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Patterns of Herbivory in Belizean Mangrove Swamps[1]

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ABSTRACT

We quantified herbivory on leaves of two mangrove species, *Rhizophora mangle* and *Avicennia germinans,* at eight sites in Belize. Amounts and types of damage were compared among three mainland sites and five mangrove cays off the coast. Several environmental and autecological factors that potentially influence herbivory were examined, including canopy cover, tree age, leaf age, tidal height, and nutrient enrichment. Herbivores damaged 4.3 percent to 25.3 percent of *Rhizophora* leaf area and 7.7 percent to 36.1 percent of *Avicennia* leaf area, figures comparable to other mangal throughout the world. On average, *Avicennia* was less frequently damaged than *Rhizophora* at all sites but one. Herbivory at a bird rookery was not significantly higher than elsewhere, indicating that nutrient enrichment of leaves did not stimulate herbivory at this site. Significant but inconsistent differences in damage were detected between the cays and mainland sites. Significant differences, dependent on tidal height, were found between seedlings and trees. *Rhizophora* seedlings growing under a canopy of adult conspecifics suffered twice as much damage as seedlings growing in areas where the adult canopy was removed. Damage types occurring on each species were consistent across all sites, but the two species did not share the same herbivores.

RESUMEN

Se ha cuantificado la herbivoría en las hojas de dos especies de manglar, *Rhizophora mangle* y *Avicennia germinans.* Cantidades y tipos de daño fueron comparado entre 3 sitios en el continente e 5 cayos de manglares lejanos de la costa. Examinamos algunos factores que pueden ejercer influencia sobre la herbivoría: la cubierta del dosel, la edad de los árboles, la edad de las hojas, el nivel de la marea, y el enriquecimiento de los nutrientes. Los herbívoros dañaron de 4.3% a 25.3% de la área de las hojas de *Rhizophora,* y de 7.7% a 36.1% de la área de las hojas de *Avicennia.* Estos resultados son comparables con los resultados recogidos en otros sitios del mundo. Por término medio, *Avicennia* fue menos dañada en todos los sítios, con una excepción. La herbivoría en una colonía de pájaros no sobrepasó la herbivoría en otras partes. Este resultado indica que el enriquecimiento de nutritivos no estimuló la herbivoría en este sítio. No descubrimos diferencias significativas entre los sítios de los cayos y el continente. En cambio, se observaron diferencias significativas entre los arbolillos y los árboles, pero estas diferencias fueron dependientes del nivel de la marea. Los arbolillos de *Rhizophora* que crecieron debajo de un dosel del árboles de la misma especie sufrieron el doble del daño de los arbolillos que crecieron donde el dosel fue removido. Los tipos de daño fueron consistentes en todas partes. Las dos especies no compartieron los mismos herbívoros.

STUDIES OF HERBIVORY IN TERRESTRIAL TROPICAL FORESTS have attempted to identify host plant properties that influence herbivore foraging preferences: plant apparency (Feeny 1976), host plant quality and secondary chemistry (Coley 1983 and references therein) and community composition (*e.g.,* polycultures *vs* monocultures, Denno & McClure 1983). Coastal mangrove forests provide a very tractable system in which to study the dynamics of herbivory. The comparatively simple structure of mangrove communities allows one to ask whether damage patterns observed on neotropical coastlines support predictions about herbivory based on host plant characteristics and island biogeography theory (MacArthur & Wilson 1967, Simberloff 1967).

In this report, we document levels of herbivory found in two species of mangroves, *Rhizophora mangle* L. and *Avicennia germinans* L. (throughout the text, these species will be referred to generically). We examined the relationship between herbivory and several autecological characteristics of these trees: relative tree age, proximity to neighbors, location with respect to tidal height, presence of a canopy, and leaf age and height above substrate. Comparisons were made among the amounts and types of

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herbivory occurring in mainland and island sites. Where possible, herbivores responsible for particular damage types were identified, allowing us to compare the relative importance of different groups of herbivores on the two species and to obtain a preliminary picture of herbivore community structure (*sensu* Okelo 1985).

In examining herbivory in Belizean mangroves, we addressed eight questions: Do damage types and amounts differ among islands and the mainland? Is there a relationship between island size and levels of herbivory? Is herbivory correlated with island distance from the mainland? These three related questions address how damage patterns, as indicators of herbivore densities and diversity, vary among island and mainland sites. Island biogeography theory predicts that offshore cays would be depauperate of herbivorous fauna (Simberloff 1967, MacArthur & Wilson 1967, Okelo 1985, Schoener 1988). Likewise, one might expect that smaller islands would support a less diverse fauna.

Within a site, do damage types and amounts vary across a tidal gradient? *Rhizophora mangle* occurs broadly from lowest low water (LLW) to highest high water (HHW). Herbivores feeding on trees that are constantly inundated by sea water may face different constraints of access, movement, and leaf chemistry from herbivores on trees that are rarely flooded.

Do damage types and amounts differ between the two species of mangrove? Previous studies of herbivory in Australasian and neotropical mangroves have raised questions about interspecific variability in damage (Onuf *et al.* 1977, Beever *et al.* 1979, Johnstone 1981, Lacerda *et al.* 1986, Robertson & Duke 1987, Smith *et al.* 1989). Different levels of herbivory between the two species could result from variation in leaf palatability, texture, chemistry, or nutrient content. Certain herbivore species assemblages may be restricted to either *Avicennia* or *Rhizophora* if host-switching is precluded by different suites of secondary defenses.

Do damage types and amounts differ between seedlings and mature trees? Another host plant feature known to influence herbivory is plant age (Coley 1983). Newbery (1980) found that infestation by a coccid, *Icerya seychellarum,* was less frequent on young *Avicennia marina* trees than on older individuals. Lacerda *et al.* (1988) found that levels of macronutrients, heavy metals and antiherbivore compounds change as *Rhizophora* propagules and seedlings develop. The performance of new seedlings may be impaired by herbivores (Smith *et al.* 1989), with consequences for community succession.

Does the presence of an adult canopy influence herbivory on mangrove seedlings in the understory? The foraging behavior of herbivores may be influenced by the local light environment (Coley 1983). Herbivores may prefer shaded leaves because these provide a cooler substrate or a refuge from visual predators. Lacerda *et al.* (1986) suggested that mangroves, as "sun" plants with long-lived leaves, may experience less herbivory than "shade" plants. Plants operating at a photosynthetic surplus may produce higher concentrations of secondary defensive compounds.

Do herbivores concentrate on *Rhizophora* leaves of a particular age class? As individual leaves age, their nutrient content may decline and their cumulative concentration of secondary compounds may increase, rendering the tissue less palatable to herbivores (Crawley 1983, Harborne 1982). We wished to determine whether herbivores preferentially attacked younger leaves. Such activity could hinder the production of new biomass by trees and seedlings, and has important implications for plant growth.

STUDY SITE AND METHODS

SITE DESCRIPTIONS.—Figure 1 depicts the location and coordinates of all sites surveyed. Mainland herbivory censuses were conducted from March to April 1988 and November to December 1988 in Placencia Lagoon, Point Placencia, Stann Creek District, Belize. This lagoon is shallow (< 1.5 m deep), tidal, and brackish; salinity values fluctuate between 12 ppt to 34 ppt (Ellison & Farnsworth, in press). Daily tidal amplitude throughout coastal Belize is ~30 cm (Rützler & MacIntyre 1982). Mangroves in Placencia Lagoon exhibit a distinct zonation of species and morphology correlated with tidal height, similar to that noted elsewhere (MacNae 1967, Lugo & Snedaker 1974). From LLW to mean water (MW), *Rhizophora* forms a monospecific stand from 20 to several hundred meters wide. Above MW, the community consists of a mixture of *Avicennia, Rhizophora,* buttonwood (*Conocarpus erectus* L.), and scattered white mangroves (*Laguncularia racemosa* (L.) Gaertn.). Above HHW the dominant vegetation comprises palmetto, *Paurotis wrightii* (Griseb. & Wendl.) Britt., on quartz sand. Only *Rhizophora* and *Avicennia* were studied at Placencia because other species were relatively uncommon. Two additional sites, "Big Creek" and "Placencia Channel" (our nomenclature; Fig. 1) were also surveyed to obtain an estimate of variability in herbivory levels among LW mangrove trees on the mainland.

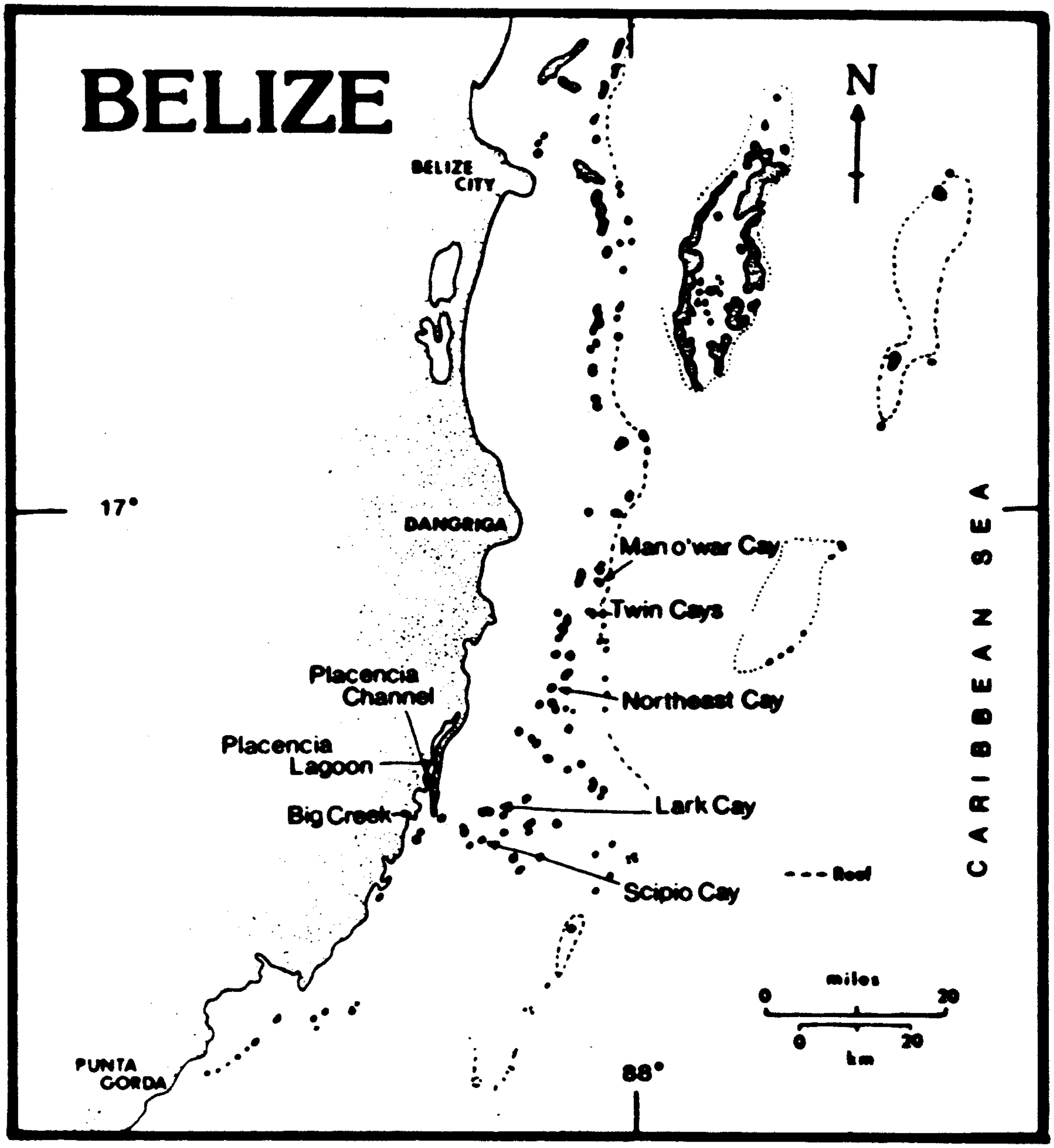

FIGURE 1. Map of coastal Belize with sampled locations. Approximate areas of cays and their distances from mainland, respectively, are as follows: Twin Cays (100 ha, 16 km); Lark Cay (3 ha, 11 km); Scipio Cay (1.7 ha, 13 km); Northeast Cay (5 ha, 19 km); Man O'War Cay (2 ha, 17 km).

The 250-km-long barrier reef complex off the coast of Belize is the largest continuous reef in the Caribbean Sea (Stoddart *et al.* 1982). Numerous cays dominated by *Rhizophora* occur between the reef and mainland. We surveyed mangroves on five separate cays in a 60 km north-south strip at various distances from the coast (Fig. 1). We later regressed our damage figures on island size and distance from the mainland.

Man O'War Cay (Fig. 1) is of particular interest in this study because it contains a rookery of Brown Boobies, *Sula leucogaster,* and Magnificent Frigatebirds, *Fregata magnificens.* The deposition of bird guano creates conditions of localized nutrient enrichment (Kohlmeyer 1986), reflected in the large size of both *Rhizophora* and *Avicennia* on the island. Onuf *et al.* (1977) reported that guano-enriched *R. mangle* in Florida lost significantly more leaf biomass to herbivores. We quantified herbivory at Man O'War Cay in July 1988 to assess effects of possible enrichment on leaf damage.

HERBIVORE IDENTIFICATION.—Herbivores were identified and linked with damage types whenever possible. Collections, photographs, and identifications to lowest possible taxon of herbivores were made when they were observed in the act of foraging. Insects were captured by hand, as sweeps with insect nets proved unsuccessful in the dense vegetation. Collections and observations of nocturnal herbivores were made on seven separate dates during 1988 in Placencia Lagoon. Herbivores, as we came to use the term, encompassed all organisms responsible for foliar damage, including insects, the mangrove tree crab, *Aratus pisonii* (Warner 1967), and the mangrove periwinkle, *Littorina angulifera* L. (Coomans 1969, Kohlmeyer & Bebout 1986).

TREE SAMPLING PROTOCOL.—*Rhizophora* occurred and was sampled for herbivory at all locations, while *Avicennia* was sampled only at HHW sites where it occurred (Placencia Lagoon, Twin Cays, Lark Cay, and Scipio Cay). At each tidal height where they were found, five to ten trees of each species were selected haphazardly for census. On each tree, we chose up to eight branches oriented in one of the four cardinal compass directions at varying heights above the substrate. Height of the midpoint of the branch (from main stem to tip) above the substrate and the compass bearing of the branch were recorded.

To quantify leaf area and damage we laid a clear plastic grid of 5 × 5 mm squares over each leaf and counted the number of squares occupied by the leaf and by each damage type (*cf.* Coley 1983, Ernest 1989). Where edges of a leaf were missing, we visually reconstructed leaf margins by extrapolating from the intact margins. Nearly symmetrical red and black mangrove leaves (Tomlinson 1986) allow for a reliable estimate of area even if only half of the leaf remains. Repeated impromptu checks of leaf areas by pairs of observers revealed high replicability in counts.

Damage types were categorized on the basis of qualitative visual distinctions. Damage defined as bites were incursions occurring along the leaf margin. Holes were punctures or openings enclosed within the leaf. Trails were made by leaf miners and other insects excavating tissue. Necrotic spots and scars were described by color: brown, black, or white.

Because leaves develop in recognizable pairs in both *Rhizophora* and *Avicennia,* it was possible to record missing leaves on the basis of leaf scars (Lowman 1984). The majority of missing leaves occurred in older leaf pairs (Farnsworth, pers. obs.), and their disappearance may have been due to senescence and not herbivory. Missing leaves were thus excluded in our analyses of herbivory.

TIDAL ZONE AND HERBIVORY.—*Rhizophora* trees and seedlings were surveyed for herbivory at all three tidal zones at Placencia Lagoon; *Avicennia* trees and seedlings were examined at the HHW zone. Trees and seedlings at other locations were surveyed at all zones in which they occurred in sufficient numbers for sampling.

STATISTICAL ANALYSES OF SITE COMPARISONS.—For purposes of comparison, individual leaf damage was calculated as the fraction of total leaf area showing damage. Resulting percent damage figures were arcsin square root transformed prior to analysis to normalize and equalize variances (Sokal & Rohlf 1981).

Overall mainland–island comparisons were analyzed using ANOVA. A two-way design, LOCATION (island or mainland) × TIDAL ZONE (LW or HHW), assessed main effects. Although ideally, a nested MANOVA should have been used to address the significance of within LOCATION variation (*i.e.,* five island sites nested within ISLAND and three mainland sites nested within MAINLAND), mangroves did not occur in both tidal zones at all sites. The consequent occurrence of empty cells in the nested design therefore precluded analysis of within-LOCATION variance in the overall ANOVA. We tested for within-LOCATION differences using one-way ANOVAs (site as main effect, MAINLAND and ISLAND considered separately) on total percent damage, and *a posteriori* Scheffé tests for multiple comparisons among means. Because only *Rhizophora* occurs in all tidal zones, interzone comparisons were only examined for this species. All statistics were performed using SPSS/PC+ v2.0 (Norusis 1988).

HERBIVORE DAMAGE TO SEEDLINGS.—Seedlings of both species were surveyed, as above, at two sites: Placencia Lagoon and Twin Cays. We defined *seedlings* as established shoots <0.5 m tall that possessed no branches and (for *Rhizophora*) where the fleshy hypocotyl was still visible. At Placencia Lagoon, 6 LW *Rhizophora* seedlings ($N = 45$ leaves), 13 MW seedlings ($N = 63$ leaves) and 12 HHW zone seedlings ($N = 70$ leaves) were surveyed *in situ.* Twelve *Avicennia* seedlings were examined in the

HHW zone ($N = 75$ leaves). At Twin Cays, 12 *Avicennia* seedlings (HHW, $N = 199$ leaves), 6 MW *Rhizophora* seedlings ($N = 83$ leaves) and 6 LW *Rhizophora* seedlings ($N = 63$ leaves) were censused for herbivory. No HHW *Rhizophora* seedlings were available at that time for census. Seedling height, number, and relative age (leaf pair) of missing leaves, status of growing tip, and distance to nearest neighbor were recorded for all seedlings.

To assess age effects, the percent damage to seedlings was compared to damage in mature trees within each zone using two-tailed t-tests.

PRESENCE OF A CANOPY AND SEEDLING HERBIVORY.—We also investigated levels of herbivory in seedlings under two light regimes. In February 1988 five 3 × 3 m quadrats were established under adult mangroves in the MW zone at Placencia Lagoon. All quadrats contained at least 40 *Rhizophora* seedlings growing naturally in the understory. The canopy of mature *Rhizophora* was removed with a machete in three of the quadrats; the other two quadrats were designated as controls. In December 1988 all seedlings were harvested and leaves scored for herbivory as described above ($N = 667$ leaves).

VARIATION IN LEAF DAMAGE WITH LEAF AGE.—Position of leaf pair on a terminal branch was used as an index of relative leaf age for *Rhizophora*; the terminal leaf pair was defined as leaf pair #1. Young leaves are positioned near the branch tip, and successively older leaves lie farther back along the branch. We recorded relative leaf age in terms of leaf pair number, and regressed leaf damage on leaf pair number. Frequent lateral branching of *Avicennia* twigs along a branch did not permit a similar index for this species.

RESULTS

DAMAGE TYPES AND HERBIVORES OBSERVED.—Figure 2 illustrates some of the herbivores found feeding on mangrove leaves, and the characteristic types of damage they inflicted. Over 66 recognizably different insect foliovores were discovered on mangrove leaves in Placencia Lagoon and Twin Cays during day and evening censuses. The most commonly observed herbivores were Lepidoptera larvae, including *Megalopyge opercularis, Automeris* sp., *Phocides pygmalion pygmalion,* and eight other unidentified specimens, which caused large elongate bites and holes within *Rhizophora* leaves. Coleoptera larvae (principally Chrysomelidae and Lampyridae) also left bites and holes on *Rhizophora* leaves. Homoptera (Blattidae, Cicadellidae, Cercopidae and Diaspididae) caused spots of necrotic tissue on the epidermis of *Rhizophora* and *Avicennia* leaves, often damaging large portions of photosynthetic tissue. Aphids (Homoptera: Aphididae) were occasionally found being tended by ants on *Avicennia* trees in the HHW zone at Placencia, but their contribution to total damage appeared negligible. Unidentified leaf miners created trails that destroyed substantial portions of the epidermal layer in both *Rhizophora* and *Avicennia* leaves. Larvae of unknown identity 0.5-cm-long were commonly found to curl the emerging leaves of *Avicennia* and to feed on leaf tissue while hidden in the curl. Two types of gall-makers were also found on *Avicennia* leaves. *Aratus pisonii,* the mangrove tree crab, destroyed large numbers of flower buds, flowers and emerging leaf tips of *Rhizophora,* although crab herbivory was confined to the LW zone at all locations, and crabs did not appear to attack older leaves. *Littorina angulifera* left distinct brown crescents on *Rhizophora* leaves, apparently by scraping the epidermis with the radula (Kohlmeyer & Bebout 1986).

At no time did we find a single herbivore species feeding on both *Rhizophora* and *Avicennia.* Based on our observations and collections, we conclude that *Avicennia* and *Rhizophora* do not share herbivore species in Belize, even where the two species grow in close proximity.

DISTRIBUTIONS OF DAMAGE TYPES.—Damage to mangrove leaves was divided into discrete categories for the purpose of identifying the herbivores responsible for the various signatures. It then became possible to compare the distributions of different damage types between trees and among sites. Figure 3 shows a typical distribution of the eight most prevalent herbivory categories found in *Rhizophora* and *Avicennia* at Placencia Lagoon. Across both species, bites constituted the most common type of damage. Altogether, bites, holes, and brown spots accounted for 57 percent to 78 percent of all damage in *Avicennia* and 69 percent to 92 percent of all damage in *Rhizophora.*

Distributions of these damage types were remarkably consistent among conspecific adults and seedlings and among the different survey locations, even though total amounts of herbivory differed significantly. G-tests were performed to ascertain intraspecific differences in herbivory types based on age class and location, but revealed no significant differences in any of the possible combinations.

Very different suites of herbivores exploit *Rhizophora* and *Avicennia,* and we could not assume

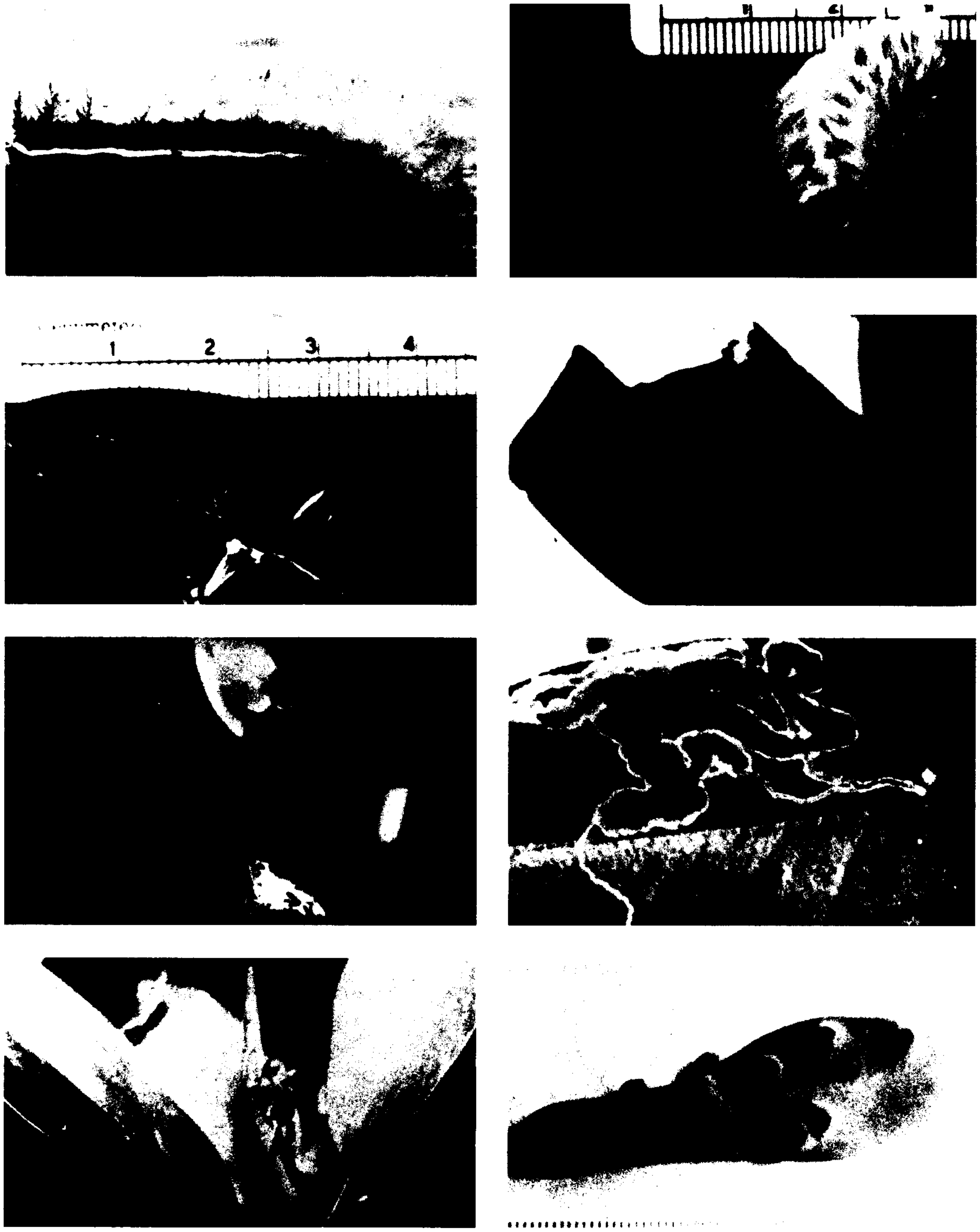

FIGURE 2. Common herbivores encountered on *Rhizophora* and *Avicennia*. Left (top to bottom): *Automeris* sp. on *Rhizophora*; *Phocides pygmalion pygmalion* on *Rhizophora*; bagworm (Lepidoptera: Psychidae) on *Rhizophora*; *Aratus pisonii* on *Rhizophora*. Right (top to bottom): *Megalopyge opercularis* on *Rhizophora*; limacodid moth larva on *Rhizophora*; leaf miners on *Rhizophora*; galls on *Avicennia*.

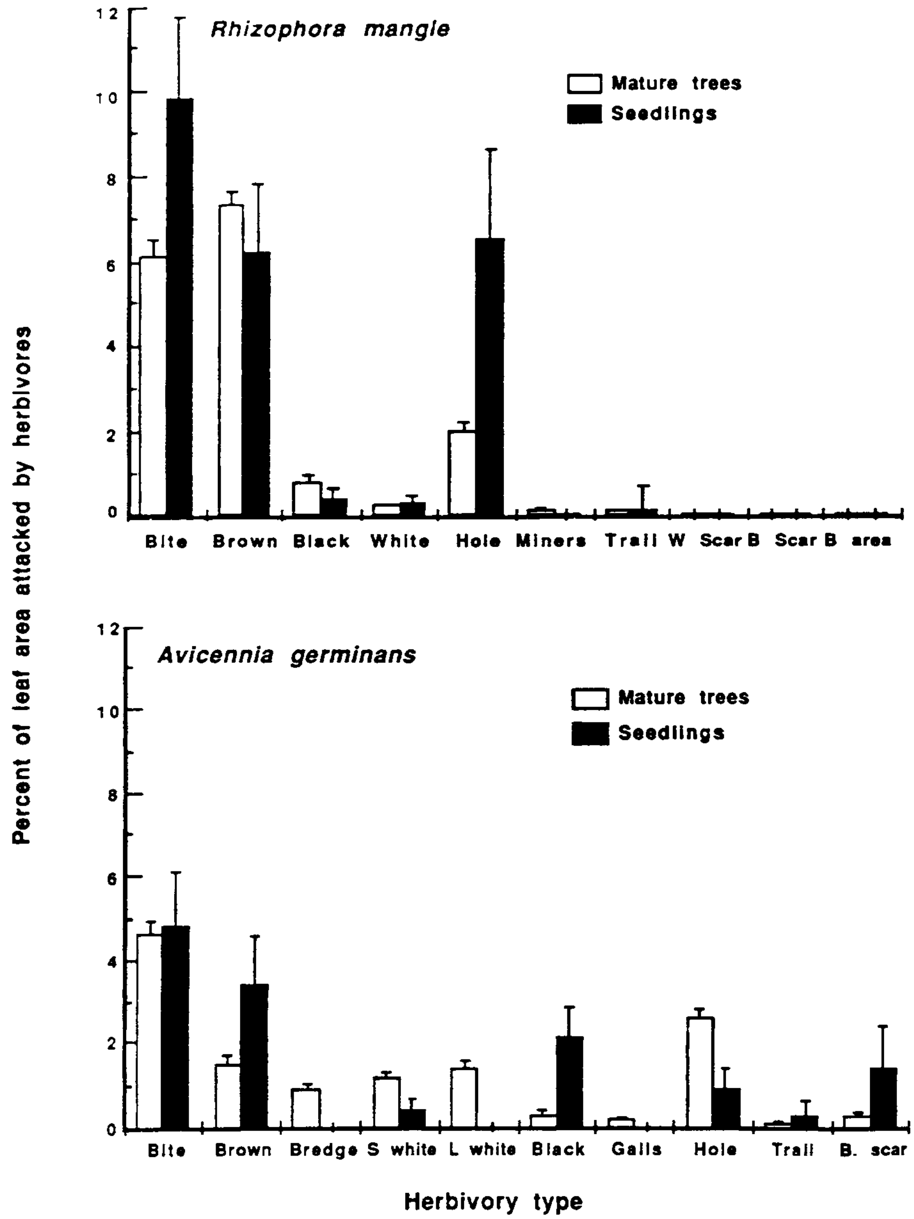

FIGURE 3. Distribution of damage types on leaves of trees and seedlings of *Rhizophora* and *Avicennia* at Placencia Lagoon. Values in the histogram are expressed as the percent of total herbivory ($\bar{x}$ ± 1 SE) in each category. These values also reflect the relative importance or rank of damage types affecting mangrove leaves. Herbivory types are described in text.

that the same herbivores were responsible for similar types of damage to the two mangrove species. Because of this qualitative nonoverlap of herbivores, we did not make comparisons of the distribution of damage types between *Avicennia* and *Rhizophora.*

LARGE-SCALE PATTERNS IN HERBIVORY.—Overall herbivory levels, expressed as percent damage per leaf across all leaves in all samples, ranged from 4.3 percent to 25.3 percent for *Rhizophora,* and from 7.7 percent to 36.1 percent in *Avicennia* (Table 1). For *Rhizophora,* ANOVA indicated significant island–mainland differences ($F_{1,2897} = 21.21$, $P < 0.0001$), tidal zone effects ($F_{1,2897} = 81.62$, $P < 0.0001$), and location × tidal zone interactions ($F_{1,2897} = 46.83$, $P < 0.0001$). For *Avicennia,* which occurred only at HHW, there were also significant island–mainland differences ($F_{1,2712} = 17.71$, $P < 0.0001$). However, separate ANOVAs on the

TABLE 1. *Percent of individual leaf area ($\bar{x} \pm SD$) damaged by herbivores. The percentage of all leaves in the sample that were damaged by herbivores and the number of leaves sampled are both given in parentheses. For each species, within a given zone, different superscripted letters indicate significant differences ($P < 0.05$, ANOVA) between adults and seedlings. Within a given zone, different superscripted numbers indicate significant interspecific differences ($P < 0.05$, ANOVA) between adults, or between seedlings.*

Location	Zone	*Rhizophora mangle*		*Avicennia germinans*	
		Adults	Seedlings	Adults	Seedlings
Placencia Lagoon	LW	6.9 ± 10.15^{a} (85.5, $N = 524$)	4.3 ± 6.04^{b} (62.5, $N = 45$)	—	—
	MW	5.5 ± 8.79^{a} (82.1, $N = 720$)	9.2 ± 13.01^{b} (90.5, $N = 63$)	—	—
	HHW	$16.6 \pm 13.94^{a,1}$ (96.5, $N = 540$)	$25.3 \pm 25.01^{a,1}$ (85.7, $N = 70$)	$14.0 \pm 22.24^{a,2}$ (65.9, $N = 1347$)	$15.1 \pm 19.15^{a,2}$ (53.3, $N = 75$)
Placencia Channel	LW	14.8 ± 21.40 (98.9, $N = 92$)	—	—	—
Big Creek	LW	14.8 ± 12.83 (94.3, $N = 194$)	—	—	—
Lark Cay	LW	18.3 ± 16.53 (98.3, $N = 173$)	—	—	—
	HHW	18.2 ± 16.21^{1} (100.0, $N = 205$)	—	7.68 ± 11.58^{2} (74.1, $N = 158$)	—
Scipio Cay	HHW	11.8 ± 13.58^{1} (92.8, $N = 207$)	—	36.1 ± 29.47^{2} (99.6, $N = 237$)	—
Northeast Cay	HHW	19.4 ± 17.69 (99.7, $N = 303$)	—	—	—
Man O'War Cay	HHW	13.4 ± 14.53 (92.5, $N = 93$)	—	—	—
Twin Cays	LW	12.4 ± 12.88^{a} (97.8, $N = 272$)	8.8 ± 13.95^{b} (52.4, $N = 63$)	—	—
	MW	—	12.5 ± 18.66 (73.5, $N = 83$)	—	—
	HHW	14.6 ± 12.37^{1} (97.4, $N = 307$)	—	$11.9 \pm 15.82^{a,2}$ (99.6, $N = 1013$)	9.5 ± 16.42^{b} (59.8, $N = 199$)

3 mainland sites and the 5 island sites revealed significant within-location differences for both species ($P < 0.001$ for all comparisons made). This variation is documented in Table 1.

Rhizophora growing on Man O'War Cay exhibited intermediate levels of percent damage (13.4%) that among the islands were significantly different only from Northeast Cay ($P < 0.05$, Scheffé test). Curiously, the most common damage type occurring on Man O'War Cay was brown spots—patches of necrotic tissue generally left by Homoptera. At all other sites, bites by Coleoptera and Lepidoptera larvae constituted the most prevalent damage type. However, this difference in damage distribution was not significant ($P > 0.10$, G-test).

Comparisons of percent damage on mature *Avicennia* trees on selected cays yielded similar results (Table 1). Scipio Cay departed significantly ($P < 0.05$, ANOVA) from the other locations, with an unusually high value for herbivory (36.1%).

Based on linear regression analysis, percent of leaves lost to herbivores did not vary consistently with island area ($P = 0.51$, F-test) or distance from the mainland ($P = 0.59$, F-test).

COMPARISONS AMONG TIDAL ZONES.—We compared herbivory levels in *Rhizophora* across several tidal zones at Placencia Lagoon, Lark Cay and Twin Cays (Table 2). Percent damage to *Rhizophora* leaves did not differ significantly between the LW and HHW zones at Lark Cay ($P = 0.825$, 2-tailed t-test), although several new types of low-level damage were found exclusively in the HHW zone there. In contrast, trees growing in the HHW zone of Placencia Lagoon and Twin Cays exhibited significantly higher amounts of damage than trees in the LW zone ($P < 0.05$, Scheffé test—Placencia; $P < 0.05$, t-test—Twin Cays).

INTERSPECIFIC COMPARISONS.—Interspecific comparisons of percent damage were made for the HHW zones of Placencia, Twin Cays, Scipio Cay and Lark

TABLE 2. *Intersite comparisons of %* Rhizophora *leaf area damaged by herbivores. All comparisons were done using Scheffé's* a posteriori *test for multiple comparisons among means, except those marked with a superscript t, which were done using a* t*-test. All comparisons are for adults, except for those in parentheses, which are between seedlings.* * P < *0.05; ns, not significantly different; — comparison not done.*

		Placencia Lagoon			Lark Cay		Twin Cays		
Location	Zone	LW	MW	HHW	LW	HHW	LW	MW	HHW
Plac. Lagoon	LW	—	ns	* (*)	*	—	*^{t} (ns^t)	—	—
	MW	—	—	* (*)	—	—	—	(ns^t)	—
	HHW	—	—	—	—	ns	—	—	ns
Lark Cay	LW	—	—	—	—	ns^t	*	—	—
	HHW	—	—	—	—	—	—	—	ns
Twin Cays	LW	—	—	—	—	—	—	—	*
	MW	—	—	—	—	—	—	—	—
	HHW	—	—	—	—	—	—	—	—

Cay. Seedlings and trees were assessed separately. Interspecific differences were found at all locations in both age classes (Table 1). *Avicennia* trees exhibited significantly lower percent damage than *Rhizophora* trees at Placencia ($P < 0.001$, ANOVA), Lark Cay ($P < 0.001$, ANOVA), and Twin Cays ($P < 0.001$, ANOVA). Likewise, *Avicennia* seedlings showed lower percent damage than *Rhizophora* seedlings in Placencia ($P < 0.001$, ANOVA). The only site at which *Avicennia* exhibited higher herbivory levels than *Rhizophora* was Scipio Cay, where *Avicennia* showed an unusually high 36.1 percent of leaf area to be damaged.

HERBIVORY ON SEEDLINGS AND TREES.—Significant differences (Table 1) between levels of herbivory on adults and seedlings in Placencia Lagoon and Twin Cays precluded pooling data from these two sites. In Placencia Lagoon, significant differences between seedlings and trees of *Rhizophora* were found only at LW and MW ($P < 0.01$, Table 1), although results from the HHW zone suggest a similar trend ($P = 0.056$). LW seedlings exhibited significantly lower levels of herbivory than LW adults ($P < 0.05$, ANOVA). However, above MW, damage to seedlings exceeded damage to trees, indicating a strong tree age × tidal height interaction ($P < 0.05$, ANOVA). No significant difference in percent damage was seen between *Avicennia* seedlings and trees at Placencia ($P = 0.69$).

At Twin Cays, as in Placencia, damage to LW *Rhizophora* seedlings was significantly lower than for mature trees ($P < 0.001$, Table 1). Leaves of *Avicennia* seedlings were less damaged than leaves of adult trees ($P < 0.001$).

Likewise, *Rhizophora* seedlings suffered significantly more herbivory at HHW than at LW or MW ($P < 0.05$, Scheffé test, Table 2), which were not themselves significantly different. Herbivory levels on seedlings of the MW and LW zones of Twin Cays also did not differ ($P = 0.086$, F-test). *Avicennia* seedlings of Placencia Lagoon displayed significantly higher damage than the seedlings of Twin Cays ($P = 0.04$, t-test).

HERBIVORY DYNAMICS UNDER A CANOPY.—*Rhizophora* seedlings growing under a monospecific canopy of *Rhizophora* trees showed significantly higher damage than seedlings growing in full sun ($P < 0.001$, ANOVA). Mean percent damage for shaded leaves was 23.5 ± 1.79 percent (SE; $N = 208$ leaves) and for sunlit leaves was 10.6 ± 0.78 percent ($N = 459$ leaves). Shaded and sunlit plants did not differ in the distribution of damage types shown (G-test, $X^2_{10} = 0.838$, NS).

VARIATION IN DAMAGE WITH LEAF AGE.—Multiple linear regression analysis was conducted to determine whether percent damage appearing on *Rhizophora* leaves was dependent on leaf age (trees and seedlings), branch height, orientation of branch (trees only), seedling height or distance to nearest neighbor (seedlings only). These analyses were done on a site-by-site basis because of the high local variance described above. Results for the regressions were themselves highly variable (Table 3). Damage increased significantly with leaf age on trees from Scipio Cay, Northeast Cay, Big Creek and Placencia, and on seedlings from Twin Cays. However, coefficients of determination (r^2 values) suggest that little of the percent damage in leaves was explained by leaf pair number alone, although the other factors included in the model did not significantly improve its fit. Regressions were not significant for trees from Lark Cay or Twin Cays, nor for seedlings from Placencia.

TABLE 3. *Results of Model I regressions of %* Rhizophora *leaf area damaged on leaf age (expressed as leaf pair number). Sample size is given in Table 1.*

Location		Zone	r^2	β	P
Plac. Lagoon	Adults	LW	0.04	+0.09	0.05
		MW	0.007	+0.02	0.27
		HHW	0.004	+0.03	0.76
	Seedlings	LW	0.19	+0.05	0.003
		MW	0.002	+0.009	0.71
		HHW	0.07	−0.08	0.02
Plac. Channel	Adults	LW	0.05	+0.06	0.05
Big Creek	Adults	LW	0.06	+0.04	0.008
Lark Cay	Adults	LW	0.08	+0.05	0.001
		HHW	0.0008	−0.004	0.69
Scipio Cay	Adults	HHW	0.091	+0.04	0.001
Northeast Cay	Adults	HHW	0.019	+0.07	0.001
Man O'War Cay	Adults	HHW	0.10	+0.05	0.002
Twin Cays	Adults	LW	0.004	+0.01	0.26
		HHW	0.002	+0.005	0.44
	Seedlings	LW	0.39	+0.16	0.0001
		MW	0.03	+0.04	0.14

DISCUSSION

Our study permitted a quantitative comparison of the importance of herbivory in *Avicennia* and *Rhizophora* in Belize, especially where they co-occur. These two mangrove species co-occur only above HHW and we encountered mixtures on Lark Cay, Twin Cays, Man O'War Cay, Scipio Cay and Placencia Lagoon. Despite the close proximity of these species at Placencia, none of the herbivores we collected was observed on both species; *Avicennia* and *Rhizophora* did not share the same herbivores.

In Belize, *Avicennia* trees and seedlings showed consistently lower leaf damage than *Rhizophora* at all locations except Scipio Cay. Moreover, only an average of 76 percent of *Avicennia* leaves were attacked, whereas an average of 88 percent of *Rhizophora* leaves showed evidence of attack (Table 1). Possible interspecific differences in leaf chemistry may influence herbivory rates. Lacerda *et al.* (1986) found that leaves of *Avicennia schaueriana* differed significantly from *Rhizophora mangle* in several chemical features including Na, N, phenols, ash, carbohydrates, and fiber, and that *Avicennia schaueriana* exhibited significantly lower levels of herbivory than *Rhizophora*. Based on cluster analysis of New Zealand mangroves, Hogg and Gillian (1984) reported that the Avicenniaceae (*Avicennia marina* (Forsk.) Vierh. and *A. marina* var. *resinifera* (Forst.) Bakhuizen) form a single chemotaxonomic cluster, distinct from the Rhizophoraceae. Ghosh *et al.* (1985) found interfamilial differences in lipid, sterol, and triterpene content in the Avicenniaceae and the Rhizophoraceae.

Differences in leaf salt content may also restrict herbivores to particular mangrove species. *Avicennia germinans* excretes salt through glands on the leaf epidermis (Tomlinson 1986), and crystals can often be seen on the leaf surface. *Rhizophora mangle* excludes salt at the roots and its leaves contain little salt. Newbery (1980) suggested that the exudate of concentrated salt solution on the leaf surface of *Avicennia marina* discouraged establishment of coccids on leaves.

Another measure of leaf quality, nutrient content, also has been correlated with attack rates, and several authors (Onuf *et al.* 1977, Johnstone 1981, Lacerda *et al.* 1986) have hypothesized that nutrient enrichment of mangroves could stimulate herbivore activity. We found that apparent nutrient enrichment of mangroves on Man O'War Cay (Kohlmeyer 1986) was not associated with significantly higher herbivory on *Rhizophora* relative to the other sites surveyed.

Overall, the damage attributable to herbivores in Belizean mangroves was comparable to the percentages found in other mangal (Onuf *et al.* 1977, Beever *et al.* 1979, Johnstone 1981, Lacerda *et al.* 1986, Robertson & Duke 1987, Smith *et al.* 1989). Johnstone (1981), Lacerda *et al.* (1986), and Robertson and Duke (1987) remarked on the high variability associated with values for leaf area damaged. Our data were no exception, yet this variability did not obscure differences between species, seedlings and trees, or populations growing at different locations throughout Belize.

When percentages were calculated as the sum of all herbivory types over leaf area, values ranged from 4.3 percent to 36.1 percent across all the populations surveyed. These values may overestimate the actual foliar tissue lost to herbivores. We calculated percent damage inflicted by all foliovores, including those, such as Homoptera and leaf miners, that did not physically remove leaf tissue. If we limit our calculations solely to types of injury that actually result in total removal of tissue, namely bites and holes, our percentages would range from 3.6 percent to 13.3 percent.

Authors have pointed out that static herbivory samples do not capture the expansion of initial damage that is caused by leaf growth and not herbivores (Reichle *et al.* 1973, Robertson & Duke 1987). Robertson and Duke (1987) suggest that hole expansion must be corrected for in estimates of herbivory by up to a factor of 2, especially if herbivores preferentially attack young, rapidly growing leaves. We will report elsewhere a study of temporal dynamics of mangrove herbivory that supports the application of the Robertson and Duke model.

We confined our study to foliovores, as the damage they inflict was readily quantifiable. However, wood borers also may significantly impact these trees (Rehm & Humm 1973, Simberloff *et al.* 1978, Perry 1988, Ellison & Farnsworth 1990), and our estimates of total herbivory may be conservative.

Percent damage on the five cays surveyed did not differ in any consistent way from the mainland sites in Belize. Percent damage was not correlated with island area or with distance from the mainland in our study. Although extensive herbivore collections were not made on the cays, we expect that these islands share the majority of their invertebrate fauna with the mainland. Mainland butterfly species, for example, have been seen over open water as far as 20 km from the coast (Farnsworth, pers. obs.).

If the cays we sampled were sufficiently isolated from the mainland, we might expect to observe a concentration of a particular herbivore or suite of herbivores on individual cays. The consistency of distribution of damage types on leaves from distant sites indicates that the same types of herbivores operate in the same relative proportions in different tidal zones on the mainland and on the cays. A model of herbivore guilds based on these damage types could be developed to describe the community of leaf consumers in these mangroves (Atsatt & O'Dowd 1976, Futuyma & Gould 1979, Smith *et al.* 1989). Guilds of invertebrate herbivores typically consist of a few common species and many other rarer species (Crawley 1983). However, Strong (1974) points out that host species with a broad geographic range accrue a higher diversity of pests than hosts with a more restricted distribution. Given the ubiquity of mangroves, we might expect a highly variable and complex assemblage of herbivores to be exploiting them. Future work should delineate the kinds of interactions between types of herbivores that may dictate dynamics of these guilds.

In this study, seedlings and mature trees differed in the amount of damage shown, but no consistent trends emerged. Neither the distribution nor total amount of damage was consistently associated with plant age, indicating that important herbivores in this system distinguish feeding substrates on the fine-grained level of the individual leaf.

Herbivory was strongly affected by the local light regime around individual seedlings. Seedlings growing in the absence of a canopy experienced only half the percent damage to leaf tissue that occurred on shaded seedlings. It is possible that understory seedlings simply may have experienced higher recruitment of herbivores dropping directly from the adult canopy, and that the canopy removal temporarily eliminated a local source of herbivores. However, there was ample time for herbivores to recolonize the quadrats during the 11 months of the experiment. Shaded and unshaded plants did not differ in the distribution of herbivory types shown, so we cannot explain the observed results on the basis of a concentration or outbreak of a single herbivore on shaded seedlings. Further study on the differences between sunlit and shaded seedlings is warranted.

Together, host plant quality, light regime, and tree distributions converge to influence herbivory in neotropical mangrove communities. While herbivores may remove only 3 percent to 20 percent of leaf tissue from the detritivore pathway, leaf damage is ubiquitous in mangroves and could substantially influence plant productivity. Herbivores and herbivore guilds deserve attention as significant structural components of mangrove communities.

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