

Small Gap Creation in Belizean Mangrove Forests by a Wood-Boring Insect¹

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ABSTRACT

We investigated the role of wood-boring insects in the creation of light gaps within mangrove forests. We compared the frequency of gaps caused by wood borers to other gap-forming processes and characterized the physical attributes of light gaps in mangrove forests on small islands in Belize. Methods of quantifying light gaps included aerial photography, ground surveys, and experimental plots. Small light gaps ($\leq 12 \text{ m}^2$) were very common in *Rhizophora mangle* fringe, comprising almost 22 percent of these forests. *Rhizophora mangle* gaps were smaller than gaps in *Avicennia germinans* forests. In *R. mangle* forests, gaps were caused by branch death, and in *A. germinans* forests, gaps were caused primarily by downed trees. More than 91 percent of the gap-forming branches and boles in the *R. mangle* fringe were killed by a wood-boring cerambycid beetle, *Elaphidion mimeticum*, indicating that it is the major cause of small-scale disturbances in these forests. No trees or branches in the *A. germinans* forest were attacked by this beetle. In *R. mangle* forests, small gaps had significantly higher light levels and soil temperatures than areas under the closed canopy; however, soil conditions for sulfide concentrations, porewater salinity, and redox potentials were similar in small gaps and under the closed canopy. Survival of *R. mangle*, *A. germinans*, and *Laguncularia racemosa* seedlings was also higher inside these small gaps, indicating their importance in regeneration of mangrove forests. Feeding by wood borers is thus an important type of indirect herbivory in mangrove forests, with a critical role in ecological processes such as gap dynamics.

Key words: *Avicennia germinans*; Belize; cerambycid; *Elaphidion mimeticum*; indirect herbivory; light gaps; mangrove; *Rhizophora mangle*; seedling survival; wood-boring insects; xylovoxy.

THE IMPORTANCE OF LIGHT GAPS TO FOREST STRUCTURE AND DYNAMICS is widely recognized (Whitmore 1978; Brokaw 1985a, b; Hubbell & Foster 1986). Research in tropical forests has focused primarily on ecological processes and plant species associated with gap colonization and regeneration, subsequent to gap creation (Denslow 1980, 1987; Brokaw 1985a, b, 1987; Hubbell & Foster 1986; Brokaw & Scheiner 1989; Denslow *et al.* 1990; Clark & Clark 1991). In many forested ecosystems, biotic agents, (*e.g.*, lianas, insects, and mammals such as elephants, moose, and beaver), are known to kill or break branches from trees, forming openings in the canopy (Eggeling 1947; Tho 1975, 1982; Putz & Chan 1986; McNaughton *et al.* 1988; Naiman 1988; Pastor *et al.* 1988; Spies & Franklin 1989; Mopper *et al.* 1991). The gap-forming mechanisms in tropical forests, however, are generally ascribed to external, abiotic forces

(Whitmore 1989). Large gaps produced by catastrophic disturbances (*e.g.*, fires, earthquakes, or hurricanes), retain indelible records of these forces. Although the specific origins of small gaps resulting from single tree or branchfalls are unknown in many cases, they are typically attributed to wind, rain, or general senescence (Dayton 1971; Paine & Levin 1981; Brokaw 1985a, b; Whitmore 1989). The view of patch creation in tropical forests as being controlled predominantly by physical forces may be contrasted with that for several other ecosystems (*e.g.*, temperate subtidal and intertidal communities, coniferous forests of the Pacific Northwest, and the Serengeti region of Africa) in which gaps are often generated by biotic forces (Dayton 1971, Sinclair & Norton-Griffiths 1979, Paine & Levin 1981, Pearson 1981, McNaughton *et al.* 1988, Pastor *et al.* 1988, Spies & Franklin 1989).

Gap dynamics in mangrove forests along tropical coastlines worldwide so far have received little attention (Putz & Chan 1986; Smith 1987, 1992; Ellison & Farnsworth 1993; Chen & Twilley 1998). In Florida, small gaps in mangrove forests

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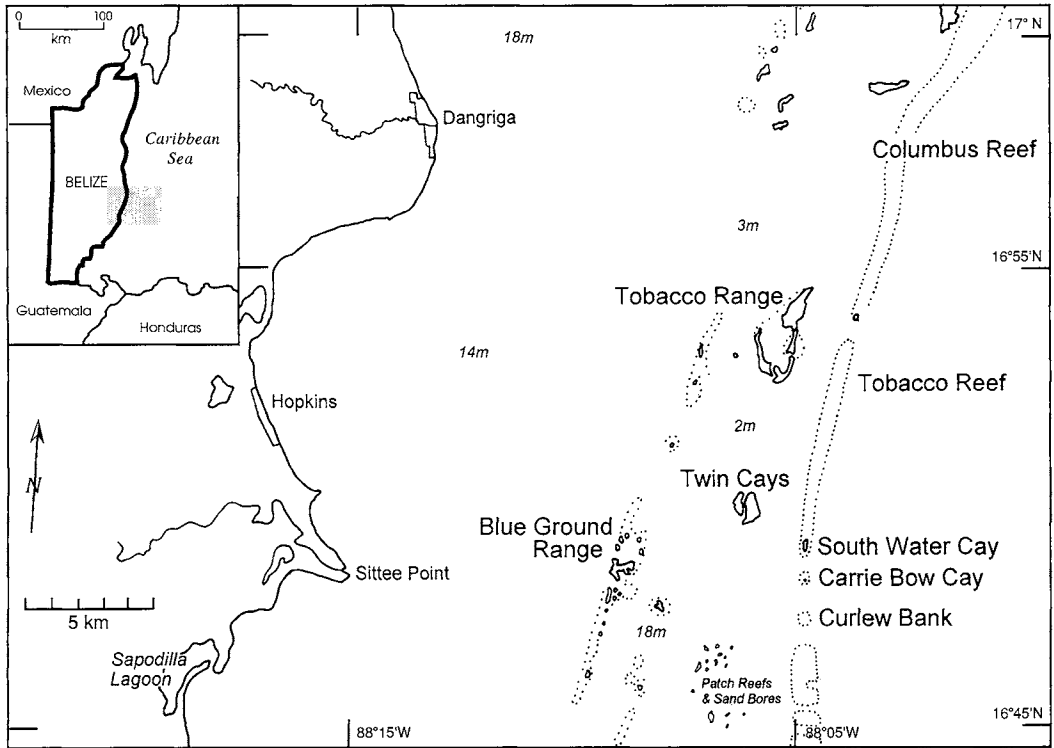


FIGURE 1. Location of the three mangrove archipelagos surveyed (Twin Cays, Tobacco Range, and Blue Ground Range) within the crest of the barrier reef off the coast of central Belize. The inset in the upper left shows the position of the study sites relative to the Belizean mainland.

are attributed mainly to lightning strikes (Craighead 1971, Smith 1992, Smith *et al.* 1994). In Malaysian mangrove forests, live-wood feeding termites attack and kill trees, creating relatively large gaps (80–140 m²; Tho 1975, 1982). In mangrove forests in Belize, trees commonly are attacked by several species of wood-boring insects, or xylovores, that feed in live trees (Feller & Mathis 1997). These xylovores are responsible for considerable losses from the mangrove canopy that can result in light gap formation (Rützler & Feller 1988, 1996; Feller 1995). Wood borers also play major roles in structuring mangrove communities (Feller & Mathis 1997). Each species of mangrove hosts several species of highly specialized primary xylovores, including larvae of longhorn beetles (Cerambycidae), weevils (Curculionidae), moths (Lepidoptera), and scolytids (Scolytidae), that girdle and/or hollow twigs and branches to cause branch pruning and localized death (Chemsak 1982, Chemsak & Feller 1988, Feller & Mathis 1997). *Rhizophora mangle* L. (red mangrove), the dominant mangrove species in many of these forests, supports a partic-

ularly large number of primary xylovores (10 species collected to date; Feller & Mathis 1997). The resulting woody debris provides critical habitats for many species of secondary xylovores (*ca* 20 species) and inquilines (*ca* 75 species; Chemsak 1982, Chemsak & Feller 1988, Feller & Mathis 1997).

The objectives of this study were to: (1) document the role of wood-boring insects in the creation of light gaps within mangrove forests; (2) compare the frequency of gaps caused by wood borers with other gap-forming processes; and (3) characterize the physical attributes of light gaps on small mangrove islands in Belize. Our approach involved aerial photography, extensive ground surveys of light gaps, and experiments to assess the roles of small gap formation in mangrove regeneration.

MATERIALS AND METHODS

This study was carried out at three mangrove archipelagos in central Belize: Twin Cays, Tobacco Range, and Blue Ground Range. These forested islands are in the outer lagoon just inside the crest

of the Belizean barrier reef, 15–18 km off the mainland coast (Fig. 1). In 1980, Twin Cays became the primary study site and experimental field laboratory for the Smithsonian Institution's National Museum of Natural History Field Station on nearby Carrie Bow Cay. Summaries of research in progress can be found in Rützler and Feller (1988, 1996, in press). Vegetation on these islands is dominated by *R. mangle*, *Avicennia germinans* (L.) Stearn (black mangrove), and *Laguncularia racemosa* (L.) Gaertn.f. (white mangrove). Typical of many island mangrove systems in the Caribbean, *R. mangle* forms a dense seaward fringe (3- to 7-m tall) on these islands (Woodruffe 1996).

Because mangrove forests typically have a single-layered canopy without an understory, our usage of "gap" refers to openings in this canopy, caused by dead or leafless branches and trees that were still standing or had fallen into the litter. The edge of the adjacent leafy canopy extending vertically to the forest floor was considered the outer margin of the gap.

We used aerial photography to estimate the percentage of mangrove forest at Twin Cays in open light gaps. A high contrast, black-and-white enlargement was subjected to image analysis (Optimas 4.0, Optimas Corporation, Bothell, Washington) to determine, in a 45-m wide section of fringe forest, the portion of the forest that was open gaps.

On one island within each archipelago, we surveyed light gaps in stands of *R. mangle* and *A. germinans*. We examined all gaps encountered in the *R. mangle* fringe within 5 m of the water's edge (around the periphery of each island) for a total of 45 gaps. In addition, 13 gaps located in stands of *A. germinans* just inland from the *R. mangle* fringe were inspected. Fewer *A. germinans* gaps were examined because there was smaller total area of this type of forest available on the study islands. Individual gaps were assumed to be independent of each other. To estimate a gap's size, we measured its width at the widest points along two axes. The average of these values was used as the diameter to calculate gap area, assuming a circular shape. We examined all dead and dying branches and boles that contributed to a gap, and determined their vegetative condition. The vegetative condition was scored as alive when a branch or bole that caused a gap was missing all or most of its leaves and appeared to be dying, but still had living apical buds on some shoots. Branches were considered standing dead if they lacked any green leaves or buds, but were attached to their tree and had all

branches, twigs, and bark intact. Our observations suggested that branches in the standing dead category probably had died within the previous year. Dead branches or boles that were still attached to their tree but had lost their terminal and lateral branches and bark were called standing snags. Many of the standing snags had been dead for several years. Branches or boles broken from their tree were categorized as fallen dead. These branches, which were on the ground, varied from long dead and well-weathered wood to recently dead branches that had broken from trees during storms. All the branches and boles contributing to the gaps sampled in this survey were inspected to determine cause of death. Potential causes of death included wood-boring insects, humans (e.g., machete and chain saw cuts), abiotic causes (e.g., lightning or wind), and were termed unknown when no conclusion could be drawn.

We also measured tree height and leaf area index (LAI) of the closed canopy at a subset of the *R. mangle* gap sites surveyed on the three island groups ($N = 10$). To measure LAI, we used a plumb bob method used previously in mangrove forest studies (Cintrón & Novelli 1984, Brown & Ewel 1987). To avoid bias, we determined LAI as the mean number of leaf contacts against a weighted plumb line, lowered five times at randomly selected points through the canopy of each tree and counted by an unbiased observer.

To quantify the effects of light gaps in the mangrove canopy on environmental conditions and mangrove survival, we conducted an experiment at Twin Cays. We randomly selected ten gaps, each paired with a control plot under the adjacent closed canopy, in the *R. mangle* fringe forest along a wide channel that separated the two largest islands in this archipelago (Fig. 1). Control plots were ca 5 m from the edge of each gap. The following variables were measured inside each of the ten gaps: vegetative condition and cause of death of all branches or boles contributing to a gap; gap size; and gap openness from hemispherical photographs of the canopy (Solarcalc®; Chazdon & Field 1987). Photosynthetically active radiation (PAR) was measured 1 m above the soil surface between 1200 and 1300 h on a clear day, in the center of the gaps and in the control plots. Values were calculated as a percentage of full sun conditions. Soil temperatures were measured in both areas at a 5-cm depth after 5-min equilibration. To quantify the effect of a light gap on edaphic factors, we measured soil redox potentials and porewater salinity, pH, and sulfide concentrations (McKee *et al.* 1988). Soil



FIGURE 2. (a) Active feeding gallery of an *Elaphidion mimeticum* larva in living *Rhizophora mangle* wood from which the bark has been cut with a machete. (b) Old feeding gallery, girdled wood, and exit holes of *E. mimeticum* in dead *R. mangle* wood in a fallen dead branch.

measurements were taken at two depths (1 cm and 15 cm) in both areas. For comparison, these measurements also were made in three large, dieback areas (0.5–3 ha) in the interior of Twin Cays. To determine the effect of light gaps on mangrove survival, we transplanted a one-year-old juvenile of *R. mangle*, *A. germinans*, and *L. racemosa* into the center of each of the ten gaps and control plots, and monitored their survival over two years.

Student's *t*-tests were used to compare the gap characteristics in our survey of light gaps in *R. mangle* and *A. germinans* forests. Data from our gap experiment for redox potentials, porewater salinity, pH, sulfide concentrations, percent full sun, soil temperatures, and seedling survival were analyzed as paired *t*-tests. Prior to analyses, percentage data were arcsine-square root transformed, and counts were square root transformed. Sulfide concentrations were log transformed. Probability values ($P < 0.05$) were considered significant differences in all statistical tests, which were made using Systat® (Wilkinson 1990).

RESULTS

NATURAL HISTORY OF *ELAPHIDION MIMETICUM*.—Branches killed by insect wood borers, in particular the wood-boring beetle *Elaphidion mimeticum* Shaeffer (Coleoptera: Cerambycidae, Cerambycinae), commonly were associated with small gaps in *R. mangle* forests in Belize. Larvae of *E. mimeticum* feed on live wood in *R. mangle* branches or boles (Fig. 2a). The products (frass, exuviae) and effects (galleries, exit holes) of this species' development are species-specific and diagnostic. They cut an *ca* 0.5-cm deep feeding gallery in the wood just beneath the bark, including both phloem and xylem. A larva feeds in a meandering pattern, but eventually, its gallery completely girdles the host branch. Damage by this wood borer severs the conductive tissue between the canopy and the root system and kills the leaves and stem tissue of the tree distal to the girdle. Although this xylovore does not consume all the wood or leaves on the branch that it girdles, its feeding is responsible for the death of the entire branch. Following emergence, adults of



FIGURE 3. A standing dead branch of *Rhizophora mangle* recently killed by *Elaphidion mimeticum*, creating a gap in the mangrove canopy.

E. mimeticum are nocturnally active and live *ca* 2 wk, during which time they reproduce but do not eat. Cerambycid adults of this size (2–3 cm) typically take up to five years to develop from egg to adult emergence (Linsley 1959). Dispersal of this species from the mainland to the offshore mangrove islands probably occurred via rafting in wood. Although adult specimens have been taken in light traps, this study provides the first larval host records, natural history, and ecological data for *E. mimeticum*.

The larval feeding gallery of *E. mimeticum* persists in the wood and remains recognizable long after the affected wood has fallen into the litter (Fig. 2b). These galleries also remain open in the wood of trees where branches have been pruned. The damage to the crown or bole is preserved in the wood and in the shape of the canopy and can be used to infer the history of *E. mimeticum* damage to *R. mangle* trees. Active attack sites and recently killed branches are also recognizable externally by rust-red stains on the bark, caused by tannins released from the underlying damaged wood. Live branches, still in the process of being girdled, have fewer, smaller, and more yellow leaves than

the surrounding canopy. The speed at which a branch is killed depends on how quickly it is girdled. The process can take several years, during which time the canopy gradually thins, eventually loses all its leaves, and opens into a gap (Fig. 3). During storms, live leaf-bearing branches in the process of being girdled by wood borers frequently break from the tree at the point of attack. It is common to see such branches broken free or dangling from trees, with their leaves still attached as aerial litter.

Although less common in these forests, branches (1–3 cm diameter) of *R. mangle* are also killed and pruned by a second cerambycine cerambycid, *Elaphidionoides* sp. Early larval instars of this species feed down the center of a host branch. Pruning occurs when a late instar larva makes very smooth, concentric, circular cuts that completely sever a branch from its tree. Like *E. mimeticum*, *Elaphidionoides* sp. is recognizable not only by its larvae, but also by its products and effects on the tree.

LIGHT GAP SURVEY.—Aerial photography of the mangrove fringe at Twin Cays showed clearly that this forest is a mosaic of many small light gaps (*i.e.*,

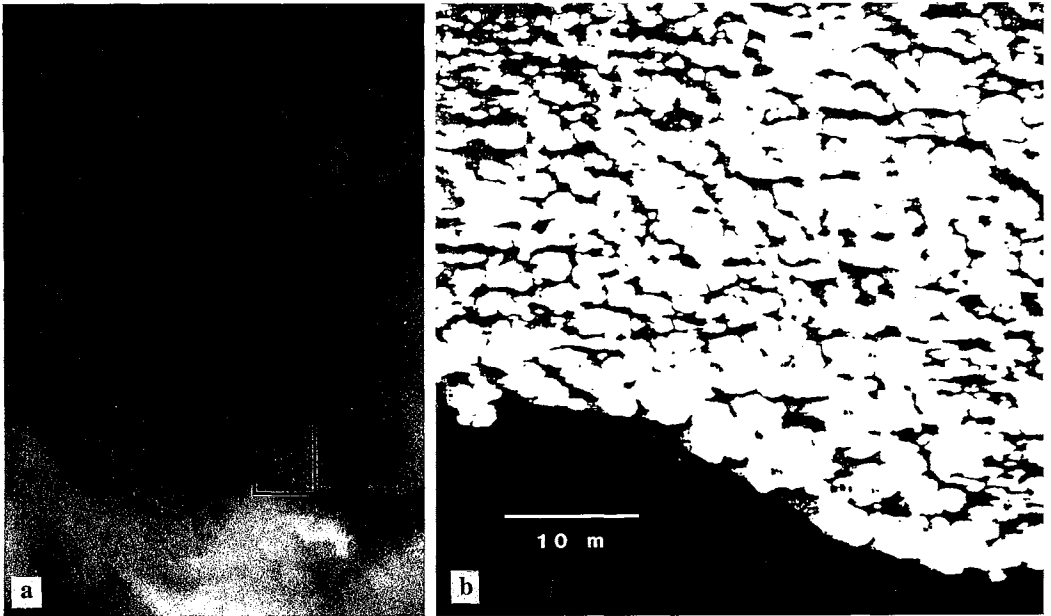


FIGURE 4. (a) Aerial photograph of the fringing red mangrove forest along the windward shoreline of Twin Cays, Belize. (b) High contrast enlargement of the 45-m shoreline section marked in (a).

irregular black patches in the photograph) and closed canopy (Fig. 4a). Based on image analysis of the enlargement (Fig. 4b), open gaps accounted for 21.6 percent of this forest.

From our gap survey of multiple islands, we found significant differences in gap size, number of contributing dead and dying branches and boles, and vegetative condition in *R. mangle* and *A. germinans* forests (Table 1A). *Rhizophora mangle* gaps were significantly smaller than *A. germinans* gaps ($t_{56} = 2.62$, $P < 0.01$). They were created primarily by branch death while *A. germinans* gaps were caused by downed trees ($t_{56} = 21.24$, $P < 0.001$). Furthermore, 90 percent of dead branches and boles in *A. germinans* gaps were strongly weathered and probably had died several years previously but persisted in the litter or as standing snags. In contrast, 35 percent of the branches in *R. mangle* gaps were dying or recently dead, as evidenced by intact terminal branches and bark. We found no evidence to suggest that any of the branches or boles contributing to either *R. mangle* or *A. germinans* gaps had been killed by lightning strikes.

In our gap survey, death of > 91 percent of the gap-forming branches and boles in the *R. mangle* fringe were directly attributable to *E. mimeticum*, as indicated by the presence of one or more

feeding galleries that completely girdled a stem (Table 1B). Almost all the remaining had evidence of *E. mimeticum* occurrence (*i.e.*, feeding galleries and exit holes), but were so weathered that we could not find galleries that may have completely girdled the stems. Vegetative conditions, ranging within a single gap from a dying branch with a few green leaves still present to fallen, strongly weathered wood, showed that gaps form slowly and are the result of multiple, asynchronous, and independent attacks on adjacent trees by *E. mimeticum* (Table 1a).

LIGHT GAP EXPERIMENT.—In our gap experiment on Twin Cays, the mean area of the ten selected gaps in the *R. mangle* fringe was $9.6 \text{ m}^2 \pm 2.2$ ($\bar{x} \pm 1$ SE). From image analysis of hemispherical photographs (Fig. 5), openness of these gaps was 31.7 percent ± 3.6 . Tree height of the adjacent closed canopy ranged from 2.5 to 7.2 m with a mean of $3.9 \text{ m} \pm 0.4$. Leaf area index of the forest around a light gap ranged from 1.8 to 6.0, with a mean of 4.0 ± 0.3 .

Although the light gaps used in this experiment were small, they had significantly higher light and soil temperature than the control plots under the closed canopy (Table 2). The closed canopy had a light deficit, but soil conditions were not much

TABLE 1. Results of survey of gaps and gap-causing agents in *Rhizophora mangle* and *Avicennia germinans* forests at three mangrove archipelagos in Belize.

A. Gap characteristics	<i>Rhizophora mangle</i>	<i>Avicennia germinans</i>
No. gaps examined	45	13
Gap size (m ²) ^a	12 ± 1.5 ^b	72.4 ± 22.7
Relative frequency of vegetative conditions ^c		
Alive	13	5
Standing dead	23	5
Standing snag	41	40
Fallen dead	24	50
No. units contributing to each gap:		
Branches	3.02 ± 0.32	0.23 ± 0.17
Boles	0.50 ± 0.12	2.62 ± 0.58
B. Cause of death of branches/boles:		
No. examined	159	37
Percentage attributed to:		
Abiotic causes	0	0
<i>Elaphidion mimeticum</i> girdle ^d	91.2	0
<i>E. mimeticum</i> evidence ^e	8.2	0
Human causes	0	18.9
Unknown cause	0.6	81.1

^a Gap area (m²) is calculated as a circle from the mean of two widest dimensions of a gap.

^b $\bar{x} \pm 1$ SE

^c Vegetative condition of branch(es) that produced each gap: (1) alive, missing all or most of its leaves, so gap was readily perceived but still had living apical buds on some shoots; (2) standing dead, with all branches, twigs, and bark intact; (3) standing snag, with terminal and lateral branches and bark absent; (4) fallen dead, with wood detached from tree but present on gap floor.

^d Branch completely girdled by feeding gallery of *E. mimeticum* larva.

^e Branch with gallery, frass, pupal chamber, pupal chamber plug, exit hole, tannin stain, or larvae, but we were unable to locate complete girdle.

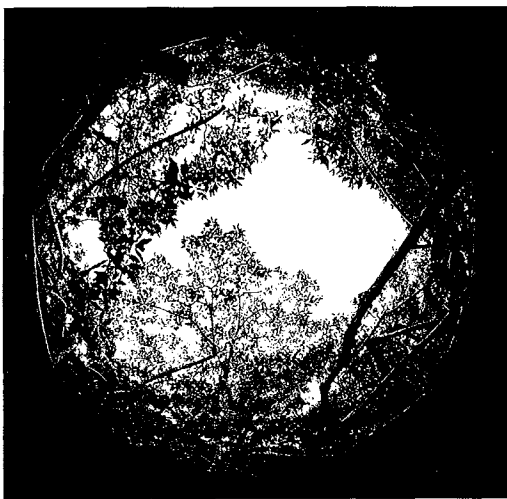


FIGURE 5. Hemispherical photograph of one of the ten gaps used in a light gap experiment in the *Rhizophora mangle* fringe forest at Twin Cays, Belize.

different from small gaps. At the other extreme, large dieback areas in the interior were characterized by high light levels, high soil temperatures, and more stressful soil conditions, such as higher sulfide and salinity levels and lower redox potentials.

Seedling survival was significantly higher inside the experimental gaps than in the plots under the closed canopy ($t_9 = 2.42$, $P < 0.05$). After two years, survival of *R. mangle*, *A. germinans*, and *L. racemosa* juveniles inside the small gaps was 70, 60, and 30 percent, respectively, compared to 40, 20, and 20 percent, respectively, under a closed canopy. In the fringe forests, the juvenile and suppressed trees within the gaps and under the adjacent canopy were primarily *R. mangle*, with an occasional seedling of *A. germinans* or *L. racemosa*.

DISCUSSION

Our research in the mangrove forests of Belize has shown that small gaps in the canopy are caused more frequently by biotic than abiotic forces. Based

TABLE 2. *Physicochemical conditions based on measurements in ten gaps and in control plots under the adjacent closed canopy in the fringe mangrove forest at Twin Cays, Belize. Values for each variable are the $\bar{x} \pm SE$. Results of paired t-tests comparing gaps and adjacent closed canopy are given. For comparison, similar measurements are given for large dieback areas (0.5–3.0 ha) in the interior of Twin Cays (N = 3). Percent photosynthetically active radiation (PAR) and sulfide were transformed prior to analysis to stabilize variances.*

Variable	Closed canopy	Small gap	Probabilities	Dieback areas
Redox potential (mV)				
at 5 cm depth	134 \pm 13	145 \pm 13	NS	-166 \pm 8
at 15 cm depth	-1 \pm 10	-6 \pm 12	NS	-175 \pm 11
Porewater salinity (‰)	33 \pm 1	33 \pm 1	NS	42 \pm 1
pH	6.2 \pm 0.1	6.2 \pm 0.1	NS	6.5 \pm 0.1
Sulfide (mM)	0.73 \pm 0.11	0.66 \pm 0.12	NS	4.93 \pm ?
PAR (% of full sun)	4 \pm 1	63 \pm 6	0.001	100 \pm 0
Soil temperature (°C)	28.4 \pm 0.3	31.6 \pm 0.6	0.001	35.1 \pm 0.4

on our gap survey, damage to *R. mangle* wood by the larvae of a live-wood eating cerambycid, *E. mimeticum*, is the major form of small-scale disturbance (compared to large-scale disturbances such as hurricanes). Our data show conclusively that most of the branches and boles forming *R. mangle* gaps in Belizean forests were killed by *E. mimeticum* (Table 1B). Our data also show clearly that this species of wood borer is the primary agent responsible for initiating subsequent gap-phase regenerative processes within the fringe forests dominating Belizean mangrove islands. This finding contrasts with studies in mangrove forests of southern Florida in which small gaps were attributed exclusively to lightning strikes (Smith 1987). Although *A. germinans* hosts other species of primary xylovores that prune branches, none of the gaps in those forests were killed by *E. mimeticum*.

The gap sizes we report are small (≤ 12 m²) compared to descriptions of gaps in other tropical forests (e.g., 20–705 m², Brokaw 1985b; 63–88 m², Putz & Milton 1996; Foster & Brokaw 1996); however, the geometry of these small gaps, that results from the low stature of the fringe mangrove forest (e.g., 3–7 m) relative to gap area, creates microenvironmental differences comparable to much larger gaps in forests with higher canopies (Denslow 1980, Smith *et al.* 1989). These wood borer-caused gaps are small, irregular patches, usually formed by the death of several overlapping primary or secondary branches from adjacent trees, rather than entire trees. The irregular shape of these small gaps is seen clearly in low elevation aerial photography (Fig. 4). These gaps are distinguishable from the lightning-caused gaps that Smith (1992) described as typically circular patches caused by the death of several trees rather than a single individual or branches.

Besides small gaps in the canopy, there are extensive dieback areas of 0.5 to 3 ha that form large gaps in the interior of many of these mangrove islands. These areas are unvegetated except for occasional dwarf trees. Old eroded stumps throughout these areas, however, indicate the presence of a forest composed of large *A. germinans* trees in the recent past (Rützler & Feller 1996). Most of the diebacks appear to have been caused by changes in abiotic conditions, such as excessive flooding, low soil redox potentials or high sulfide concentrations (K. McKee, pers. obs.). The inability of *A. germinans* to regenerate in these areas may be due to its earlier establishment under different conditions no longer present. On the other hand, *R. mangle* in a fringe forest experiences constant (if severe) conditions that likely contribute to increased seedling survival in these areas.

In general, our data suggest that the small gaps we found in the fringe mangrove forest offer the best conditions for seedling survival. These findings are consistent with previous studies in which we found that: (1) mangrove seedling recruitment varies spatially depending on physicochemical conditions (McKee 1995a); and (2) mangrove seedling growth in a 2.3-ha rectangular gap caused by clear-cutting was enhanced by shading (50% full sunlight) and by nutrient enrichment (McKee & Feller 1994). We also found that seedling survival for *R. mangle* in large dieback areas at Twin Cays was 63 percent \pm 22, which is similar to *R. mangle* seedling survival we measured in small gaps in the fringe forest at Twin Cays; however, seedling survival was 0 percent for both *A. germinans* and *L. racemosa* in the dieback areas.

Discovery of a gap-forming insect in the canopy of *R. mangle*, which is widespread in the mangrove forests in Belize that we have visited, forces

reconsideration of small gap-creation processes in other mangrove forests and tropical forests in general. Some of the gap-forming branchfalls in tropical forests that previously had been attributed to wind, rain, or general senescence may have been killed by primary xylovores. Determination of gap origin by a wood borer can be accomplished by examining pieces of fallen wood if the life history of the insect is understood. We frequently have collected this species and observed its characteristic damage in mangrove forests all along the Belizean mainland and cays. This genus is widespread in the Neotropics. Little information, however, is available about the natural history and ecological roles of such long-lived, wood-feeding insects. Possibly because of the difficulty in locating, rearing, and identifying larvae of this group of insects, their contributions to the cumulative feeding damage suffered by tropical forest plants generally have been overlooked, or assumed to be secondary (*i.e.*, feeding on dead wood) rather than primary consumption (*i.e.*, feeding on living plant tissue). Species related to *E. mimeticum* probably have similar feeding behaviors and may have similar impacts on their hosts (Duffy 1960).

Brokaw (1985a) has pointed out that the size of gaps and treefall units (*e.g.*, trees or branches) determines forest structure and dynamics, and that species-specific modes of death affect gap size. For example, a tree that dies standing and drops limbs typically forms small gaps. Adjacent areas dominated by either *R. mangle* or *A. germinans* in Belizean forests are consistent with this prediction. Our results suggest that these two species have different mechanisms of gap creation, different sizes of gaps, and different dynamics of regeneration. Gaps in *A. germinans* forests may be relatively large compared to the small gaps in the *R. mangle* fringe forest (Table 1). In the dieback areas (0.5–3 ha),

weathered stumps and a dearth of live trees or saplings are evidence that these areas are old with little regeneration to forest. In contrast, *R. mangle* forests are mosaics of numerous small gaps and trees in all stages of forest development. Differential growth responses by mangrove species to availability of light and nutrients during the seedling stage (McKee 1995b) further emphasizes the potential importance of gap dynamics to regeneration patterns and structure of Neotropical mangrove forests.

Implications of this study extend beyond mangrove-forest ecology. Factors that affect wood borer population dynamics and rates of xylovores by wood feeders (*e.g.*, nutrients, moisture, CO₂, and natural enemies) indirectly may influence rates of gap formation and subsequent regenerative processes in these and other tropical forests. How this process of gap formation affects subsequent regeneration within the clearing has not been studied. Although most research in tropical forests has focused exclusively on direct removal of leaf tissue by folivores, this study points out that primary consumption by wood borers can be a major form of indirect herbivory with a critical role in ecological processes such as gap dynamics.

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