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Primary Herbivory by Wood-Boring Insects along an Architectural Gradient of *Rhizophora mangle*¹

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ABSTRACT

We investigated the distribution of primary xylovores in *Rhizophora mangle* (red mangrove) first-order branches, *i.e.*, “twigs”, along an architectural gradient on Belizean mangrove cays. Greater structural diversity in *R. mangle* architecture, xylovore availability, occurrence of natural enemies, and habitat do not result in variable xylovore species richness. Despite large differences in architectural complexity, tall, fringe, dwarf, and sapling trees host the same set of primary twig borers. However, tall trees support greater diversity and abundance of twig inquilines than other tree forms. Primary twig borers have a key role in structuring these mangrove communities because their galleries and pupal chambers provide habitats for numerous species of secondary xylovores and inquilines. We also measured the amount of leaf area removed from *R. mangle*'s canopy by wood- and leaf-feeding herbivores. Vigorously growing tall and sapling trees sustain greater losses because of twig borers than dwarf trees. However, xylovores in fringe trees was not different from any of the other categories. Cumulative herbivory was greatest in the tall trees. In most cases, leaf-area loss as an indirect or collateral result of primary xylovores equaled or exceeded leaf-area loss as a direct result of folivory.

Key words: diversity; herbivory; inquilines; mangrove; plant architecture; primary xylovores; *Rhizophora mangle*; species richness; twig-feeding guild; wood-boring insects.

DESPITE THE PAN-TROPICAL DISTRIBUTION and importance of mangrove forests (Chapman 1970, Heald 1971, Odum 1971, Tomlinson 1986), the insect fauna associated with these communities has not been sampled thoroughly except at a few locations (Wilson & Simberloff 1969, Chemsak 1982, Chemsak & Feller 1988, Mathis 1989, 1997; Murphy 1990, Feller 1993, 1995). The consensus has been that mangroves are so well protected by tannins that they are essentially inedible by most herbivorous insects (Huffaker *et al.* 1984). Tomlinson (1986) suggested that coevolutionary processes giving rise to close animal-plant interactions do not occur in mangroves. However, our recent studies in Belize (Rützler & Feller 1988, 1996, *in press*; Feller 1993, 1995; Mathis 1989, 1997) indicate that the diversity and significance of the insect fauna associated with mangroves are greater than previously described. In addition to primary consumption by foliage feeders or folivores, we have found that first-order branches (hereafter ‘twigs’) of *Rhizophora mangle* L. (red mangrove) are commonly attacked by several species of specialized, primary wood-boring insects or xylovores (Chemsak 1982, Chemsak & Feller 1988). The goals of this study

were to determine the species of primary consumers associated with *R. mangle* twigs, to quantify their contribution to herbivory of this species, and to compare the level of herbivory caused by these wood borers with that caused by folivores.

Hypotheses explaining differences in herbivory have not been extensively tested in mangrove systems. Most previous studies have based their herbivory measurements exclusively on damage to leaves by folivores but have not considered losses to primary xylovores. In Florida, Beever *et al.* (1979) suggested that differences in herbivory of *R. mangle* leaves by the mangrove tree crab (*Aratus pisonii* H. Milne Edwards) may be the result of differential crab recruitment caused by topological differences between mangrove swamps and fringing mangrove relative to the seaward perimeter.

Several studies examined the relationship between leaf damage and nutrient availability in mangrove swamps, but yielded contradictory results (Onuf *et al.* 1977, Johnstone 1981, Lacerda *et al.* 1986, Farnsworth & Ellison 1991, Feller 1993, 1995). In Florida, Onuf *et al.* (1977) found that herbivory was correlated with nutrient availability, plant growth, and leaf N content, with a greater loss of leaf material at a *R. mangle* island rookery (high nutrient) than at a mangrove island lacking a large bird population (low nutrient). However, in

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Brazilian mangroves, Lacerda *et al.* (1986) found that leaf ash, crude fiber, and water content were negatively correlated with herbivory, that carbohydrates and total phenolics were positively correlated with herbivory, but that total nitrogen was not correlated with herbivory. In Papua New Guinea, Johnstone (1981) found that none of the parameters he measured in 23 species of mangroves, including leaf N content and nutrient availability, correlated well with leaf damage by folivores. In Belize, Farnsworth and Ellison (1991) reported differential folivory along a tidal gradient, but they found no evidence that herbivory was correlated with nutrient availability. Also in Belize, in a controlled nutrient enrichment experiment in a stand of dwarf *R. mangle*, Feller (1995) found that rates of herbivory by generalist folivores were unchanged in response to increased nutrient availability; however, herbivory by two species of specialized endophytic insects, *i.e.*, a microlepidopteran stem miner (*Marmara* undescribed sp.) and a bud moth (*Ecdytoplopha* sp.), increased dramatically in phosphorus-fertilized trees. In that study, there were no differences in rates of damage to twigs by xylovores after 2 yr of fertilizer treatment.

Although essentially monocultures, *R. mangle* forests are composed of tree stands of varying degrees of nutrient availability and diverse structural or architectural complexity, *e.g.*, riverine, fringe, and dwarf mangrove types (Lugo & Snedaker 1974). Because of increased resource diversity and size, the plant architecture hypothesis (Lawton 1978, 1983, 1986) predicts that larger plants, such as riverine or fringe *R. mangle*, provide more complex habitat structures and will support a more diverse insect fauna than smaller, less structurally complex plants, such as dwarf *R. mangle*. A number of studies have found that interspecific variation in architectural complexity in plants, ranging from herbs to shrubs to trees, is an important factor in determining faunal diversity and patterns of insect herbivory (see Lawton 1983 for references). Effects of intraspecific architectural variation on abundance and species richness of phytophagous insects have received less attention (Bach 1981, 1984). However, Lawton (1983) predicted that insect species richness should also increase with intraspecific architectural complexity, *e.g.*, from seedling to sapling to mature tree. Alternatively, the plant-vigor hypothesis (Price 1991) predicts that herbivory by specialized, endophytic herbivores such as the primary twig borers in *R. mangle* will be greater on the more vigorous plants or plant modules in a population. The structurally diverse stands of *R.*

mangle in the mangrove forests of Belize provide a natural model to test these hypotheses.

The objectives of this research were to document and quantify primary consumption by a guild of twig borers on *R. mangle's* twigs along a tree-height gradient. We asked: 1) Are intraspecific differences in tree architectural complexity related to levels of xylovores and diversity of xylovores in *R. mangle*? 2) What is the contribution of these primary xylovores to the overall herbivory suffered by *R. mangle*, and how does it compare with herbivory by folivores? Further, we sought to document and quantify the importance of *R. mangle* twigs as a habitat for a large number of mangrove occupants. We asked: 3) Are twigs killed by primary xylovores preferred as habitat byinquilines generally and ants specifically over dead twigs not killed by stem borers? 4) Do inquilines classified as predators and parasites differentially influence levels of xylovores along the tree-height gradient?

NATURAL HISTORY

Although the mangrove canopy is notoriously monotonous, with little or no vertical stratification (Janzen 1985, Lugo 1985), the primary wood-boring insect fauna associated with *R. mangle* on Belizean mangrove cays is distinctly stratified. Based on our surveys, live *R. mangle* is attacked by several species of primary wood borers, including larvae of longhorn beetles (Cerambycidae), weevils (Curculionidae), moths (Lepidoptera), and scolytids (Scolytidae). Some of these borers girdle and/or hollow stems, causing pruning of branches distal to the point of attack and localized death. The resulting dead wood and wood-borer galleries in wood are used by numerous, secondarily invading insects and other arthropods for shade, refuge, and food. *Rhizophora mangle* not only sustains considerable losses of woody tissue as a result of this direct primary consumption by wood borers, but it also loses the attached leaves in greenfall as an indirect result of xylovores.

The twigs of *R. mangle* host a well-defined feeding guild (*sensu* Root 1967) of primary xylovores. This guild is composed predominately of seven species of twig borers: *Methia rhizophorae* Chemsak and Feller, *Ataxia cayensis* Chemsak and Feller, *Anatinomma alveolatum* Bates (Cerambycidae), *Pseudoacalles sablensis* Blatchley (Curculionidae), and three moths (larvae) unidentified to species (Tortricidae, *Ecdytoplopha* complex; Pyralidae, Phycitinae; and Cossidae). Another group of small, wood-boring insects feeds on wood of dead twigs,

including *Urgleptes ozophagus* Chemsak and Feller, *Styloleptus rhizophorae* Chemsak and Feller (Cerambycidae), *Tricorynus vacuus* Fall (Anobiidae), *Hypothenemus africanus* Hopkins and *H. columbi* Hopkins (Scolytidae), *Chrysobothris* sp. (Buprestidae), etc. In addition, larger live *R. mangle* branches and boles host at least two species of large, primary stem-boring cerambycids, *Elaphidion mimeticum* Shaeffer and *Elaphidionoides* sp., whose larvae deeply girdle wood under the bark and cause death of branches and boles distal to the girdled area. Dead-wood xylovores, including termites (*Nasutitermes* sp.) and cerambycids (e.g., *Anelaphus inermis* (Newman), *Derancistrus felleriae* Chemsak, and *Leptostylopsis latus* Chemsak and Feller), feed in the resulting dead wood. Also, the live woody tissue of young aerial roots and root radicles of propagules is attacked by *Coccotrypes rhizophorae* Hopkins (Scolytidae).

Consistent with the narrow definition of guild (Root 1967, 1973; Simberloff & Dayan 1991), members of the twig-feeding guild exploit *R. mangle* twigs in a similar manner. The larvae feed down the center of twigs, and create hollow cylinders of wood. Although larval galleries of some of these twig borers may occasionally extend a few centimeters proximal to terminal branch nodes, feeding activity is initiated in the region of twig terminals, and it kills twigs. Based on rearings, estimates for the time required for larval development of twig borers range from five to seven months. Life-history stages (i.e., larvae, pupae, and adults) have been determined for all beetles of this feeding guild. In addition, products (i.e., frass and exuviae) and effects (i.e., galleries and exit holes) are diagnostic. With rare exception, a twig hosts a single individual of one of these primary xylovores. Although larvae are generally well protected in twigs, they are subject to attack by natural enemies, including several species of parasitic Hymenoptera and predaceous clerid and elaterid beetles.

In addition to wood borers, we have collected numerous species of other insects and arthropods from hollowed, dead *R. mangle* twigs. These dead twigs persist on trees up to 1.5 yr before falling into the litter. Exit holes of emerged wood borers expose the empty larval galleries and pupal chambers in twigs. These spaces are frequently reutilized as *domatia* by a large suite of inquilines, including more than 20 species of ants (J.F. Lynch, pers. comm.), as well as spiders, isopods, myriapods, pseudoscorpions, scorpions, crickets, scales, psocopterans, mites, moths, flies, roaches, thrips, buprestids, tenebrionids, anobiids, termites, and cer-

ambycids. So far, we have found as many as 70 arthropod species associated in some way with *R. mangle* twigs on Belizean mangrove cays. However, some *R. mangle* twigs die from unknown causes that cannot be attributed to the primary, stem-boring xylovores. As they desiccate, some of these twigs frequently split lengthwise down the center, creating long cavities. This natural split is fusiform in cross section and is readily distinguishable from species-specific galleries created by wood borers. Although inquilines can use these spaces, it seems likely that they have more ready access via exit holes to galleries created by wood borers.

METHODS

STUDY SITE.—This study was carried out on Twin Cays (92 ha) and Man-of-War Cay (2 ha). These mangrove islands are located in the outer lagoon just inside the crest of the barrier reef of central Belize, approximately 22 km SE of the coastal town of Dangriga (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 are found in Rützler and Feller (1988, 1996, in press).

Like many Caribbean mangrove systems, Twin Cays and Man-of-War Cay are dominated by *R. mangle*, *Avicennia germinans* (L.) Stearn (black mangrove), and *Laguncularia racemosa* (L.) Gaertn.f. (white mangrove). Topographic features of Twin Cays include several tidal creeks, unvegetated flats, and shallow ponds. Man-of-War Cay, 4 km northwest of Twin Cays, lacks this topographic diversity and is vegetated by a stand of uniformly tall trees. This small island has long served as a year-round rookery for magnificent frigate birds (*Fregata magnificens* Matthews) and brown boobies (*Sula leucogaster* (Boddaert)).

The architectural diversity of *R. mangle*'s growth form at our study sites can be described with reference to a tree-height gradient (Lugo & Snedaker 1974), ranging from vast stands of tiny bonsai-like dwarf trees (1–1.5 m tall) that dominate the interior of Twin Cays, to a 10–15 m wide zone of fringe trees (3–6 m tall) around the periphery of Twin Cays, and to 10–13 m tall, straight-trunked trees on Man-of-War Cay. The tree-height gradient for *R. mangle* on Twin Cays and Man-of-War Cay parallels a nutrient gradient, with the dwarf plant form (architecturally most simple) produced at the most nutrient-poor sites

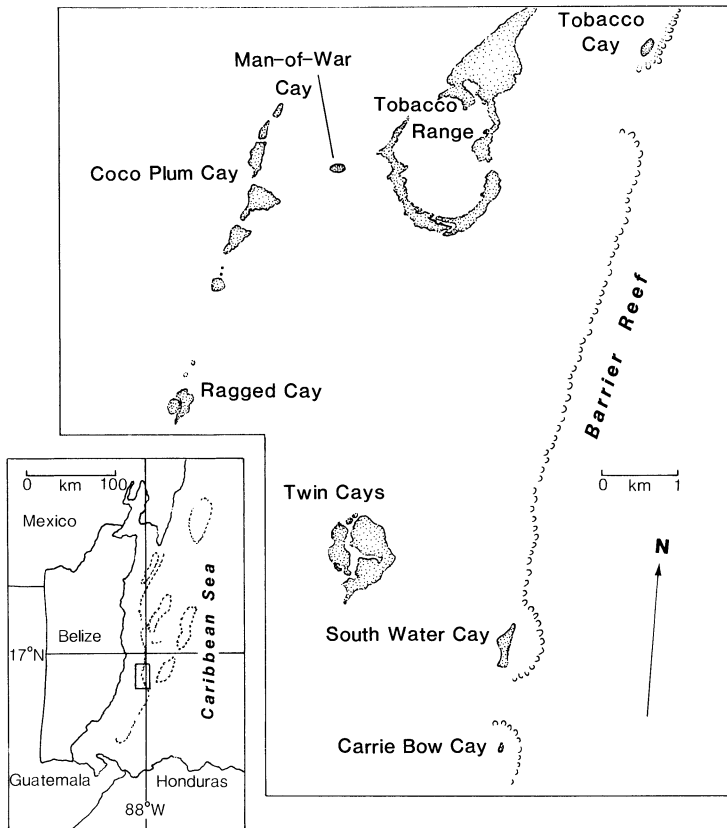


FIGURE 1. Locations of Twin Cays and Man-of-War Cay inside the crest of the barrier reef off the coast of central Belize.

and the tall plant form (architecturally most complex) at a constantly fertilized rookery site. Based on long-term fertilization studies, the dwarf trees in the interior of Twin Cays are phosphorus limited (Feller 1995).

Tall, fringe, and dwarf *R. mangle* trees are distinguishable by other attributes of vigor in addition to tree height. In describing *R. mangle* growth patterns, Gill and Tomlinson (1971) gave leaf number, internodal length, flowering, and branching frequency as indicators of vigor. On Twin Cays, twigs on dwarf trees produce 1–2 pairs of leaves per year, and lateral branching and flowering are infrequent. Twigs have congested internodes with approximately 3–4 pairs of well-preserved leaf scars per centimeter, and 3–4 pairs of leaves in close succession at the most distal portion of a twig (Feller 1995). Based on leaf scar counts and leaf production rates, many trees in the dwarf stands at Twin Cays are over 50 yr old (Feller 1995). Fringe trees at Twin Cays exhibit similar characteristics of low

vigor, *i.e.*, congested internodes and infrequent branching. The tall *R. mangle* trees at the Man-of-War Cay rookery display characteristics associated with increased vigor, *i.e.*, rapid growth, elongate internodes, and frequent lateral branches (Gill & Tomlinson 1971). Branches of young *R. mangle* trees (hereafter saplings) growing along lee shores of interior ponds also exhibit these vigorous growth patterns; however, tall trees are older and have many more twigs and more orders of branch reiteration than do saplings.

We sampled in four architectural categories of *R. mangle* based on tree height: 1) dwarf trees (1–1.5 m) growing in shallow ponds in the interior of Twin Cays; 2) fringe trees (3–6 m) growing along the seaward margins of Twin Cays; 3) tall trees (10–13 m) growing on Man-of-War Cay; 4) saplings (1–1.5 m) at Twin Cays. Although saplings are similar in height to dwarf trees, they have vigorous growth attributes more similar to tall trees, *i.e.*, long internodes and frequent branching. This

category was included to isolate the height or size component *per se* of *R. mangle* architecture as the determining factor for herbivory. The sapling and dwarf categories are non-overlapping and are readily distinguishable based on growth rates, internodal lengths, branching patterns, and leaf area index (Feller 1995). For this study, we located 10 stands of saplings along the lee shores of shallow, interior ponds at Twin Cays. These areas are enriched with allochthonous input of organic material composed of decomposing algae from adjacent ponds.

To characterize trees in the four categories by attributes in addition to height, we determined branch reiterations, numbers of living and dead twigs, and leaf area per tree. Estimates were based on 30 trees per category. Branch reiteration was counted as the number of branching events between the bole and the leaf-bearing twigs. To estimate the number of twigs per tree, we multiplied the total number of primary branches per tree by the total number of twigs (living and dead) on one primary branch. To determine what constituted a primary branch, the canopy of each tree in this survey was subdivided into approximately equal-sized parts, based on visual inspection. For the dwarf, fringe, and sapling trees, we were able to select randomly the primary branches on which to count twigs. However, because of the height of the tall trees, we had to count twigs on primary branches that could be visually silhouetted from the tops of the buttressing prop roots. To determine dead twigs per tree, we multiplied the number of dead twigs on a primary branch by the number of primary branches per tree. To estimate leaf area per tree, we multiplied mean leaf area per twig by the number of twigs per tree. Leaf area was measured with a LI-COR 3000 portable leaf area meter (Li-Cor, Inc., Lincoln, NE, USA), and means are based on 30 leaf-bearing twigs haphazardly selected per tree-height category. To describe stand characteristics, we measured tree density and bole diameter (immediately above the uppermost buttressing prop root) in three 25 m² plots/category. From these data, we estimated mean stand density (stems/ha) and basal area (m²/ha) (Snedaker & Snedaker 1984).

For the woody portions of the 30 harvested twigs, we counted nodes, measured total twig and internodal length, and determined wood density. Wood density ($\rho = m/V$) was based on the dry weight and volume of the 5-cm section around the midpoint of each harvested twig. To evaluate nutritional differences in the woody tissue among the four categories, we also measured percent water,

carbon, nitrogen, acid-detergent (ADF) fiber, and neutral-detergent (NDF) fiber.

XYLOVORY STUDY.—We used *R. mangle* twigs killed by stem borers as population indices to compare species richness and herbivory along a tree-height gradient. Because members of the twig-feeding guild cause twigs to die, we used measures of dead twigs or “deadhearts” as equivalent to absolute estimates of the total number of these invading insects (Southwood 1978). A twig was considered “dead” when it lacked leaves and an apical bud. Occupancy of twigs by more than one species of primary xylovore or by more than one individual of the same species was extremely rare (*i.e.*, 5 per 4000 twigs), and thus was overlooked.

We initially collected 10 samples of 100 dead twigs from *R. mangle* stands on Twin Cays and Man-of-War Cay from each of the four tree-height categories: tall, fringe, dwarf, sapling. Only solitary dead twigs (rather than twigs from a larger dead branch) were collected to avoid twigs killed by other feeding guilds. Twigs were removed from the tree at the branch node and were dissected with a pocket knife. We recorded: 1) cause of death (primary twig borer or other); 2) if other, presence or absence of a natural split in the center of the twig; 3) species of twig borer; 4) life phase of twig borer; 5) presence or absence of inquiline and secondary xylovore; and 6) type or species of inquiline. These data were used to calculate the proportion of twigs in the samples that were killed by twig borers. Inquilines were categorized according to their use of the twig, *i.e.*, parasite, predator, nest site, refuge, secondary xylovore. Organisms found in the twigs were preserved in 70% ethanol. Because we have not worked out the life histories of the tortricid, pyralid, and cossid twig borers in *R. mangle*, data for these three species are lumped in a “moth” category. Larvae of these moths are distinguishable, but we are not able to make species determinations based on galleries, frass, and exit holes.

We used the twig-sample data to compare species richness of the twig-feeding guild and to determine the contribution of twig xylovore to overall herbivory among the four tree-height categories. For each category, the proportion of twigs killed by twig borers in the 100-twig samples was multiplied by the mean number of dead twigs per tree to estimate the number of twigs per tree lost to xylovore. These data along with the total number of twigs per tree were used to calculate the proportion of the canopy in each category that was lost to twig borers.

TABLE 1. Stand and tree characteristics, including density (stems/ha), bole diameter (cm), basal area (m²/ha), number of twigs per tree, leaf area (m²) per tree, and number of branching orders of tall trees on Man-of-War Cay, and fringe, dwarf, and sapling trees on Twin Cays, Belize. Values are means \pm 1 SE.

Stand characteristics:	Tree-height categories			
	Tall	Fringe	Dwarf	Sapling
Density	6267 \pm 933	8267 \pm 990	26,600 \pm 8867	25,467 \pm 9590
Bole diameter	14.0 \pm 0.9	6.0 \pm 0.3	2.5 \pm 0.1	2.7 \pm 0.1
Basal area	78.6 \pm 15.7	20.5 \pm 8.6	12.9 \pm 9.1	16.4 \pm 5.8
Twigs	2985 \pm 256	629 \pm 81	48 \pm 6	139 \pm 6
Leaf area	928.9 \pm 70.5	61.6 \pm 21.3	15.3 \pm 7.7	44.6 \pm 18.3
Branching orders	7.4 \pm 0.1	8.3 \pm 0.3	6.3 \pm 0.2	3.7 \pm 0.2

FOLIVORY STUDY.—To determine the contribution of folivory to overall herbivory, we also measured leaf damage in each of the four tree-height categories. Samples of 100 leaves were chosen blindly from the leaves removed from 30 haphazardly selected twigs per category. Tracings of these leaves were measured using AUTOCAD Release 9© 1982. Following the contour of the leaf margin, we reconstructed the complete leaf outline and measured the intact, whole leaf area plus damaged area on each leaf. Values for intact leaf area and damaged area were used to calculate leaf area and percentage leaf area removed. This estimate along with leaf area per twig and number of twigs per tree were used to calculate the amount of leaf area lost per tree to folivores.

STATISTICAL ANALYSES.—Counts of twig-borer species in the 100-twig samples were analyzed as a Kruskal-Wallis nonparametric analysis of variance, using the Systat® 1991 software package for inferential statistics. Nonparametric multiple comparisons (STP) were used to locate significant differences among tree-height categories (Sokal & Rohlf 1981). Frequency distribution of twig-borer species among tree-height categories was analyzed with a G-test for goodness of fit. Variables based on harvested materials, measurements, and proportions were analyzed as a one-factor ANOVA. To analyze for heteroscedasticity, probability plots of all variables and ANOVA residuals were examined. Data were transformed as needed to reduce variance. When an ANOVA found a significant effect, we used the Bonferroni multiple comparison to locate differences among the categories.

RESULTS

CHARACTERISTICS OF THE TREE-HEIGHT CATEGORIES.—Data on stand structure of the tall, fringe,

dwarf, and sapling *R. mangle* trees are presented in Table 1. The stands of dwarf and sapling trees at Twin Cays are similarly stocked, both with over 25,000 stems/ha. They are more than three times as dense as the fringe stands at Twin Cays and more than four times as dense as the tall stands at Man-of-War Cay. Despite having the lowest stand density, the mean basal area (m²/ha) of the tall trees is three to six times greater than for the other categories of trees. Although they have similar height and stand density, saplings have approximately three times more twigs and leaf area as dwarf trees (Table 1). The number of twigs and leaf area per tree show that the architecture of the tall trees is the most complex, followed in order of complexity by fringe, sapling, and dwarf *R. mangle*.

There were no significant differences in the twig length among the four categories, but twigs of tall and sapling trees had significantly fewer nodes than fringe and dwarf trees (Table 2). The number of leaf nodes divided by the number of leaves produced per year provides an estimate of the time interval between branching events. Internodal length of each category was different with the longest internodes in sapling and tall trees. Wood densities for twigs of tall and sapling trees were similar, but twig wood in tall trees was significantly less dense than for fringe and dwarf trees. Percent water content was similar among all four categories of trees. However, the percent N content of the twig wood was significantly different, with similar values for dwarf and fringe that were almost half the values for tall and sapling twigs. Fiber analysis indicated that twigs from tall trees had significantly higher levels of acid-detergent fiber (ADF) than fringe, dwarf, or sapling trees. For neutral-detergent fiber (NDF), tall trees and saplings had significantly higher values than dwarf trees, and NDF values were similar in dwarf and fringe trees.

HERBIVORY RESULTS.—The same species of primary

TABLE 2. Twig characteristics, including wood density (mg/cm), number of nodes per twig, twig length (cm), internodal length (cm), and percent water, acid-detergent fiber (ADF), neutral-detergent fiber (NDF), carbon, nitrogen, for tall trees on Man-of-War Cay, and for fringe, dwarf, and sapling trees on Twin Cays, Belize. Values are means \pm 1 SE. Means with the same letter superscript within a row are not significantly different (ANOVA; $P > 0.05$).

Twig characteristics:	Tree-height categories			
	Tall	Fringe	Dwarf	Sapling
Wood density	0.461 ^a \pm 0.017	0.556 ^b \pm 0.016	0.509 ^b \pm 0.012	0.540 ^{ab} \pm 0.025
Nodes per twig	8.3 ^a \pm 1.0	23.4 ^b \pm 2.3	40.3 ^c \pm 2.9	4.9 ^a \pm 0.4
Twig length	17.92 ^a \pm 0.85	15.70 ^a \pm 0.91	16.47 ^a \pm 1.01	19.78 ^a \pm 1.01
Internodal length	2.39 ^a \pm 0.29	0.83 ^b \pm 0.9	0.44 ^c \pm 0.03	4.40 ^d \pm 0.28
Percent water	61.0 ^a \pm 0.9	54.0 ^a \pm 0.3	55.0 ^a \pm 0.5	59.0 ^a \pm 0.5
Percent ADF	60.23 ^a \pm 7.1	53.87 ^b \pm 8.8	51.5 ^b \pm 7.2	55.20 ^b \pm 13.6
Percent NDF	70.10 ^a \pm 9.5	62.00 ^{bc} \pm 7.9	58.9 ^c \pm 20.3	66.90 ^{ab} \pm 6.7
Percent C	30.00 ^a \pm 1.6	32.12 ^a \pm 9.3	30.07 ^a \pm 0.9	32.11 ^a \pm 12.9
Percent N	0.43 ^a \pm 0.03	0.28 ^b \pm 0.02	0.19 ^b \pm 0.01	0.40 ^a \pm 0.05

twig-boring insects were present in all four categories of *R. mangle* trees sampled on Twin Cays and Man-of-War Cay (Fig. 2). *Pseudoacalles sablensis* was the dominant twig borer in tall- and sapling-tree samples, accounting for almost half of the twigs killed by twig borers in these samples. It was encountered over five times more often in these twig samples than in fringe- or dwarf-tree samples. Although *M. rhizophorae* was common in all the tree-height categories, this cerambycid was the dominant twig borer in the fringe and dwarf stands. The other two cerambycids, *A. alveolatum*

and *A. cayensis*, were present at consistently low levels in all categories. Distribution of the three moth borers was variable among the four categories, ranging from 2 to 18 per 100 twigs and accounting for 8.5–26.0 percent of the twigs killed by twig borers. However, there were no significant differences in the overall frequency distribution of these twig borers among the four tree-height categories (G -test: $X^2 = 16.312$, $df = 12$, $P > 0.05$).

Although the same set of twig-borer species were present in tall, fringe, dwarf, and sapling trees, there were significant differences among tree-height

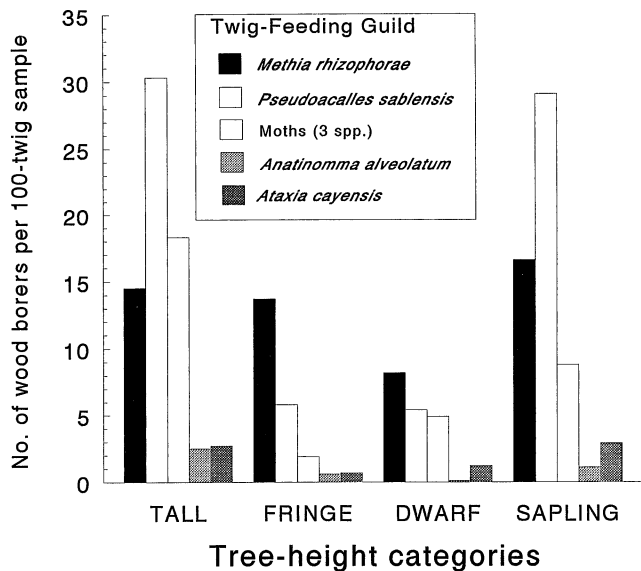


FIGURE 2. Occurrence of the twig-feeding guild (*Methia rhizophorae*, *Pseudoacalles sablensis*, 3 moths, *Anatinomma alveolatum*, and *Ataxia cayensis*) in *Rhizophora mangle* tall, fringe, dwarf, and sapling trees, based on 10 samples of 100 twigs from each tree-height category.

categories in the levels of herbivory attributable to indirect removal of leaf tissue via twig death caused by these primary xylovores, (Fig. 3A; ANOVA: $F = 6.830$, $df = 3$, $P < 0.001$). The percent of twigs lost per tree to twig borers in dwarf trees was significantly lower than in sapling or tall trees. However, dwarf and fringe trees suffered similar levels of this type of loss. Our data show that despite large differences in architectural complexity (Table 1), twig xylovores among tall, fringe, and sapling trees was similar. Although percent C, N, wood density, and fiber content of twigs varied significantly among the four categories of trees (Table 2), there were no significant correlations between twig xylovores and these variables.

There were also significant differences among the tree-height categories in the levels of herbivory attributable to direct removal of leaf tissue by folivores (Fig. 3B; ANOVA: $F = 9.013$, $df = 3$, $P < 0.001$). The tall trees at Man-of-War Cay lost almost 8 percent of their canopy to folivory, which was significantly higher than in any of the other tree-height categories. The fringe, dwarf, and sapling trees at Twin Cays all suffered similar levels of damage by folivores. Because both xylovores and folivores are responsible for loss of portions of the leafy canopy, we combined estimates of the damage caused by these two feeding guilds to provide a more complete picture of herbivory in *R. mangle* (Fig. 3C). Combined values range from approximately 6 percent in dwarf trees to almost 16 percent in tall trees. The cumulative herbivory by leaf feeders and twig borers in tall trees was approximately twice the level measured in dwarf and fringe trees and 40% greater than the level measured for saplings.

SECONDARY USE OF TWIGS.—Secondary use of dead *R. mangle* twigs by arthropods was not evenly distributed among the tree-height categories (Kruskal-Wallis test: $H = 14.47$, $df = 3$, $P \leq 0.002$). Tall-tree twigs on Man-of-War Cay were reutilized by inquilines significantly more frequently than were twigs in either fringe or dwarf trees on Twin Cays (Nonparametric multiple comparison (STP): $U = 93.5$ (fringe), $U = 85.5$ (dwarf), critical $U = 83.98$; $P < 0.05$). The sapling category overlapped all other tree types in frequency of reutilization. Furthermore, we found approximately twice as many types of inquilines in tall trees as in fringe or dwarf. Also, individual tall-tree twigs commonly housed two or three different species of inquilines, e.g., ants, isopods, and scales or roach egg case and centipedes, etc., whereas fringe and dwarf twigs

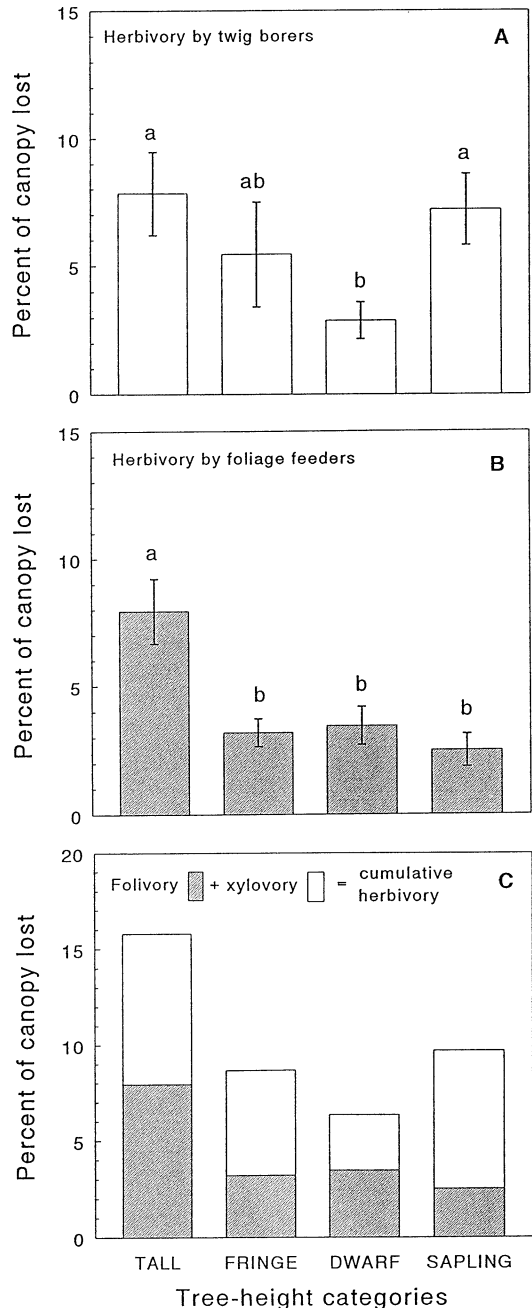


FIGURE 3. Percent of canopy lost (means \pm 1 SE) from tall, fringe, dwarf, and sapling *Rhizophora mangle* trees as a result of (A) primary herbivory by twig borers, (B) herbivory by foliage feeders, and (C) cumulative herbivory by both twig xylovores and folivores. Levels of damage are based on ten 100-twig samples per category. Within a graph, bars with the same letter are not significantly different (ANOVA; $P > 0.05$).

TABLE 3. Summary of inquiline distribution in hollow *Rhizophora mangle* twigs in tall, fringe, dwarf, and sapling trees. If a twig contained a hollow space, it was characterized as either a wood borer's gallery or a natural split. Values are means based on 10 samples of 100 twigs in each category.

	Tree-height categories			
	Tall	Fringe	Dwarf	Sapling
Twigs with galleries	54.7	22.2	16.9	49.7
Twigs with natural splits	15.3	56.3	61.8	21.6
Inquilines in galleries	23.0	5.8	5.9	14.6
Inquilines in natural splits	1.8	3.1	3.7	1.8
Inquilines in galleries (%)	93.5	64.2	56.1	88.5
Inquilines in natural splits (%)	6.5	35.8	43.9	11.5
Galleries with inquilines (%)	42.4	26.1	34.9	29.4
Natural splits with inquilines (%)	11.3	5.5	6.0	8.3

typically housed a single species of inquiline. Sapling twigs housed 80 percent as many inquiline types as tall trees, but a given twig rarely contained more than one inquiline species.

Although both vacated wood-borer galleries and natural splits in *R. mangle* twigs housed inquilines, our data show that inquilines were not evenly distributed among these two types of hollow twigs (Table 3). On average, 56–94 percent of the inquilines occurred in galleries rather than in natural splits. Among all the tree-height categories, 26–42 percent of the wood-borer galleries that we found were being used by inquilines, compared to 6–11 percent of the naturally split twigs. Twigs with galleries were significantly more frequently inhabited by inquilines than were naturally split twigs in each category: (Tall: $X^2 = 49.42$, $P < 0.001$; Fringe: $X^2 = 44.19$, $P < 0.001$; Dwarf: $X^2 = 110.19$, $P < 0.001$; Sapling: $X^2 = 15.78$, $P < 0.001$).

Because twig-nesting ants are the numerically dominant group of insects in mangrove systems (Cole 1983) and were the most consistently encountered inquiline group in hollow *R. mangle* twigs at our sites, we evaluated their preferences for galleries vs. naturally split twigs. In each tree-height category, between 10–15 percent of the wood-borer galleries were occupied by ants, whereas only 1–4 percent of the naturally split twigs were occupied by ants. For all categories, significantly higher proportions of the ants present were in twigs with wood-borer galleries rather than in twigs that had split naturally (Tall: $X^2 = 10.59$, $df = 1$, $P < 0.001$; Sapling: $X^2 = 15.17$, $df = 1$, $P < 0.001$; Fringe: $X^2 = 22.60$, $df = 1$, $P < 0.001$; Dwarf: $X^2 = 15.36$, $df = 1$, $P < 0.001$). In tall and sapling trees, over 90 percent of the twig-dwelling ants that we found were in galleries made by wood borers. In fringe and dwarf trees, fewer twigs

housed ant colonies, and they were nearly evenly distributed among natural splits and galleries. However, many more fringe and dwarf twigs were split naturally than were hollowed by wood borers.

Because several inquiline species are potential predators, (e.g., spiders and clerids) or parasitoids (Hymenoptera) on the twig borers, they may influence primary xylovoxy of the twigs. Secondary utilization of dead twigs by potential natural enemies (exclusive of ants) of the primary xylovores was evenly distributed among the four categories of trees (Kruskal-Wallis Test: $H = 5.43$, critical $X^2 = 7.815$, $df = 3$, $P > 0.05$). If ants are included as part of the set of predators, secondary utilization by potential natural enemies was still not significantly different among the four tree types (Kruskal-Wallis test: $H = 6.18$, $df = 3$, $P > 0.05$). Our data may underestimate the amount of secondary twig utilization because some of the secondary occupants, e.g., spiders, are quite mobile and may have escaped from samples before twigs could be tallied. We assume this possibility to be a variable common to all samples.

DISCUSSION

PRIMARY WOOD-BORERS IN *RHIZOPHORA MANGLE*.—In contrast with other lowland tropical forests, mangrove forests are often cited for their lack of species richness, not only plant species but the associated fauna also. Nevertheless, *R. mangle* in Belize does host numerous insect species, including specialized species of primary wood-boring insects (Chemsak 1982, Chemsak & Feller 1988, Rützler & Feller 1988, 1996, in press; Feller 1995). Of these, a seven-member feeding guild of twig borers mine twigs. Larval stages of each of these borers feed lengthwise down the center of a twig, killing the twig and creating a hollow cylinder of wood in the

process. Vast monospecific stands of *R. mangle* provide an essentially unlimited food source for these insects. Although adult wood-borers are rarely collected, larvae along with their effects and products can be used to evaluate xylovoxy. It became obvious during this study that *R. mangle* loses considerable amounts of its leaf area as an indirect consequence of xylovoxy. For example, a tree loses 100 percent of the leaves on every twig attacked by a twig borer. Furthermore, because this type of damage destroys the apical meristem, it also loses any future wood and leaf production by that twig. Risley and Crossley (1988) made a similar observation with respect to greenfall in the southern Appalachians; they cautioned that failure to consider this collateral source of leaf loss may cause herbivory to be underestimated. Based on our data, leaf loss because of twig borers in the twig-feeding guild is equal to or greater than the amount lost to folivores.

TREE ARCHITECTURE AND LEVELS OF XYLOVOXY.—Twig xylovoxy in the guano-fertilized, tall trees on Man-of-War Cay is three times higher than in the fringe and dwarf *R. mangle* on Twin Cays. Although the highest measure of twig xylovoxy occurred in the most architecturally complex stand of *R. mangle* in our study, that measure was not significantly different from Twin Cays' sapling stands, which are more similar in architecture to dwarf trees. Likewise, dwarf trees experienced a similar level of twig xylovoxy to fringe trees. Consequently, the height or size component *per se* of plant architecture does not explain these differences and similarities in the level of xylovoxy by *R. mangle*'s twig borers in our study areas. Because all trees on both Twin Cays and Man-of-War Cay hosted the same set of twig xylovores, xylovoxy differences are not due to differences in xylovoxy availability or habitat. Further, variation in xylovoxy cannot be explained by differential predation because all tree-height categories had similar occurrences of potential predators and parasitoids.

The patterns of damage by primary twig borers in *R. mangle* are more consistent with the plant-vivory hypothesis, which predicts increased herbivory by specialized, endophytic insects in the more vigorous plants or plant modules in a population (Price 1991). The tall and sapling trees sampled in this study have very localized sources of nutrient enrichment (*i.e.*, bird guano at the tall tree stand at Man-of-War Cay and algal compost at sapling stands on Twin Cays) and display vigorous growth characteristics (Table 2). In contrast, fringe and dwarf trees on Twin Cays lack these sources of en-

richment and exhibit suppressed growth characteristics. In a fertilization experiment of dwarf *R. mangle* trees at Twin Cays, increased availability of phosphorus resulted in vigorous growth pattern similar to the tall and sapling categories, *e.g.*, increased number of leaves, twigs, and aerial roots, leaf area per twig, and internodal length (Feller 1995). Although nutrient enrichment caused significant increases in phenolics and decreases in leaf toughness, Feller (1995) reports that damage by leaf-feeding herbivores dominated by a group of generalist feeders was unchanged. However, herbivory by two specialized endophytic insects, *i.e.*, a bud moth and a stem miner, increased dramatically in phosphorus-fertilized trees.

TREE ARCHITECTURE AND DIVERSITY.—Species richness of primary twig borers is essentially uniform for tall, fringe, dwarf, and sapling *R. mangle* trees. Despite many-fold differences in height (1 m *vs.* 13 m), and resource diversity (*i.e.*, number of twigs, structure of branching, internodal length, and leaf distribution), dwarf mangrove trees host the same species of twig borers as tall trees. Perhaps determining composition and abundance of a single feeding guild (*e.g.*, twig-feeding or leaf-feeding) is insufficient to evaluate the effects of intraspecific architectural differences of a host plant on herbivore diversity. It may be that *R. mangle* twigs become saturated as a habitat for primary xylovores at about seven species. A complete faunal list that also includes primary folivores for each architectural type may confirm Lawton's (1983) prediction that more complex, intraspecific plant forms should support more species. If secondary phytophages and inquilines are considered, tall trees support a richer fauna than fringe or dwarf trees. However, species richness in fringe and dwarf trees still does not differ with respect to inquilines, and saplings support an inquiline fauna more similar to tall trees.

HABITAT VALUE OF TWIGS.—To our knowledge, more species are associated with *R. mangle* twigs than with any other single arboreal habitat in Belizean mangrove swamps. Besides supporting primary xylovores, twigs hollowed by wood borers are used as nest sites by ants and spiders, as diurnal refuges by nocturnal insects, as food sources by numerous dead-wood feeders, as prey sites for predators, and as host sites for parasites. Tall trees that have the highest level of twig xylovoxy also have the highest incidence and diversity of twig inquilines. These data suggest that the twig-feeding guild

has a key role in structuring Belizean mangrove communities by making *R. mangle* twigs a suitable habitat for numerous inquilines and secondary phytophages.

HABITAT EFFECTS OF TWIG BORERS ON LEAF FALL.—In Belize, large stands of dwarf trees vegetate huge areas behind a dense, marginal fringe of *R. mangle*. A dwarf tree has, on average, 48 twigs so that loss of just one twig to a twig borer accounts for ≈ 2 percent of its total leaf surface; whereas, evaluation of leaf area damaged or removed by folivores indicates that only 3–6 percent has been lost to a suite of folivores (Feller 1995). Unlike tall and sapling trees, dwarf trees seldom branch so they cannot overcome the loss. Unbranched, first-order branches with 40+ consecutive pairs of leaf scars that produce two to three pairs of leaves per year are evidence that no branching has occurred in approximately 13 to 20 yr. From this, it seems that dwarf trees, in particular, are at great risk from primary wood borers. Yet, it is interesting to note that many of these little trees have survived wood borers as well as hurricanes and are more than 50 yr old (Feller 1995). For example, in 1961, Hurricane Hattie killed and flattened most of the larger *R. mangle*, *A. germinans*, and *L. racemosa* on many Belizean cays (Stoddart 1963), but entire stands of the dwarf *R. mangle* trees survived, relatively unscathed.

CONCLUSION

This study demonstrates that to appreciate the diversity of insects associated with mangroves it is necessary to look beyond the leaf surface. Based on the evidence presented here, arboreal, wood-boring insects play important roles as primary xylovores in Belizean mangrove swamps. Infestation by wood

borers is extensive regardless of architectural complexity. Any evaluation of insect species richness, insect-plant interactions, community structure, or the effects of insect herbivory on primary productivity in mangrove systems should take the activities of wood borers into account. Differential levels of xylovores among tall, fringe, dwarf, and sapling trees do not support the architectural complexity hypothesis (Lawton 1983). The pattern of xylovores that we measured across this tree-height gradient is more consistent with the plant-vigor hypothesis (Price 1991). Further investigations are needed to determine the underlying causes for differential twig xylovores in *R. mangle* on Belizean mangrove cays. However, the explanation probably lies in the physical and chemical differences in plant tissues resulting from the impact of localized, environmental gradients on resource availability for tree growth.

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