrove, *Laguncularia racemosa* (L.) Gaertn. (Combretaceae), dominate more inland sites (Davis 1940; Lugo & Snedaker 1974; Chapman 1976). Although it is often assumed that the dynamics of mangrove forests are regulated

by environmental factors that vary across the intertidal gradient, the mechanisms that generate spatial patterning in mangroves are poorly understood (reviewed in Smith 1992).

Disturbances play a central role in determining the distribution and abundance of tree species in forests (Pickett & White 1985). Disturbances create canopy openings that provide the opportunity for tree recruitment, and the scale, intensity and spatial pattern of tree mortality defines the consequences of disturbance for forest vegetation composition. Hence, a clear understanding of forest dynamics is not possible without a comprehensive understanding of the disturbance regime. Hurricanes are common in many areas characterized by mangroves, and these large-scale stand-initiating disturbances are known to influence the regeneration dynamics of such forests (Roth 1992; Smith *et al.* 1994; Baldwin *et al.* 1995). However, depending upon the position of particular mangrove forests relative to the tracks of intense tropical cyclones (hurricanes, typhoons), the frequency of large-scale, stand-replacing disturbances may vary markedly among mangroves.

Small-scale disturbances also are common in many mangrove forests (Paijmans & Rollet 1977; Smith 1992; Smith *et al.* 1994). Several authors have suggested that canopy gaps might be important in the establishment, recruitment and growth of mangroves (Watson 1928; Macnae 1968; Rabinowitz 1978; Ball 1980; Putz & Chan 1986; Smith 1987; Jimenez 1990; Smith 1992; Smith *et al.* 1994), although few studies have examined the patterns of small-scale disturbances and their role in regulating species' replacement patterns. If canopy gaps provide opportunities for the recruitment of new individuals to the canopy, then gap regeneration may contribute to the maintenance of existing tree species' distributions. Moreover, even where large-scale disturbances are common, small-scale disturbances may still play an indirect role in determining forest community pattern. Smith *et al.* (1994) observed that post-hurricane survival of individuals growing in pre-existing canopy gaps was greater than for individuals growing in the surrounding canopy of the mangrove forest. The authors proposed that these surviving individuals might provide an important seed source for recolonization following large-scale disturbances. Hence, the ability of a species to colonize a canopy gap may play an important role in determining the future species composition of mangrove forests regardless of the frequency of large-scale disturbances.

Lightning has been identified as a common disturbance agent in many mangrove forests, including Papua New Guinea (Paijmans & Rollet 1977), Australia (Smith 1992), Malaysia (Anderson 1964), Panama (Smith 1992; W.P. Sousa, University of California, Berkeley, personal communication) and

Florida (Craighead 1971; Odum *et al.* 1982; Smith *et al.* 1994). Although the mechanism by which lightning causes group tree mortality is not known, where it occurs the effect is almost always to kill groups of trees in a 20–30-m diameter circle, and the trees remain standing dead for several years (Anderson 1964; Bruenig 1964; Paijmans & Rollet 1977; Smith 1992). Given their ubiquity, lightning-created gaps may be an important force regulating tree distribution and abundance in mangroves.

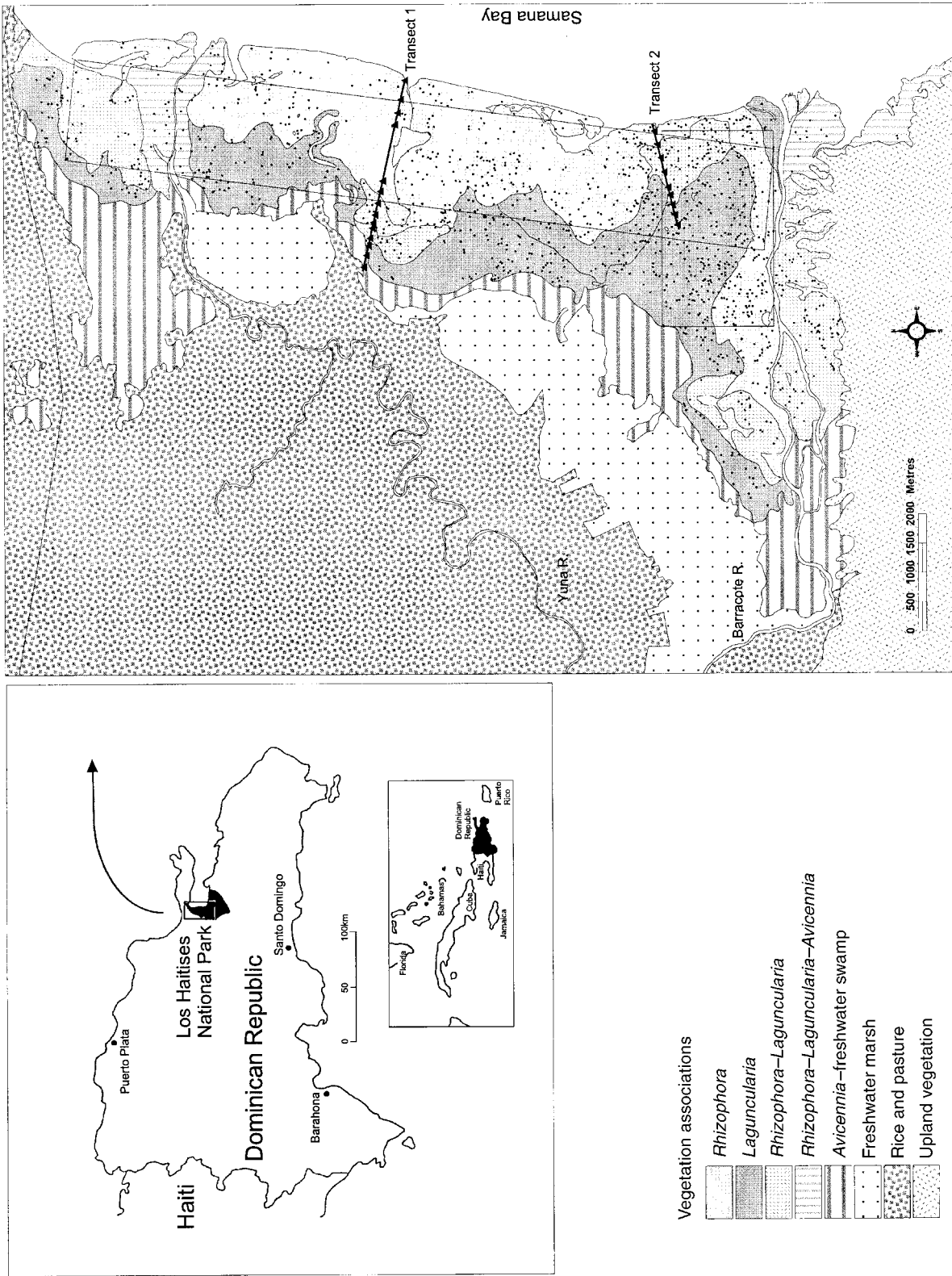
The goal of the present study was to improve understanding of the role of lightning-created canopy gaps in regulating tree distributions in mangrove forests. We studied a deltaic mangrove forest on the island of Hispaniola. The study site provided an exceptional opportunity to address this question because of its large extent (47 km²) and lack of human disturbance. Our objectives were to quantify (i) the spatial patterns of overstorey and understorey tree distributions; (2) the spatial and temporal patterns of lightning-created gap formation; and (3) tree regeneration in lightning-created gaps and beneath the closed forest across the intertidal zone. In this paper, we examine the disturbance regime associated with lightning-created gaps only. We hypothesized that gap regeneration would maintain and reinforce species' distribution patterns in this mangrove ecosystem.

Methods

STUDY SITE

This study was conducted in a mangrove forest located at the western end of Samaná Bay in the Los Haitizes National Park, Dominican Republic, in the broad delta created at the mouths of the Yuna and Barracote rivers (19°10' N, 69°40' W; Fig. 1). The forest is dominated by the red mangrove (*R. mangle*) and white mangrove (*L. racemosa*), with a lesser amount of the black mangrove (*A. germinans*). The inland border is formed by a freshwater swamp, marsh and a region of extensive rice production. Mean annual temperature is 26.3°C and rainfall averages 2065 mm year⁻¹, with the driest months being February and March when rainfall averages 100 mm month⁻¹ (Oficina Nacional de Meteorología, Dominican Republic). Mean tidal amplitude is approximately 0.6 m.

Soils were field classified as fine-silty isohyperthermic typic hydraquents. Throughout most of the forest, the soil was characterized by an organic peat mat approximately 30–50 cm in thickness, underlain by a highly decomposed organic layer about 1 m in thickness. The surface peat mat consisted primarily of living roots, whereas the deeper organic soil layer contained few living roots. Underlying the organic soil was a firm clay substrate. The peat mat was absent nearer the coast, where the soil was predomi-



Mangrove forest 1996

Fig. 1 The mangrove forest study area in the Los Haitises national park, Dominican Republic, depicting the forest associations, location of lightning-created gaps, transects and plots used for field sampling (heavy solid lines and triangles, respectively), and the two sampling rectangles (large box = coastal rectangle; small box = inland rectangle) used for the spatial analysis (see text).

nantly an allochthonously derived silty-clay marl that extended approximately 250 m inland. At the upland margin of the forest, the clay layer surfaced and the organic peat mat was absent.

A tidal wave destroyed much of the mangrove in 1946 (Sachtler 1973; Alvarez & Cintrón 1984). Since then, the forest has recolonized and expanded in total area from 32.7 km² in 1959 to 47.1 km² in 1996 (based on aerial photographs; see below). There have been no large-scale disturbances since 1946 and the forest presently is in a relatively pristine state largely unaffected by humans.

STAND STRUCTURE

To characterize the composition, structure and spatial pattern of the forest and the relationship of these variables to environmental features, we established permanent plots along two transects in 1994 (Fig. 1). Field reconnaissance suggested complex riverine effects, and the two sampling transects were positioned to minimize this complicating influence. One transect extended 3.1 km inland from the coast to the transition to the freshwater marsh, and a second transect extended from the coast inland for 1.8 km. Fourteen 30-m diameter plots were positioned along transect 1 so that each of the different vegetation associations, as delineated by aerial photography (see below), was sampled. We spaced nine 30-m diameter plots along the second transect at uniform 200-m intervals. All plots were located in closed canopy forest.

In each plot, all trees greater than 5 cm diameter at breast height (d.b.h.) were measured and tagged to allow estimates of stem density and basal area. Although stem diameter measurements for *R. mangle* were made above the highest prop root, we refer to these measurements as d.b.h. The height of the four tallest canopy trees in each plot was measured using a clinometer. To estimate sapling and seedling density, all saplings (1 m tall and < 5 cm d.b.h.) were counted and identified in each plot, and seedlings (< 1 m tall, including young-of-the-year) were enumerated by species in a total of 12 subplots, each 1 × 1 m, spaced evenly along perpendicular transects set out north-south and east-west from the centre of each plot. All seedling counts were made in December 1994 and sapling counts in November 1994. Based on our litter fall collections (unpublished data), both *R. mangle* and *A. germinans* produce seeds year-round, whereas for *L. racemosa* most seed production occurs in December and January.

GAP CHARACTERISTICS

Lightning-created gaps were located near each permanent plot (up to four per plot when present) and

a total of 52 gaps was sampled. Canopy gaps varied in age from newly formed to at least 10 years old. Gap area and the composition and density of the vegetation growing in each of the gaps were quantified. To calculate expanded gap area (A), we measured the longest axis (A_{major}) between the trunks of border trees and the longest axis perpendicular to this (A_{minor}), and fit these measurements to the formula for an ellipse: $A = (A_{\text{major}} \times A_{\text{minor}})/4$. To calculate actual gap area, directly under the canopy opening, we corrected expanded gap area for crown extension from border trees. The average crown area per tree was calculated as the inverse of overstorey tree density and used to derive the radius of the average tree crown, which was then subtracted twice from A_{major} and A_{minor} . Gap shape was described by eccentricity ($A_{\text{major}}/A_{\text{minor}}$): a value of 1 indicates a circular shape whereas a value > 1 indicates an elliptical shape (Battles & Fahey 1996). Seedling and sapling density in each gap were estimated by counting individuals in 1 × 1-m plots spaced every 5 m along the two perpendicular axes, and recorded by species.

In November 1995, saplings (> 1 m tall and 5 cm d.b.h.) were measured and tagged in each of the 23 permanent plots and in a subset ($n = 17$) of the gaps surveyed along transect 2, and used to estimate growth and mortality rates. Gaps nearest to permanent plots were selected for sapling growth measurements in order to permit paired comparisons of sapling growth rates in canopy gaps and under the forest canopy. Our target sample size was 25 saplings of each species in each plot and gap, but because few saplings of species other than *R. mangle* were found (see the Results) the actual sample size ranged from 0 to 25 individuals of each species. The diameter of each tagged sapling was measured at a height indicated with flagging and then remeasured in January 1997 for growth estimates. Relative growth rates were computed as: $\ln[\text{DBH}_2] - \ln[\text{DBH}_1]$ (Evans 1972), and expressed on an annual basis.

UNDERSTOREY LIGHT LEVELS

The availability of light in the understorey was quantified using the gap light index (GLI) (Canham 1988; Canham *et al.* 1990). This technique quantifies the percentage of photosynthetically active radiation transmitted to a particular point in the forest floor over the course of the growing season. The GLI ranges from 0 for a completely closed canopy to 100 for a completely open site. Four fish-eye photographs were taken in a random location in each of four quadrats in each permanent plot and three photographs were taken in random locations in 13 canopy gaps. Field acquisition, digital conversion and GLI analysis follow the protocols described in Battles (1999). We re-analysed more than 10% of

the photos and calculated precision as the root mean square of the difference in GLI between the two analyses. The absolute precision associated with the GLI measurements was 1.0 GLI and the average relative error was 4%.

GAP ABUNDANCE AND DISTRIBUTION

A time-series of aerial photographs of the mangrove forest was obtained from the Military Cartographic Institute, Dominican Republic, for the following years: 1959 (1:60 000), 1967 (1:20 000), 1983 (1:40 000), 1993 (1:20 000) and 1996 (1:20 000). The 1993 and 1996 photographs were in colour whereas earlier years were black and white. The 1993 aerial photographs covered only 36 km² of the total 47.1 km² of forest.

Aerial photographs were examined stereoscopically; lightning-caused canopy gaps and other landscape features were mapped onto clear acetate overlays and all features were transferred to a base map. Major vegetation types were delineated for the 1996 photographs based on changes in canopy colour and texture. Field reconnaissance was used to verify photo interpretations. Lightning-created gaps were readily distinguished due to the uniformity of the forest canopy and the discrete, circular nature of the gaps, and we were able to perform a complete census of lightning-created gaps in the mangrove forest for all photographed years except 1993. We calculated the percentage of forest area in gaps at each time period by multiplying the total number of gaps by the average gap size as measured in the field. We assumed average gap size was constant for all years because it was not possible to measure gap size from the aerial photographs.

The base map was made from a 1:50 000 topographic map (Military Cartographic Institute, Dominican Republic). The base map and acetate overlays were enlarged to 1:20 000 scale using a photocopier. Each base map was then digitized into a geographical information system (GIS) using ESRI ARC/INFO software (Environmental Systems Research Institute, Inc., Redlands, CA, USA). A composite map consisting of information from all photographs was drawn to reconstruct the development of the forest since 1959. We classified the forest into four different age classes (before 1959, 1959–67, 1967–83, 1983–96) to illustrate forest recovery following the 1946 tidal wave. The GIS data provided the location of each gap and also the aerial coverage of the different forest types (vegetation and age classifications).

GAP FORMATION

To estimate annual gap formation rate, we compared gap locations on the aerial photographs

between years and quantified the number of new gaps appearing in the more recent photographs. We calculated annual formation rates from 1959 to 1967, 1967 to 1983, 1983 to 1993 and 1993 to 1996. On the colour photographs, we were able to quantify the number of gaps that had formed and subsequently closed in the time interval between photographs because the vegetation of recently closed gaps has a characteristic dark green colour. However, it was difficult to detect recently closed gaps in the black and white photographs and, as a result, formation rates may be underestimated for the two earliest periods (1959–67, 1967–83), when only black and white photographs were available.

SPATIAL ANALYSIS

We quantified the spatial distribution of gaps using a combination of point-based and quadrat-based measurements. To make the spatial analysis more tractable, two rectangles were used to represent the mangrove forest: one (12 000 m north–south by 2200 m east–west) was orientated so that the long axis ran parallel to the coast (coastal rectangle), and one in the southern corner (2200 m north–south by 3300 m east–west) was orientated so that the long axis lay parallel to the river (inland rectangle; Fig. 1). The rectangles were used to search for directionality in gap location (anisotropy) in two opposing directions. Given the configuration of the mangrove forest, it was necessary to divide the mangrove into two regions to maximize the distance along the two axes for the analysis. The overlap between the two rectangles would not affect the results. The two rectangles incorporated approximately 61% of the area of the mangrove and 70% of the gaps. We used the gap centres to define the point location of the gaps (determined by GIS from aerial photographs).

To examine gap dispersion, we first tested the null hypothesis of complete spatial randomness. We examined patterns at multiple scales using the K-function (Cressie 1991) and calculated confidence intervals (99%) from simulations of random point fields, as implemented in S+ Spatial Stats (Mathsoft Inc., Seattle, WA). Pairwise correlations were used to examine anisotropy in the spatial distribution (Stoyan & Stoyan 1994).

To quantify spatial patterns in terms of gap density, we divided the coastal rectangle into 60 contiguous quadrats [200 m (north–south) by 2200 m (east–west), area = 44 ha] and the inland rectangle into 33 quadrats [2200 m (north–south) × 100 m (east–west), area = 22 (ha)]. The size of the quadrat in each rectangle was chosen to minimize the fre-

quency of quadrats with no gaps present. The number of gaps in each quadrat was counted.

STATISTICAL ANALYSIS

Non-parametric statistics were used to analyse vegetation composition because the data were heteroscedastic and transformations did not normalize the data. Therefore, in addition to means and standard deviations, we report medians and quartiles in the results. We used Mann–Whitney *U*-tests for two sample comparisons and Kruskal–Wallis one-way non-parametric ANOVA for multiple comparisons across single factors. Sapling growth in plots and gaps was compared using two sample *t*-tests. One-way ANOVAs were used to compare growth rates among species. All of the above analyses were performed using Minitab (Minitab Inc., State College, PA).

Results

FOREST COMPOSITION AND STRUCTURE

A monospecific stand of *R. mangle* occupied the lower intertidal zone of both transects, with a gradual transition inland to a forest dominated by *L. racemosa* (Fig. 2a). Along transect 1, a sharp transition from a *Laguncularia*- to an *A. germinans*-dominated forest occurred near the inland margin, followed by an abrupt transition to a narrow band of freshwater marsh and then an extensive rice production area. Field reconnaissance indicated that the *Laguncularia*-dominated forest along transect 2 (at 1325–1800 m inland; Fig. 2a) extended beyond the end of the transect to the inland mangrove edge and, although *Avicennia* became more abundant, it did not achieve dominance as on transect 1. Although an *Avicennia*–freshwater swamp association occurred along the inland border (Fig. 1), *A. germinans* was not a dominant species in this region of the freshwater swamp (see below). Canopy height averaged 24 m across all plots, with maximum canopy heights of 30 m attained in the more inland stands (Fig. 2d). Surface water salinity generally decreased along the spatial gradient from the coast to the upper mangrove regions (Fig. 2e).

Using the 1996 aerial photographs, we identified five forest associations and determined their areas (km²): *Rhizophora* (18.5), *Rhizophora*–*Laguncularia* mix (8.7), *Laguncularia* (16.0), *Rhizophora*–*Laguncularia*–*Avicennia* mix (3.9), and an *Avicennia*–freshwater swamp mix (14.7) (Fig. 1). *Avicennia germinans* was grouped with the larger classification of freshwater swamp because it was not possible to distinguish this species using the aerial photographs; however, *A. germinans* had a limited distribution

and occurred primarily along the inland border of the mangrove forest and did not extend far into the freshwater swamp. Vegetation associations classified from transect data (Table 1) corresponded with those identified by aerial photography (Fig. 2a). The resolution was not as fine using the aerial photographs, so that transects showed small-scale heterogeneity and the *Rhizophora*–*Laguncularia*–*Avicennia* mixed forest occurred in large areas only in regions not encountered by the transects.

Highest basal areas (up to 38 m² ha⁻¹) were attained in *Laguncularia*-dominated stands (Table 1). Along transect 1, tree density was greatest in the *Rhizophora*-dominated forest and decreased further inland (Table 1). Total tree density was more variable among plots along the second transect and was greatest where *Laguncularia* was most abundant (Table 1).

GAP CHARACTERISTICS

All 52 gaps surveyed were created by lightning. Expanded gap area ranged from 300 to 1600 m², averaging 724 m² (i.e. mean diameter was 30.4 m) (Fig. 3). Actual gap size averaged 506 m² (25.4 m diameter), based on an average tree crown size of 20.4 m². Average gap shape was slightly elliptical, with a mean eccentricity of 1.3 ± 0.04 . Canopy gaps did not differ in size or shape between transects (*t*-test, $P = 0.59$ and $P = 0.10$, respectively) or among the different vegetation zones (one-way ANOVA, $P = 0.61$ and $P = 0.95$, respectively). Transmission of photosynthetically active radiation to the forest floor was significantly ($P < 0.01$) greater in canopy gaps (GLI = 23.5 ± 1.7) than under the intact forest canopy (2.9 ± 0.2). The GLI differed significantly among gaps, increasing linearly with gap size ($r^2 = 0.67$, $P = 0.004$).

We identified a total of 1257 lightning-created canopy gaps in the 1996 photographs (Fig. 1). The gap fraction (% forest area in gaps) was 1.9% based on expanded gap area, and 1.4% based on actual gap area. The expanded gap fraction increased through time from 0.1% in 1959 (47 gaps), to 0.6% in 1967 (349 gaps), 1.0% in 1983 (627 gaps), 1.4% (696 gaps based upon 76% of the forest area) in 1993, and 1.9% in 1996. Gap formation rates averaged 0.01% year⁻¹ from 1946 to 1959; 0.07% year⁻¹ from 1959 to 1967; 0.06% year⁻¹ from 1967 to 1983; 0.15% year⁻¹ from 1983 to 1993; and 0.23% year⁻¹ from 1993 to 1996. In the 1996 aerial photographs we identified 59 areas as representing recently closed gaps that had not been present in 1983, and thus had formed and closed in less than 13 years.

Persistence of canopy gaps was estimated by comparing aerial photographs among years. Most gaps present in one photograph closed during the time

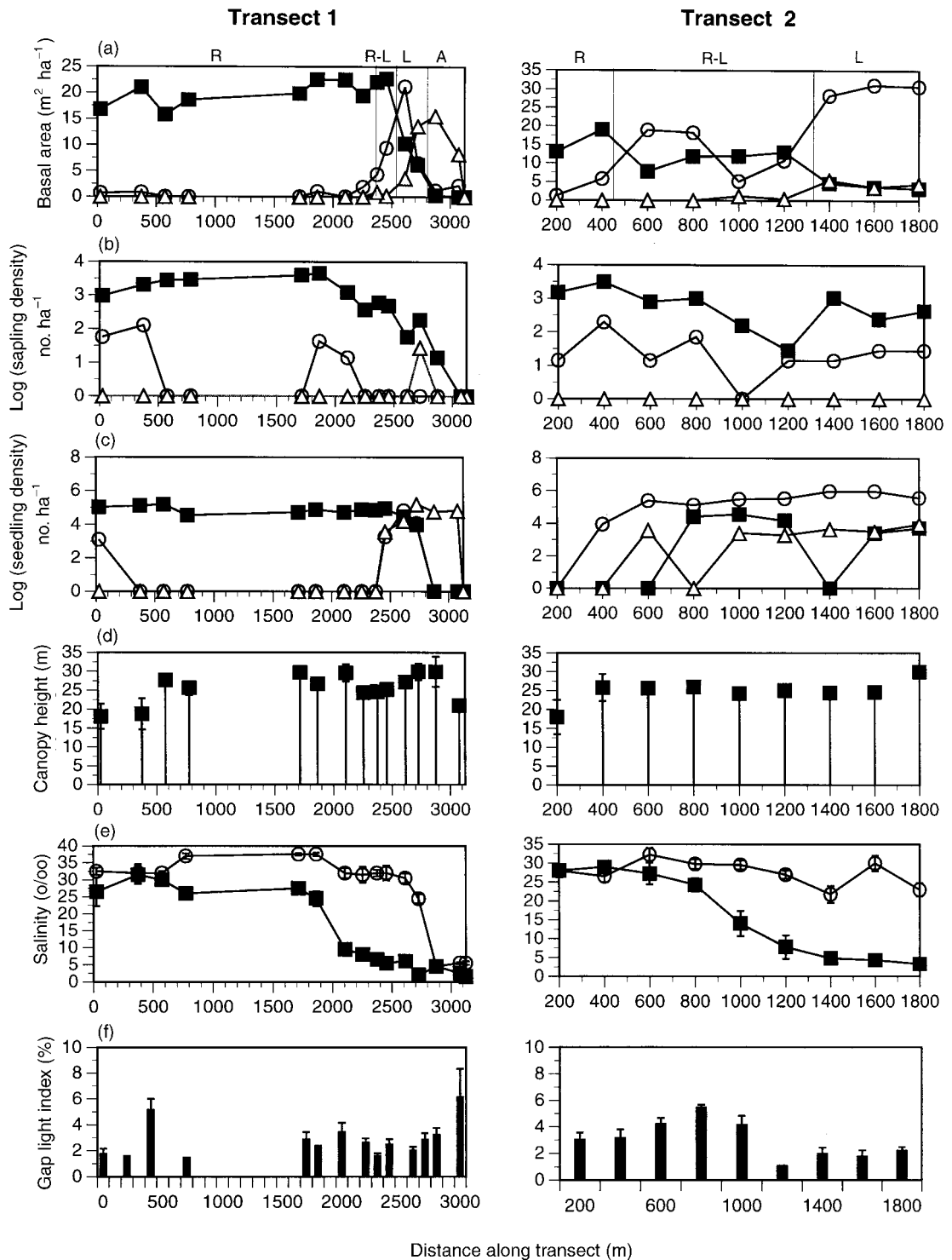


Fig. 2 Basal area of adult (a), and density of sapling (b) and seedling (c) populations of three mangrove species (*R. mangle* ■, *L. racemosa* ○, *A. germinans* △), canopy height (d), changes in salinity (e) measured at two depths (surface water ■ and 50 cm ○) and the gap light index (f) measured in plots along two transects across the intertidal zone of a neotropical mangrove forest (see Fig. 1 for location of transects). Error bars in panels (d) (e) and (f) represent the standard error of the mean. The different forest associations, as delineated independently using aerial photographs, are also indicated in (a), and forest transitions along the transect are delineated by the vertical line (R = *Rhizophora*, R-L, *Rhizophora-Laguncularia*; L = *Laguncularia*; A = *Avicennia*).

Table 1 Species' importance values (sum of relative basal area and relative density) for each permanent plot located along two transects, their resulting classification into different forest associations, and the total basal area and total density (trees > 5 cm d.b.h.) for each plot

Distance inland (m)	Importance value			Community type	Total basal area (m ² ha ⁻¹)	Total density (no. ha ⁻¹)
	<i>Rhizophora</i>	<i>Laguncularia</i>	<i>Avicennia</i>			
Transect 1						
25	192	8	0	<i>Rhizophora</i>	17.4	2080
275	200	0	0	<i>Rhizophora</i>	21.8	1429
575	200	0	0	<i>Rhizophora</i>	15.8	877
775	200	0	0	<i>Rhizophora</i>	18.6	1457
1715	200	0	0	<i>Rhizophora</i>	19.8	1217
1865	189	11	0	<i>Rhizophora</i>	23.5	1288
2105	200	0	0	<i>Rhizophora</i>	22.5	651
2255	178	22	0	<i>Rhizophora</i>	21.3	538
2375	156	39	5	<i>Rhizophora</i>	27.2	849
2455	130	67	3	<i>Rhizophora-Laguncularia</i> mix	32.3	778
2615	64	109	27	<i>Laguncularia</i>	35.0	1217
2725	79	34	87	<i>Rhizophora-Avicennia</i> mix	26.3	793
2875	12	14	174	<i>Avicennia</i>	17.1	424
3075	0	40	160	<i>Avicennia</i>	10.4	226
Transect 2						
200	189	11	0	<i>Rhizophora</i>	14.3	637
400	151	49	0	<i>Rhizophora</i>	24.8	778
600	68	132	0	<i>Rhizophora-Laguncularia</i> mix	28.9	1189
800	85	112	3	<i>Rhizophora-Laguncularia</i> mix	30.0	1358
1000	138	51	11	<i>Rhizophora</i>	18.2	934
1200	114	83	3	<i>Rhizophora-Laguncularia</i> mix	24.0	991
1400	55	120	26	<i>Laguncularia</i>	38.2	1528
1600	36	147	17	<i>Laguncularia</i>	38.3	1160
1800	26	151	23	<i>Laguncularia</i>	38.2	1259

interval before the next; hence, assuming that gap formation and closure rates were relatively constant through time, gap closure can be estimated to range from 8 to 16 years. Canopy turnover time (gap longevity/fraction of forest in gaps) ranged from 421 to 842 years.

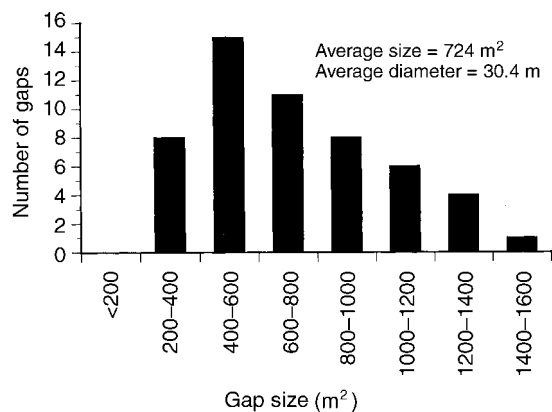


Fig. 3 Frequency distribution of expanded gap area ($n = 52$) for gaps created by lightning in a neotropical mangrove forest.

SPATIAL AND TEMPORAL PATTERNS IN GAP DISTRIBUTION

The spatial distribution of lightning-created gaps in 1967, 1983 and 1996 did not fit the null hypothesis of complete spatial randomness. Results from the pairwise correlation analyses for the coastal rectangle demonstrated strong directionality in gap density along the north-south axis for the 1996 and 1983 data, with significantly greater gap density in the southern region of the forest, decreasing with distance to the north. In 1967 no spatial trends in gap density were evident but strong clustering of gaps was observed.

In the coastal rectangle in 1996, gap density averaged 57 gaps km⁻² for the first 1600 m from the Barracote River northwards, declined to 33 gaps km⁻² from 1800 to 6200 m north of the Barracote River, and decreased further to 17 gaps km⁻² between 6400 and 12000 m (Fig. 1). For the inland rectangle in 1996, mean gap density averaged 47 gaps km⁻², with no significant indication of a coast-inland trend (east-west) in gap density. Because of the spatial clustering of gaps, canopy turnover time varied across the forest, ranging from 194-387 years in the more southern region of the

forest to 650–1300 years in the more northern region.

We also calculated gap density by forest age and community type. The mangrove forest increased in size from 32.7 km² in 1959 to 47.1 km² in 1996. The older more inland stands that had developed by 1967 appeared to have developed as the pre-existing forest regenerated following the tidal wave, with high water areas recovering more slowly; however,

since 1983, new stands have formed on abandoned agricultural lands (along the Yuna River) and on new substrate being deposited near the mouths of the two rivers (Fig. 4). The percentage of forest in gaps appeared to increase with stand age, with 2.1% area in gaps in stands that established before 1967; 1.5% in stands that established between 1967 and 1983; and 0.6% in stands that established between 1983 and 1996 (Fig. 4). The percentage of forest in

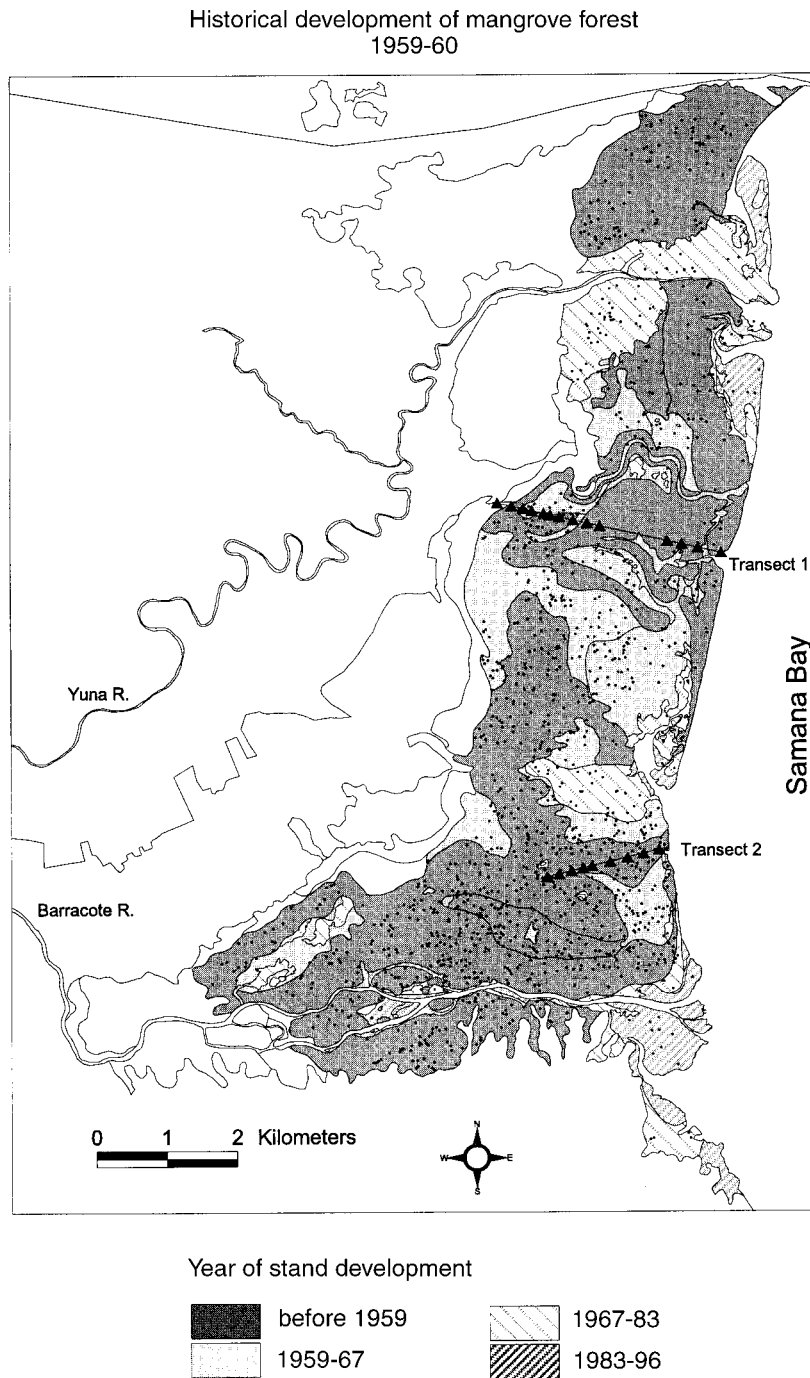


Fig. 4 Map of the mangrove forest ecosystem in the Los Haitises National Park, Dominican Republic, depicting the different aged stands of forest and the distribution of lightning-created canopy gaps.

gaps was similar in most forest types: *Rhizophora* (1.8%), *Laguncularia* (2.2%) and *Rhizophora*–*Laguncularia* mix (1.8%); however, in the *Rhizophora*–*Laguncularia*–*Avicennia* mixed forest, only 0.9% was in gaps (Fig. 1). Canopy gaps could not be distinguished in the *Avicennia*–freshwater swamp forest because of its uneven and more open canopy.

REGENERATION PATTERNS

Seedling density under the closed canopy varied greatly among plots, ranging from 0.5 to 9.2 seedlings m^{-2} , and species composition of seedlings generally reflected the overstorey composition (Fig. 2c).

Sapling abundance ranged from 1000 to 5000 saplings ha^{-1} in the lower tidal region and decreased to densities of less than 30 ha^{-1} in the more inland sites (Fig. 2b). The understorey was dominated by *R. mangle* regardless of position in the tidal zone or nature of the canopy. Although the GLI varied among plots, ranging from 1% to 6% (Fig. 2f), no strong correlations were found between GLI and seedling or sapling abundance ($r < 0.25$).

Seedling densities in canopy gaps were highly variable and, when data were compared across all plots and gaps, the seedling density of each species in canopy gaps was not different compared with under the intact canopy ($P > 0.2$ for all three species). However, when examined by vegetation zones,

Table 2 Seedling and sapling densities measured under the forest canopy and in canopy gaps in the different vegetation zones of a neotropical mangrove forest

	Seedling density (no. ha^{-1})			Sapling density (no. ha^{-1})		
	<i>R. mangle</i>	<i>L. racemosa</i>	<i>A. germinans</i>	<i>R. mangle</i>	<i>L. racemosa</i>	<i>A. germinans</i>
<i>Rhizophora</i> forest						
Understorey						
Mean	77 533	795	0	2201	21	0
SD	37 653	2637	0	1269	39	0
Median	71 228	0	0	2008	0	0
Q1	51 235	0	0	1230	0	0
Q3	107 468	0	0	2913	42	0
Canopy gap						
Mean	49 907	725	750	5362	0	0
SD	40 210	2251	3000	4035	0	0
Median	33 084	0	0	4833	0	0
Q1	21 132	0	0	2904	0	0
Q3	66 000	0	0	6116	0	0
<i>Rhizophora</i> – <i>Laguncularia</i> forest						
Understorey						
Mean	32 579	295 179	7319	503	16	0
SD	27 329	313 725	7942	426	31	0
Median	26 242	221 808	3749	537	0	0
Q1	16 245	36 864	1874	42	0	0
Q3	45 611	408 627	18 744	962	14	0
Canopy gap						
Mean	27 032	21 249	305	2856	57	0
SD	17 821	26 548	212	2799	228	0
Median	19 667	8697	0	2500	0	0
Q1	13 295	0	0	693	0	0
Q3	35 536	50 104	0	4450	0	0
<i>Laguncularia</i> forest						
Understorey						
Mean	3749	731 654	4374	551	23	0
SD	3902	319 300	1250	404	8	0
Median	2499	910 350	4374	424	28	0
Q1	625	363 015	3124	226	14	0
Q3	8123	921 597	5623	1004	28	0
Canopy gap						
Mean	24 028	286 361	7521	17 337	247	544
SD	37 214	346 822	8425	56 156	587	1720
Median	9625	160 833	4134	1818	0	0
Q1	716	5330	2159	0	0	0
Q3	30 916	393 825	11 896	4147	0	0

different patterns emerged (Table 2). Density of *R. mangle* seedlings was significantly greater under the canopy than in canopy gaps in the *Rhizophora*-dominated forest ($P < 0.05$). In the mixed *Rhizophora*–*Laguncularia* forest, *A. germinans* and *L. racemosa* seedling densities were greater in the forest understorey than in gaps ($P < 0.01$), whereas *R. mangle* seedling density was similar in gaps and forest ($P = 0.53$). In the *Laguncularia* forest, seedling density was not different between the closed canopy and gaps for any of the three species ($P > 0.2$).

The density of *R. mangle* saplings was significantly greater in canopy gaps than under the intact canopy in all vegetation zones across the tidal gradient ($P < 0.05$), and the density of *R. mangle* saplings was significantly greater than the other two species both in gaps and under the forest canopy (Table 2). There were no statistical differences between sapling densities in gaps and under the canopy for either *L. racemosa* or *A. germinans* because very few were observed (Table 2).

SAPLING GROWTH AND MORTALITY RATES

Diameter increment was not significantly different among species for saplings growing in canopy gaps ($P = 0.064$), but because of differences among species in the mean initial size of saplings, relative growth rates were significantly greater for *A. germinans* than *R. mangle* and *L. racemosa* ($P < 0.001$; Table 3). Growth rates of *R. mangle* and *L. racemosa* saplings in gaps were significantly greater than under the intact forest canopy ($P < 0.01$); comparisons could not be made with *A. germinans* saplings because only one *A. germinans* sapling survived under the closed canopy.

Sapling mortality rates differed significantly among the three species. The highest rates both in canopy gaps and under the closed canopy were observed for *A. germinans*, with intermediate rates for *L. racemosa* and much lower rates for *R. mangle* ($P < 0.01$; Table 3). Although sapling mortality tended to be greater under the canopy than in canopy gaps (Table 3), this difference was not statistically significant.

Discussion

Our results did not support the hypothesis that patterns of tree regeneration in lightning-created gaps would maintain existing tree species' distribution patterns across the intertidal gradient in the mangrove forest. *Rhizophora mangle* dominated the sapling layer in all canopy gaps, as well as under the intact forest canopy, and therefore in the absence of any large-scale disturbance this species would be expected to increase in abundance throughout the

Table 3 Number of individual saplings tagged for estimates of growth rates in canopy gaps and under the closed canopy, their initial sizes, diameter growth rates, and mortality rates over a 1-year period

Species	Number of tagged saplings		Initial sapling size (cm) average diameter \pm SE		Growth rates (cm) diameter increment \pm SE		Relative growth rates (%) diameter increment \pm SE		Mortality (%)	
	Gaps	Closed canopy	Gaps	Closed canopy	Gaps	Closed canopy	Gaps	Closed canopy	Gaps	Closed canopy
<i>R. mangle</i>	292	400	1.9 \pm 0.06	2.3 \pm 0.06	0.58 \pm 0.025	0.086 \pm 0.011	29.6 \pm 1.2	4.8 \pm 0.6	9	16
<i>L. racemosa</i>	100	15	1.7 \pm 0.11	1.8 \pm 0.84	0.46 \pm 0.041	0.108 \pm 0.056	29.8 \pm 2.6	9.2 \pm 7.0	32	40
<i>A. germinans</i>	30	8	1.3 \pm 0.25	1.7 \pm 0.45	0.51 \pm 0.041	–	46.3 \pm 5.8	–	56	88

forest given the present disturbance regime. This forest arose following a tidal wave in 1946 that destroyed most of the pre-existing forest (Sachtler 1973; Alvarez & Cintrón 1984) and, although the factors that resulted in the present spatial pattern remain unknown, our results suggest that it would not be reinforced by regeneration in canopy gaps following lightning disturbance.

GAP REGIME

This study was designed specifically to examine the gap regime associated with lightning-created gaps, and we did not sample smaller canopy gaps such as those resulting from the death of large branches or individual trees. Termites (Putz & Chan 1986) and wood-boring beetles (Feller & McKee, in press) are important mortality agents in many mangrove forests and, although the consequent gaps are substantially smaller than those created by lightning, they can be an important component of the disturbance regime (Feller & McKee, in press). Hence, because our estimates of gap area, gap formation rates and canopy turnover times are based on lightning gaps only, the overall role of small canopy gaps on the dynamics of this forest is underestimated.

Gap closure depended almost entirely upon the establishment and growth of new seedlings, because lateral encroachment by surrounding understorey trees would not be significant in such large gaps and, at our site, lightning kills all advance regeneration (pre-existing seedlings and saplings) in gaps. Pajmans & Rollet (1977) observed that lightning-created gaps present in 1957 aerial photographs of a Papua New Guinean mangrove were no longer visible in 1972, indicating a maximum closure time of less than 15 years, which is comparable to our estimate of 8–16 years. However, in other regions advance regeneration may survive lightning disturbance (e.g. Panama; W.P. Sousa, personal communication), and the rate of canopy closure of gaps might therefore vary markedly across regions.

The strong spatial component in the gap regime indicated that some areas of the forest were more disturbed than others. The important ecological question is whether this patterning is sufficient to influence regeneration processes and consequently forest composition. The high density of gaps and consequent shorter canopy turnover time in the southern region of the forest indicates that gap regeneration should have a stronger influence on forest composition in this part of the forest. Smith *et al.* (1994) suggested that the canopy gap regime might influence patterns of mangrove forest recovery from large-scale disturbances, and we would therefore expect the significant spatial variation across the mangrove forest in lightning-created

canopy gaps to influence the pattern of forest recovery from catastrophic disturbances.

Spatial patterning in the disturbance regime of other forests has been associated with physical gradients such as elevation and slope position (Battles *et al.* 1995), exposure (Lawton & Putz 1988) and slope (Martinez-Ramos *et al.* 1988). The cause of the spatial pattern of gap formation observed at our study site is not clear because the mechanistic behaviour of lightning as a disturbance agent is not well understood. Bruenig (1964, 1973) also observed clustering of lightning gaps, as well as an increase in gap formation rates over time, in a *Shorea albida* peat swamp forest in Sarawak. He found that the forest community with the tallest canopy suffered the greatest amount of damage. However, the spatial distribution patterns of gaps at our study site were neither entirely consistent through time nor clearly related to forest age, canopy height, understorey composition or environmental gradients across the tidal zone. The distribution observed at our study site may be related to storm patterns as the southern margin of the mangrove forest abuts against a karst platform with hills that exceed 200 m. These hills may form an obstruction to the horizontal movement of the trade winds, triggering thunderstorms and increasing the frequency of lightning strikes along this boundary (Byers & Braham 1949; Gosz *et al.* 1995).

CANOPY GAPS AND TREE REGENERATION PATTERNS

In general, canopy gaps influence the forest regeneration cycle by providing local resource-rich habitats for understorey individuals. Differences among tree species in establishment, germination, survival, growth and canopy recruitment in the gap environment explain the role of canopy gaps in shaping forest composition. At our site, recruitment from newly established seeds is necessary following lightning disturbance because all advance regeneration is killed and, because all three species exhibit some degree of vivipary (Tomlinson 1986), there is no buried seed bank. The successful establishment of seedlings was not constrained by germination requirements because seeds germinate either while still attached to the parent tree or during dispersal, and therefore seedlings established in gaps and understorey conditions equally well. However, successful recruitment to the sapling stage appeared to be facilitated by the high light conditions of canopy gaps, as both survivorship and growth rates of all three species were enhanced in the canopy gaps compared with the forest understorey. Together with literature observations of enhanced mangrove regeneration and growth in the high light environment of gaps (Smith 1987; Clarke & Allaway 1993; Ellison & Farnsworth

1993), these results suggest that canopy gaps provide an important regeneration niche for mangroves.

Rabinowitz (1978) suggested that both *L. racemosa* and *A. germinans* were light requiring (i.e. gap-dependent) species. Similarly, Ellison & Farnsworth (1993) noted the absence of *A. germinans* in the understory of an *A. germinans*-dominated forest at their study site in Belize, and suggested that this species was a true gap specialist, dependent on chance disturbance events for successful establishment. Both Wadsworth (1959) and Ball (1980) observed very little regeneration of *L. racemosa* in the understory of mature *L. racemosa* stands, and suggested that this species was shade intolerant. A gap dynamics model predicted that regeneration of *L. racemosa* was restricted to early stages of gap development because of this species' high light requirements (Chen & Twilley 1998). However, we saw very little regeneration of either *L. racemosa* or *A. germinans* in gaps. Craighead (1971) noted that *R. mangle* was typically the most abundant species regenerating in lightning-created gaps in a south Florida mangrove, even in stands where it was not the canopy dominant. The recruitment success of *R. mangle* at our site apparently can be attributed to its lower mortality rate, as differences in growth rates between species were relatively small, both in the understory and in gaps.

The soil physical-chemical environment in gaps can be significantly different from that under the surrounding canopy (Smith 1987; Ewel *et al.* 1998) and may influence post-establishment survivorship of seedlings and saplings. Clarke & Allaway (1993) found survival in gaps in an Australian mangrove to be patchy, and suggested that adverse soil conditions might be important in limiting tree recruitment. In the present study, the most striking effect of canopy gaps on the soil environment was the collapse of the dense root mat and consequent increase in water levels. We repeatedly visited canopy gaps over a period of 4 years and noted that about 2 years after gap formation a reduction occurred in the surface level of the peat soils. This phenomenon of soil collapse has been reported in Florida following the removal of mangrove stands; in some stands the oxidation of the peat and subsequent collapse of the soil increased water levels to an extent that prevented the successful re-establishment of the forest (Lugo 1997).

McKee (1995) found that, in the absence of biotic factors, survivorship of mangrove seedlings over 2.5 years was ultimately determined by sensitivity to physicochemical factors such as flooding and salinity. The success of *R. mangle* in gap regeneration observed in the present study may be due in part to its greater tolerance of flooding conditions (McKee 1993). However, collapse of the soil does not always follow the formation of lightning gaps in mangrove

forests. For example, this phenomenon was not observed in a Panamanian mangrove and all species were able to establish successfully in lightning gaps so that species' replacement patterns did reflect the composition of the forest overstorey (W. P. Sousa, personal communication). Thus, the role of canopy gaps in tree regeneration processes appears to depend both on the straightforward increase in light and the complex and variable changes in the soil environment.

The species composition of neotropical mangrove forests probably depends in part on the balance between large-scale and small-scale disturbances. Within the Caribbean basin the frequency of large-scale disturbances varies markedly because hurricanes are very common in northern locations but rare in southern areas. Where the interval between stand-replacing disturbances is longer, canopy gaps would play a more important role in determining species' distribution patterns. However, the exact pattern of replacement in gaps seems to depend upon changes that occur in the soil environment. Hence, understanding regional and local variation in regeneration success among species under different disturbance regimes and geomorphological settings is necessary to understand the effect of gap regeneration on the distribution and abundance of species in mangrove forests.

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