

The role of herbivory by wood-boring insects in mangrove ecosystems in Belize

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The roles wood-boring insects play in modifying mangrove ecosystems were examined on small, offshore mangrove islands in Belize. Several species of xylem- and phloem-feeding woodborers consume the wood of living mangrove trees. By girdling, pruning, and hollowing, woodborers killed over 50% of the *Rhizophora mangle* canopy in experimental plots arrayed across a tidal-elevation gradient. In contrast, leaf-feeding herbivores removed less than 6% of the canopy. In the plots, stem girdlers killed over three branches per tree. The patterns of herbivory by three functional feeding groups were heterogeneous and did not vary consistently with tidal elevation. Because *R. mangle* lacks viable axillary buds or the ability to produce epicormic shoots to replace pruned branches, the canopy architecture was significantly modified by this damage. The branches that were pruned by stem girdlers created numerous small holes or gaps in the mangrove canopy. Shoot growth and flowering increased in *R. mangle* trees with 50% of their branches experimentally girdled. Because branches and twigs attacked by woodborers lost their leaves prematurely as greenfall, the quantity and quality of leaf litter were altered when a leaf-bearing branch was girdled or hollowed. These changes suggest that wood-boring insects also significantly affect internal and external nutrient cycling processes in mangrove ecosystems.

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Disturbance within an ecosystem can create well-defined patches and alter the structural and functional properties of that system. Large-scale physical disturbances to an ecosystem caused by abiotic forces, such as the trees in a mangrove forest knocked down by a hurricane, leave distinctive scars on the landscape (Stoddart 1969, Smith et al. 1996). In contrast, disturbances that originate from biotic interactions may be less conspicuous, but not necessarily less important. Animals can cause distinctive physical disturbances that alter the environment and have major impact on ecosystem processes and other organisms (McNaughton et al. 1988, Naiman 1988, Jones et al. 1994, 1997). Defoliating insects are also widely recognized agents of ecosystem disturbance that can have an impact on forest production and nutrient cycling, and their outbreaks events can create large-scale disturbances

(Mattson and Addy 1975, Barbosa and Schultz 1987, Filion et al. 1998, Eshleman et al. 2000).

Wood-feeding insects attack live trees, which can create widespread disturbances in forests (Schowalter 2000a). In temperate forests, primary consumption by wood-boring insects can cause structural and functional disruption of primary and secondary growth of trees (Barbosa and Wagner 1989), and can affect tree architecture, growth, reproduction, and sex expression (Whitham and Mopper 1985). Woodborers also play important ecological roles in nutrient cycling, gap formation, and succession in temperate ecosystems (Amman 1976, Schowalter 1981, Lundquist 2000), and influence the composition and hydrology of forests (Bethlahmy 1975, Lundquist and Negron 2000). Woodborers can prune, weaken, or kill standing trees, thereby reducing the timber quality of both temperate

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and tropical species (Grijpma 1970, Grijpma and Gara 1970, Raffa and Berryman 1983, Howard 1991, Yamazaki et al. 1992, Rodgers et al. 1995). However, the ecological consequences of herbivory by wood-boring insects in tropical forests have not been widely investigated. It seems likely that functional feeding groups of tropical woodborers play important ecological roles similar to their temperate analogues. In this study, I examine the role of wood-boring insects in a coastal tropical forest dominated by *Rhizophora mangle* L. (the red mangrove).

Herbivory by mangrove leaf feeders has been quantified in several locations in the neotropics (Onuf et al. 1977, Beever et al. 1979, Lacerda et al. 1986, Farnsworth and Ellison 1991, Feller 1995) and in the Indo-Pacific (Johnstone 1981, Piyakarnchana 1981, Whitten and Damanik 1986, Robertson and Duke 1987, Murphy 1990, Lee 1991, Anderson and Lee 1995). The levels of defoliation reported in these studies ranges from negligible in dwarf trees in Belize (Farnsworth and Ellison 1991, Feller 1995) to > 75% of the canopy leaf area in severe outbreak events in Hong Kong (Anderson and Lee 1995), Thailand (Piyakarnchana 1981), Singapore (Murphy 1990), and Indonesia (Whitten and Damanik 1986). Most studies of mangroves suggest that herbivores consume < 10% of the canopy leaf area, which is similar to levels of defoliation reported from other tropical and temperate ecosystems (Mattson and Addy 1975, Coley and Aide 1991). In general, insect grazing of mangrove leaves is considered inconsequential and not an important regulator of litter dynamics (Odum and Heald 1975, Lee 1991).

In the mangrove forests of coastal Belize, primary consumption by woodborers may be responsible for greater losses from the canopy than consumption by folivores (Feller and Mathis 1997, Feller and McKee 1999). In general, larvae of phloem-feeding woodborers girdle stems, and larvae of xylem feeders hollow stems (Barbosa and Wagner 1989). Both types of damage cause pruning of branches distal to the point of attack and localized wood death. Phloem-feeding herbivores sever the conductive tissue between the branch and the bole, disrupting translocation of nutrients and other solutes, and eventually causing the death of the branch (Sullivan et al. 1993). The larvae of some insect borers literally prune branches from the tree by making smooth, circular cuts at right angles to the main axis of the stem (Solomon 1995). These insect borers destroy meristems and kill leaf-bearing shoots, large branches, and even entire trees by girdling, pruning, or hollowing. Thus, it is reasonable to hypothesize that the activities of insect borers may have important ecological consequences for mangrove ecosystems. Because *R. mangle* is the dominant tree in Belizean coastal forests, I measured woodborer damage in this species to examine the ecological significance of this type of herbivory in a

mangrove ecosystem. The morphologies of larval feeding galleries, pupal chambers, and exit holes of woodborers of *R. mangle* are diagnostic. The history of an individual tree can be inferred from these indelible secondary population indices that persist in dead wood and remain recognizable long after the adult insects have emerged. These signs indicate internal insect damage and can be used to measure herbivory, to assemble biological diversity data, and to provide historic evidence of woodborers' influence on mangrove ecosystem dynamics. Active attack sites in living or recently dead branches can be recognized by conspicuous rust-red stains on the bark, caused by tannins leaching from the underlying damaged tissue. Branches that are being attacked by woodborers are obvious because they typically either have lost all their leaves or have fewer, smaller, and more yellow leaves than surrounding, undamaged parts of the canopy.

The objectives of this study were: 1) to measure the levels of damage to *R. mangle* caused by woodborers; 2) to compare woodborer damage to *R. mangle* with damage caused by foliage-feeding herbivores; 3) to compare patterns of herbivory by three functional feeding groups across a tidal-elevation gradient; 4) to quantify other responses by *R. mangle* to woodborer damage; and 5) to assess the ecological significance of insect woodborers in a mangrove ecosystem.

Materials and methods

Study site – The experimental part of this study was conducted Twin Cays, Belize (16.50°N 88.06°W), a 92-ha archipelago of six mangrove islands, ~12 km from the mainland (Rützler and Feller 1999). These islands are located in a carbonate setting in the outer lagoon just inside the crest of the central barrier reef. *Rhizophora mangle* typically forms a seaward fringe, 5–10 m wide, with extensive stands of dwarf trees in shallow ponds in the hinterlands of these islands (Woodruffe 1995, Koltes et al. 1998). *Avicennia germi-nans* (L.) Stearn. (black mangrove), and *Laguncularia racemosa* (L.) Gaertn.f. (white mangrove) are also common and usually occur landward to the *R. mangle* fringe.

To determine the wood-boring insect fauna associated with the mangrove, I used standard sampling methods (i.e., light traps, Malaise traps, insectical fog, beating) to collect adults (Southwood 1978). Larval woodborers were reared to associate larval, pupal, and adult stages and to determine feeding patterns. Galleries, frass, pupal chambers, exit holes, and feeding behaviors were determined for the common species and used to quantify damage from external inspection of a tree and to identify species in the field. Voucher specimens of adults and larvae were deposited at the National Museum of Natural History, Washington, DC.

Quantifying damage – To confirm that girdling by woodborers causes branches to die, I artificially girdled branches and compared their responses with adjacent, undamaged control branches on the same tree. Thirty trees were haphazardly selected along navigable creeks at Twin Cays. I selected two living, undamaged primary branches per tree in similar positions within the canopy. Treatment (girdled versus control) was assigned randomly. (A primary branch was defined as a branch that originates directly from the bole.) For the girdled treatment, I ringed the stem by cutting away a 2-cm wide circle of bark and wood around the stem's circumference, 0.5 cm deep and 5 cm from the branch gap. These branches were monitored quarterly for 2 yr.

I assessed damage in the mangrove canopy caused by three functional groups of herbivores, specifically: 1) stem-girdling woodborers, which girdle or prune branches and boles; 2) folivores, which feed directly on leaves; and 3) twig borers, which feed in terminal, leaf-bearing shoots. Spatial variation in herbivory was measured along three replicate transects, ~0.5 km apart, at Twin Cays. Transects were oriented perpendicular to the shoreline and subdivided into five plots (10 m × 10 m) at 5-m intervals across a tidal-elevation gradient. Tidal elevation increased from the fringe mangrove at lowest low water (LLW) in Plot 1 to highest high water (HHW) in Plots 3 and 4 and decreased again to LLW in Plot 5. This gradient was chosen because other studies have reported significant differences in herbivory and seedling predation along tidal gradients (Smith 1987, Farnsworth and Ellison 1991, McKee 1995). The greatest tree height (~6 m) and lowest tree density (25 trees per plot) occurred in Plot 1; tree height decreased to a dwarf stand (≤ 1.5 m) in Plot 5 where tree density increased to ~75 trees per plot. Plots 1 and 5 contained monospecific stands of *R. mangle*. Plots 2, 3, and 4 were dominated by *R. mangle* with *A. germinans* and *L. racemosa* intermixed.

In each plot, herbivory by stem girdlers, folivores, and twig borers was measured in 10 trees selected by an unbiased observer. All branches were categorized as: 1) alive (no apparent damage); 2) dead (no leaves or live buds); or, 3) partially dead (missing all or most of its leaves but with living apical buds on some shoots). For each dead and partially dead branch, I measured order and stem diameter, and identified the cause of death or damage, as in Feller and McKee (1999), i.e., stem girdlers, human (e.g., machete or chain-saw cuts), abiotic (e.g., lightning or wind), and unknown (when no conclusion could be drawn). If a woodborer's feeding gallery encircled a stem with live wood proximal and dead wood distal to the gallery, the cause of death or damage was attributed to stem girdlers. Dead branches were characterized as: 1) standing dead (attached to tree, lacking any green leaves or buds with terminal shoots and bark intact); 2) standing snag (attached to tree but missing lateral branches and bark); 3) fallen

dead (broken from tree, varying from long-dead and well-weathered wood to recently dead). Branches in the fallen-dead category were included only if they could be clearly associated with a particular tree. For each dead or partially dead branch, I estimated the proportion of the canopy that it represented. For example, if one of a tree's five approximately equal primary branches was killed by a woodborer, then that branch was scored as "1 of 5" or a 20% loss of the canopy. Values for individual branches were summed to determine the total proportion lost per tree per cause of death or damage.

Folivory measurements were based on 100 leaves per plot, chosen randomly from the leaves off five branches collected by an unbiased observer, from each of the 10 trees per plot. Leaf area damaged was determined for digitized images of each leaf using SigmaScan Pro 4.0 image analysis software (SPSS, Inc., Chicago, IL). These data were used to estimate the proportion of the canopy removed by folivores.

To determine the proportion of the canopy damaged by the twig borers, I counted the total number of live and dead twigs and collected all dead twigs in each of the 10 trees per plot. (A twig was defined as a terminal, unbranched leaf-bearing shoot.) Each dead twig was dissected to identify those killed by twig borers, as in Feller and Mathis (1997). These data were used to estimate the proportion of the canopy killed by twig borers. Differences in the proportion of the canopy killed or damaged by stem girdlers, folivores, and twig borers among transects and plots were analyzed with a nested analysis of variance (ANOVA).

I also surveyed the wood-boring insect fauna and quantified damage by stem girdlers on two other offshore mangrove archipelagos [Blue Ground Range (16.31°N 88.06°W) and Pelican Cays (16.26°N 87.98°W)] and on the Belizean mainland at Punta Yacacos (15.89°N 88.39°W) using the point-centered quarter method. At each site, I sampled four trees at each of 20 points spaced at 5 m intervals along transects perpendicular to the shoreline, for a total of 80 trees per transect (Cintrón and Schaeffer Novelli 1984).

Measuring impact of woodborers – To assess *R. mangle*'s ability to compensate for herbivory by stem girdlers, I tracked growth and flowering for 1 yr following simulated stem girdling. Five pairs of saplings (i.e., ~2 m tall and 5–10 yr old) were selected from an open stand of trees in the interior of Twin Cays. The members of a pair were ~1 m apart and had similar height and architecture. In each pair, 50% of the primary branches of one member were girdled as described above; the undamaged member served as a control. I tagged five twigs in sunlit positions in the outer part of the canopy of each tree. In the 50%-girdled trees, these five twigs were in the undamaged half of the canopy. Leaves in the apical position on each twig were labeled with waterproof ink on their abaxial surfaces to mark

the starting point for growth measures. I measured shoot elongation (cm), and number of lateral shoots, leaves, and flowers produced between July 1994 and August 1995. In August 1995, I also counted the number of flowers produced by the girdled branches. All tests of the experimental treatment were based on paired comparisons, and the data were analyzed in a paired t-test.

To quantify the effects of stem girdlers on leaf-level processes, I compared leaf size and nutrient concentration in a pair of primary branches (one with an active stem girdler and one undamaged control) in each of 10 trees located along the Main Channel at Twin Cays. Samples of five penapical leaves were collected from each branch in February 1995. To compare growth and flowering, I measured the response of five twigs haphazardly selected in a sunlit position of the upper canopy on both branches per tree in February and August 1995. Each primary branch used in this survey was inspected to find the attack site where the girdling occurred or, for controls, to verify that it was undamaged. Leaf area was determined for each leaf with a Li-Cor 3000 Portable Area Meter (Li-Cor, Lincoln, NE, USA). Leaf samples were dried in a convection oven at 70°C and ground in a Wiley Mill to pass through a 40-mesh screen. Concentrations of carbon (C) and nitrogen (N) were determined with a Perkin-Elmer 2400 CHN Analyzer at the Smithsonian Environmental Research Center, Edgewater, MD, USA. Concentrations of phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), manganese (Mn), iron (Fe), boron (B), and aluminum (Al) were determined using an inductively coupled plasma spectrophotometer (ICP) by Analytical Services, Penn State University, State College, PA, USA. I used paired t-tests to compare branch pairs (girdled and control) for differences in leaf size, leaf and flower production, and nutrient concentration.

To compare chemical and structural differences in leaf litter from girdled versus undamaged branches, I collected samples of 5–6 leaves of greenfall (i.e., pre-senescent leaf litter) and naturally senescent leaves from 18 *R. mangle* trees selected as they were encountered along a transect across Twin Cays. Senescent leaves were yellow with a well-developed abscission layer. Greenfall was collected from aerial litter on branches that had broken free from trees at woodborer galleries, but were still dangling in the canopy. Leaf area and leaf nutrient content were determined as described above. Tests for differences between greenfall and senescent leaves were based on paired comparisons.

Probability values (p) less than 0.05 were considered to be significant in all statistical tests. Statistical calculations were made using Systat 8.0® (Wilkinson 1990). To analyze for homogeneity of variance, probability plots of all variables and residuals were examined. Data were transformed where necessary to correct for normality.

Results

Insect surveys – Wood-boring insects that attack trees and girdle branches were found in all sites that I surveyed in mangrove forests on offshore islands and the mainland coast of Belize. The woodborers *Elaphidion mimeticum* Shaeffer and *Elaphidinoides* sp. (Cerambycidae: Cerambycinae) were the two most frequently encountered members of this community. For *E. mimeticum*, a larva typically began feeding in the canopy in a live branch or bole. In branches 1–2 cm diameter, larval feeding consumed almost the entire woody content of stems inside the bark. In larger stems (> 2 cm), larvae cut deep, routed feeding galleries into the wood, and consumed the cambium, phloem, and outer parts of the xylem, but not the bark. Branches died when these extensive feeding galleries girdled them. For pupation, a larva extended its feeding gallery deep into the xylem of the branch or bole and excavated a pupal chamber that was slightly larger than its body. The pupal chamber was plugged with undigested wood fibers. Pupation lasted ~3 wk. After eclosion, an adult beetle remained in its pupal chambers for an undetermined period before it emerged. In captivity, the nocturnally active adults of *E. mimeticum* lived ~2 wk, during which time they did not eat. The larvae of *Elaphidinoides* sp. were typically found in *R. mangle* branches < 4 cm in diameter. Near the end of its larval development, this species feeds at right angles to the main axis of the branch, which severs the branch from the tree.

Quantifying damage – At Twin Cays, the portion of the canopy lost because of the stem girdling and pruning ranged from 37–56% (Fig. 1A), but it did not vary significantly among five plots along a tidal-elevation gradient ($F = 1.003$, $df = 12$, $p = 0.449$). On average, the stem-girdler damage removed (mean \pm 1 SE) 46.3 \pm 2.3% of the canopy. In contrast, leaf feeders were responsible for 4–7% (5.5 \pm 0.5%) loss of the canopy (Fig. 1B). Folivory varied significantly among the plots ($F = 6.518$, $df = 12$, $p = 0.000$). On average, values were highest at HHW (Plots 2–4) and lowest at LLW in the fringe (Plot 1) and in the dwarf stands (Plot 5). However, folivory did not vary consistently with tidal elevation (Table 1). Twig borers were responsible for another 6–11% (9.0 \pm 0.4%) loss from the canopy (Fig. 1C). Their damage varied significantly among the plots ($F = 3.843$, $df = 12$, $p = 0.000$). Although values in Plots 1–4 were variable from site to site, the damage by twig borers was generally lowest in Plot 5 (Table 1). Cumulative losses per tree to leaf feeders, twig borers, and stem girdlers ranged from 44–67%. In the 15 plots sampled, damage by sources other than stem girdlers accounted for less than 1% of the dead and dying branches in the 150 trees I examined. In those cases, the cause of damage was unknown with no evidence of wind, lightning, or human activities.

In the 150 trees sampled in the plots at Twin Cays, I found 490 branches with stem girdler galleries. The frequency of stem-girdler attacks ranged from 0 to 15 per tree. Most of the trees sampled in the plots suffered 1–5 stem girdler attacks, with an average of 3.3 ± 0.3 attacks per tree (Fig. 2). Fifteen trees had 0 attacks, whereas 5 trees had between 11 and 15 attacks. However, the number of attacks per tree did not vary significantly among plots ($F = 0.751$, $df = 12$, $p =$

0.699). Approximately 85% of the stem girdler galleries that I found were associated with dead branches that had been completely girdled; the remaining ~15% were associated with partially dead branches. Half of the dead branches were standing dead, i.e., recently dead with bark and smallest branches intact. About 35% were standing snags, i.e., long dead with bark missing and only the large, basal parts of affected branches still attached to the tree. More than 90% of stem-girdler attacks occurred in lateral branches with stem diameter of 3.0 ± 0.1 cm. Less than 10% of the attacks were directly in the bole. Consequently, this damage pruned large sections out of the canopy, but it typically did not kill entire trees.

Damage levels by stem girdlers similar to those at Twin Cays occurred at two other mangrove archipelagos and on the mainland (Table 2). At the Pelican Cays, Blue Ground Range, and at Punta Ycaos, stem girdlers had attacked 90–93% of the *R. mangle* trees.

Impact of woodborers – Experimental girdling caused branches to die in about 1.5 yr; none of the control branches died in that time. Within 4 mo, the experimentally girdled branches had an appearance similar to observed branches that were being attacked by stem girdlers, i.e., they had fewer, smaller, and more yellow leaves than on adjacent, non-girdled control branches (personal observation). Experimental girdling had significant effects on growth and flowering. Over a 6-mo period, shoot elongation of undamaged branches on saplings with 50% of their branches artificially girdled was significantly greater than on control trees (Table 3). Girdling had no significant effect on leaf production, or the number of new lateral shoots produced by the girdled saplings. The number of flowers produced by branches in the undamaged half of the girdled saplings and comparable branches on the control plants were similar. However, the branches that were girdled produced more flowers than branches on the control trees and on their undamaged half.

Woodborers had significant effects on litter nutrient chemistry (Table 4). Greenfall had higher concentrations (mg/g) of C, N, and P than did naturally senescent litter. As a result, the C:N and N:P ratios in greenfall were approximately double that of naturally senescent leaves. Senescent leaves had significantly higher concentrations of Ca, Mg, Fe, B, and Al than did greenfall. Concentrations of K, Mn, and Zn were similar in greenfall and senescent litter.

In *R. mangle* trees along the Main Channel at Twin Cays, branches with active stem-girdler galleries produced fewer leaves over a 6-mo period (2.7 ± 1.0) per twig than did undamaged control branches (11.1 ± 0.6) on the same tree ($t = 5.909$, $df = 9$, $p = 0.000$). Leaf size was significantly smaller on the girdled branches than on the control branches (13.4 ± 5.7 cm vs 35.2 ± 7.5 cm; $t = 11.806$, $df = 9$, $p = 0.000$). Girdled branches

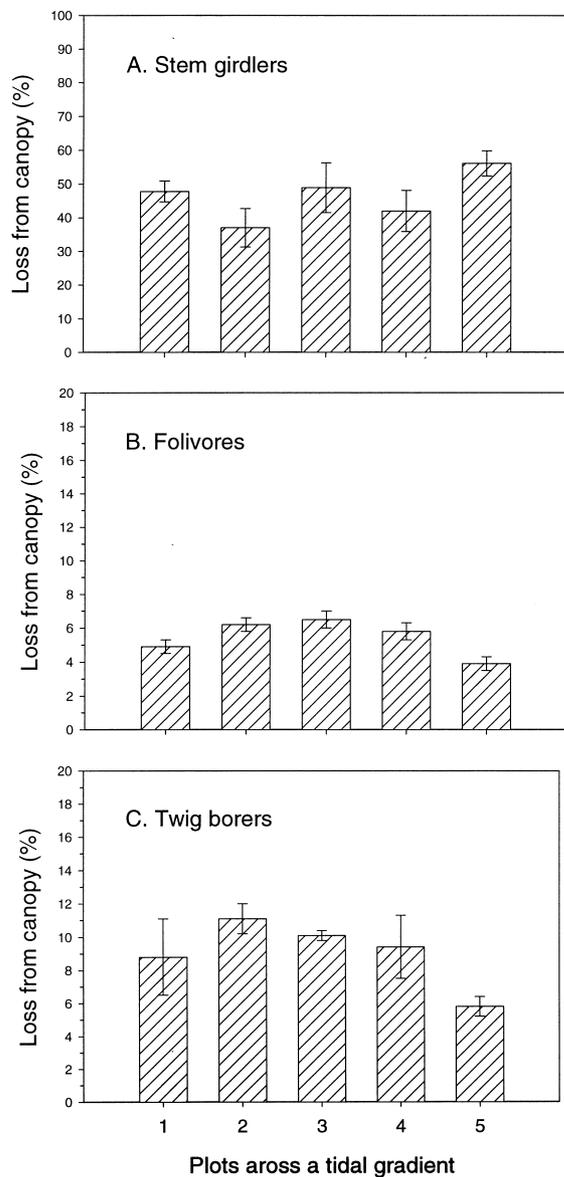


Fig. 1. Damage to the canopy of *Rhizophora mangle* in five 10×10 m plots in each of three transects evenly spaced across a tidal-elevation gradient from a fringe forest in Plot 1, through a mixed scrub forest in Plots 2–4, and to a dwarf forest in Plot 5 in the interior of Twin Cays by (A) stem girdlers, (B) folivores, and (C) twig borers. Data sets for each type of herbivory were analyzed using a nested analysis of variance.

Table 1. Probabilities from a pairwise comparison of plots based on a post hoc Fisher's Least-Significant-Difference Test comparing losses from the canopy by folivores and twig borers in five plots at each of three transects across a tidal-elevation gradient at Twin Cays. Data sets were analyzed using a nested analysis of variance.

Pairwise comparison	Folivory			Twig borer damage		
	Site 1	Site 2	Site 3	Site 1	Site 2	Site 3
Plot 1 vs 2:	0.000	0.086	0.632	0.010	0.455	0.073
Plot 1 vs 3:	0.184	0.000	0.411	0.012	0.171	0.264
Plot 1 vs 4:	0.000	0.334	0.077	0.0131	0.956	0.311
Plot 1 vs 5:	0.366	0.670	0.005	0.642	0.005	0.042
Plot 2 vs 3:	0.021	0.002	0.732	0.9542	0.531	0.492
Plot 2 vs 4:	0.998	0.456	0.190	0.914	0.489	0.005
Plot 2 vs 5:	0.000	0.031	0.021	0.034	0.018	0.000
Plot 3 vs 4:	0.021	0.000	0.334	0.960	0.188	0.034
Plot 3 vs 5:	0.025	0.000	0.045	0.039	0.079	0.002
Plot 4 vs 5:	0.000	0.162	0.313	0.044	0.002	0.302

also had significantly more flowers per twig than control branches (5.2 ± 0.6 vs 0.7 ± 0.3 ; $t = 8.081$, $df = 9$, $p = 0.000$).

Discussion

Canopy losses in *R. mangle* to herbivory by two groups of woodborers, specifically twig borers and stem girdlers, far exceeded the loss of leaf tissue caused by folivores. My data document a recurrent pattern of intense herbivory by woodborers in mangrove ecosystems in Belize and support the hypothesis that insect borers play an important ecological role in this tropical forest ecosystem. Wood-boring insects are widespread in the mangrove forests of Belize (Chemsak and Feller 1988, Feller and Mathis 1997). The natural histories of individual species of woodborers provide essential clues for recognizing the historic evidence of their activities and for understanding their influence on this ecosystem. This study provides the first larval feeding and host record for *E. mimeticum*. This genus is widespread in the Neotropics, and a number of related species with similar feeding behaviors may have similar effects on their hosts (Duffy 1960). Although adult woodborers were seldom collected, their larvae and feeding damage were in >90% of the *R. mangle* trees in Belize's mangrove forests.

At Twin Cays, damage to *R. mangle* by stem girdlers and twig borers caused indirect defoliation that was ~7–35 times greater than that resulting from direct removal of leaf tissue by folivores. Stem girdlers killed large branches and were responsible for most of the dead and dying wood observed in the *R. mangle* canopy at Twin Cays. Experimental girdling of *R. mangle* branches caused responses similar to stem girdlers and demonstrated that this type of damage caused branches to die. In all cases, the wood distal to the gallery that girdled a branch was dead or dying, whereas the wood proximal to the gallery was alive. Several species of small, xylem-feeding woodborers also attack and kill

individual leaf-bearing twigs of *R. mangle*. These twig borers attack near the apical meristem and subsequently hollow out the stem, thereby killing the whole twig. Furthermore, by hollowing out woody stems for their galleries and pupal chambers and increasing the availability of woody resources, twig borers modified the mangrove habitat to provide critical habitats for numerous species of inquilines (Feller and Mathis 1997). In that study, we found more than 70 species of arthropods associated with these hollow twigs for food, refuge, and nest sites.

Branches girdled by woodborers were clearly visible as leafless or nearly leafless sections of the mangrove canopy. Branches attacked by these herbivores prematurely dropped their leaves as greenfall, and the wood eventually died. Over half of the canopy of each tree examined in this study was missing because of primary consumption by these two groups of woodborers.

Chronic and acute infestations of insect herbivores can have major negative consequences on a host plant's growth and reproduction (Morrow and LaMarche 1978, Kinsman and Platt 1984, Whitham and Mopper

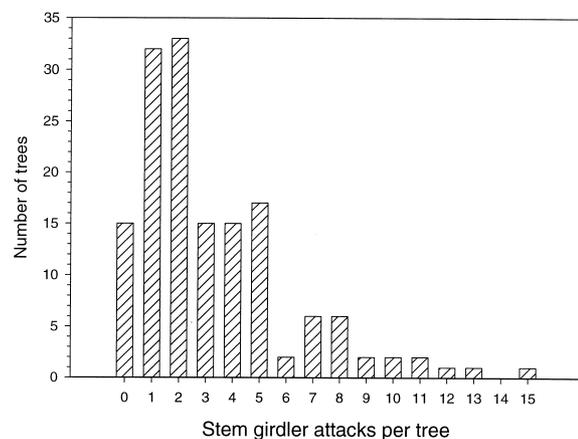


Fig. 2. Frequency distribution for attacks by stem-girdling woodborers per tree of 150 *Rhizophora mangle* trees in 15, 10 × 10 m plots at Twin Cays.

Table 2. Number of stem-girdler attacks and percent of the *Rhizophora mangle* canopy killed by stem-girdling woodborers in mangrove forests in Belize on three offshore archipelagos and on the mainland.

Location	Number of attack per tree (mean \pm 1 SE)	Portion of canopy dead or dying (%)
Twin Cays	3.3 \pm 0.3	46.3% \pm 2.3
Pelican Cays	2.6 \pm 0.3	38.3% \pm 3.6
Blue Ground Range	2.5 \pm 0.3	46.2% \pm 8.6
Mainland (Punta Ycacos)	2.3 \pm 0.2	38.6% \pm 2.7

1985, Rodgers et al. 1995). Although *R. mangle* lacks viable axillary buds to replace pruned branches (Gill and Tomlinson 1969), the increased growth by saplings with 50% of their branches experimentally girdled indicated that this species may be able to compensate for some of the heavy losses from its canopy caused by wood borers. The artificially girdled branches also became more reproductive. In nature, branches girdled by stem girdlers produced more flowers and propagules than undamaged branches. The increased production of flowers and propagules in *R. mangle* may partially offset the loss of fitness to woodborer damage by using resources in the damaged branches which cannot be transported into other parts of the tree because of severed conductive tissue.

Woodborer damage to meristems and shoots may severely alter a plant's form (Whitham and Mopper 1985, Schowalter 2000b). The history of such damage can be inferred from tree shape and from the enduring evidence on branches and boles, such as feeding galleries, exit holes, and tannin stains (Oliver and Larson 1996). By killing and pruning out large sections of the canopy, woodborers such as *E. mimeticum* and *Elaphidinoides* sp. alter the architecture of individual *R. mangle*. Because *R. mangle* lacks viable axillary buds, it cannot create a new leader to replace pruned apical growth (Gill and Tomlinson 1969). Multiple attacks by these woodborers killed an average of over three

branches per tree, which resulted in approximately 46% loss of the canopy structure (Fig. 1A). Although pruning reduces the structural complexity of individual trees, the creation of light gaps by woodborers may increase the overall structural complexity of the mangrove forest.

Disturbance events that create canopy gaps in mangrove forests are important for forest dynamics because mangrove seedlings and trees in gaps survive at a higher rate than in adjacent forests and may a source for recolonization and regeneration (Pimm et al. 1994, O'Grady et al. 1996, Clarke and Kerrigan 2001). Stem-girdler damage is by far the single-most important form of small-scale disturbance to the *R. mangle* canopy at Twin Cays and the principal agent responsible for creating small light gaps in these forests (Feller and McKee 1999). In Florida, most small gaps in mangrove forests are caused by lightning, which causes circular patches where a number of trees are killed rather than a single individual (Smith 1992). In Belize, we found no evidence of small gaps being caused by abiotic forces, including lightning strikes (Feller and McKee 1999). We found that gaps caused by woodborers were small, irregular patches, usually formed by the death of several overlapping branches from adjacent trees, rather than entire trees. Because approximately half of the canopy of each tree is killed in this manner, these gaps are common and cumulatively important. The low stature of the mangrove canopy relative to gap area creates micro-environmental differences that are comparable to much larger gaps that form in tropical forests with higher canopies (Denslow 1987, Smith et al. 1989). Despite their small size, soil temperatures increased by 3°C and light levels in these gaps were 15 times greater than under the adjacent closed-canopy forest (Feller and McKee 1999). The effects of small-scale disturbance on these factors have been shown to be important to the survival and growth of *R. mangle* seedlings (Ellison and Farnsworth 1993).

Other studies that measured herbivory in Neotropical mangrove forests focused exclusively on direct grazing

Table 3. Comparison of shoot variables from similar pairs of *Rhizophora mangle* trees in which one member was experimentally girdled on 50% of its primary branches and the other member was an undamaged control. In the first four variables, the comparison is for the undamaged half of 50%-girdled trees and for the control trees. In the fifth variable (*), the comparison is for the undamaged branches and for the girdled branches of the 50%-girdled trees. ($n = 10$).

Variable	Treatment	Mean \pm 1 SE	<i>t</i>	Probability
Shoot length (cm):	Control	3.1 \pm 0.8	3.022	0.039
	Girdled	10.5 \pm 2.6		
Number of leaves:	Control	13.2 \pm 1.9	1.180	0.303
	Girdled	19.0 \pm 4.3		
Number of lateral shoots:	Control	0.6 \pm 0.2	1.486	0.211
	Girdled	1.6 \pm 0.6		
Number of flowers:	Control	0.1 \pm 0.1	0.784	0.447
	Girdled	0.3 \pm 0.2		
*Number of flowers on girdled trees:	Undamaged	0.3 \pm 0.2	8.294	0.000
	Girdled	16.1 \pm 1.9		

Table 4. Comparisons of nutrient concentrations (mg/g) in two sources of leaf litter from the same *Rhizophora mangle* tree: (1) greenfall from a branch girdled by a wood-boring insect; and (2) naturally senescent leaves from an undamaged, control branch. Girdled branches n = 18. Control branches n = 18.

Variable	Greenfall (mean \pm 1 SE)	Natural Senescence (mean \pm 1 SE)	<i>t</i>	Probability
C	452.066 \pm 2.865	436.544 \pm 3.668	3.932	0.001
N	9.541 \pm 2.936	5.027 \pm 3.256	15.567	0.000
P	0.458 \pm 0.025	0.129 \pm 0.019	16.383	0.000
K	8.506 \pm 1.073	7.861 \pm 1.336	0.672	0.511
Ca	14.289 \pm 0.655	17.989 \pm 0.545	4.205	0.011
Mg	8.417 \pm 0.333	10.344 \pm 0.238	5.062	0.000
Mn	0.006 \pm 0.000	0.005 \pm 0.000	0.690	0.500
Fe	0.022 \pm 0.008	0.027 \pm 0.001	4.406	0.000
B	0.086 \pm 0.007	0.117 \pm 0.006	4.891	0.000
Al	0.015 \pm 0.001	0.019 \pm 0.001	4.786	0.000
C:N	48.1 \pm 1.4	91.8 \pm 4.9	9.892	0.000
N:P	22.0 \pm 1.5	46.6 \pm 4.0	6.998	0.000

on leaves by folivores (Onuf et al. 1977, Beever et al. 1979, Lacerda et al. 1986, Farnsworth and Ellison 1991). As was also true in this study, the reported levels of folivory were low, but variable from site to site. Because nearly intact leaves fall into the litter, the grazing pathway is thought to have little influence on nutrient cycling in most mangrove forests (Heald 1971, Lee 1991). Odum et al. (1982) pointed out that litterfall is a major ecological process in mangrove ecosystems because it provides detritus for foodwebs in mangrove swamps. Woodborers that kill leaf-bearing branches contribute to this process by increasing input of both leaf and wood litter. Because the leaves on a dead branch or tree killed by a woodborer die and enter the litter prematurely as greenfall, this type of herbivory may cause a change in the quality and quantity of litterfall. At Twin Cays, over half of the *R. mangle* canopy becomes litter via this route.

In contrast to previous studies, my results suggest that herbivory by wood-boring insects in the canopy can affect nutrient cycling in mangrove forests at the ecosystem level and at the individual plant level. At an ecosystem level, consumption by woodborers can add a major grazing step into litter dynamics regardless of whether they are controlled by geophysical processes (Twilley et al. 1986, Twilley 1995) or detritivory (Robertson 1986, Robertson and Daniel 1989, Twilley et al. 1997). At the level of the individual plant, woodborers alter internal nutrient recycling pathways. Because leaves die and fall from the tree still green, this type of damage precludes resorption of nutrients prior to leaf fall during natural senescence. Nutrient resorption from senescing leaves has been shown to be an important mechanism for conserving nutrients in some mangrove forests (Feller et al. 1999). Woodborer-caused greenfall had four times as much P and twice as much N as naturally senescent litter. The nutrient ratios in greenfall, e.g., N:P, C:N, which are considered important indices of the decomposability of leaf litter (Bedford et al. 1999), were dramatically altered.

In summary, extremely high levels of canopy damage and defoliation resulting from primary consumption by wood-boring insects were detected in the *R. mangle* on mangrove cays in Belize. Because of their feeding strategies and physical alterations to the mangrove environment, woodborer activities have diverse ecological consequences in mangrove ecosystems. At the level of an individual, woodborers affect canopy architecture, growth, reproduction, and internal nutrient cycling. Scaling up, woodborers impact forest structure and dynamics by creating light gaps. On the ecosystem level, woodborers potentially impact nutrient cycling processes by altering both the quality and quantity of litter. Furthermore, woodborers affected the community structure of the mangrove by providing habitat for many species of other arthropods. Results from this study also suggest that factors affecting the population dynamics and primary consumption levels of wood-boring insects may also modify forest dynamics and nutrient cycling processes in these, and perhaps other, tropical forests.

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