PLANT ANIMAL INTERACTIONS

Herbivore responses to nutrient enrichment and landscape heterogeneity in a mangrove ecosystem

Ilka C. Feller · Anne Chamberlain

Abstract Complex gradients in forest structure across the landscape of offshore mangrove islands in Belize are associated with nutrient deficiency and flooding. While nutrient availability can affect many ecological processes, here we investigate how N and P enrichment interact with forest structure in three distinct zones (fringe, transition, dwarf) to alter patterns of herbivory as a function of folivory, loss of yield, and tissue mining. The effects of nutrient addition and zone varied by functional feeding group or specific herbivore. Folivory ranged from 0 to 0.4% leaf area damaged per month, but rates did not vary by either nutrient enrichment or zone. Leaf lifetime damage ranged from 3 to 10% of the total leaf area and was caused primarily by the omnivorous tree crab *Aratus pisonii*. We detected two distinct spatial scales of response by *A. pisonii* that were unrelated to nutrient treatment, i.e., most feeding damage occurred in the fringe zone and crabs fed primarily on the oldest leaves in the canopy. Loss of yield caused by the bud moth *Ecdytolopha* sp. varied by zone but not by nutrient treatment. A periderm-mining *Marmara* sp. responded positively to nutrient enrichment and closely mirrored the growth response by *Rhizophora mangle* across the tree height gradient. In contrast, a leaf-mining *Marmara* sp. was controlled by parasitoids and predators that killed >89% of its larvae. Thus, nutrient availability altered patterns of herbivory of some but not all mangrove herbivores. These findings support the hypothesis that landscape heterogeneity of the biotic and abiotic environment has species-specific

effects on community structure and trophic interactions. Predicting how herbivores respond to nutrient over-enrichment in mangrove ecosystems also requires an assessment of habitat heterogeneity coupled with feeding strategies and species-specific behavior measured on multiple scales of response.

Keywords *Aratus pisonii* · Belize · Leaf miners · Loss of yield · *Rhizophora mangle*

Introduction

A major challenge for ecologists is to assess the impact of nutrient over-enrichment on ecosystem function in spatially heterogeneous landscapes (National Research Council 2001; Lovett et al. 2005). In forested ecosystems, biotic and abiotic factors (e.g., diversity, nutrients, geology, topography, and hydrology) contribute to structural complexity across the landscape (Silver et al. 1994; Sollins 1998). Variations in forest structure and resource availability along abiotic gradients influence a range of ecological processes, including primary productivity and herbivory. In the tropics, most studies have focused on the relationship between heterogeneity and biodiversity in species-rich rainforests (Morin 2000; Condit et al. 2002). Although mangrove ecosystems comprise a small percentage of tropical forests and are confined to a relatively narrow coastal fringe, these floristically depauperate systems exhibit complex gradients in abiotic conditions that generate distinctive patterns in species zonation and extreme spatial variation and heterogeneity in canopy structure and productivity (Lugo and Snedaker 1974; Farnsworth 1998; Rodriguez and Feller 2004). Mangroves occur along a wide spectrum of nutrient conditions from oligotrophic to eutrophic, and

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form forests characterized by vast differences in phenotypic response. For example, in nutrient-rich riverine systems or bird rookeries of the Neotropics, trees of the red mangrove, *Rhizophora mangle* L., grow to more than 40 m tall (Golley et al. 1975). However, behind the coastal fringe or in nutrient-poor areas on offshore islands, old-growth forests of this species are dominated by stunted or "dwarf" trees, ≤1.5 m tall (Lugo 1997). Dramatic gradients in tree height and productivity also occur within mangrove forests (Cintròn et al. 1985). Differences in mangrove forest structure and nutrient availability are strongly tied to soil factors that vary with a tidally driven hydrology (McKee 1995). Tidal action and evapo-transpiration influence salinity, soil redox, movement and availability of nutrients, and concentrations of toxins such as sulfide. These factors affect and are modified by the activities of the mangrove plants and associated fauna (McKee 1993, 1995; Holmer et al. 1999).

Mangroves are often described as detritus-based ecosystems in which primary consumption plays only a minor role (Odum and Heald 1975). However, recent studies have found that levels of herbivory in these systems (Farnsworth and Ellison 1991, 1993; Feller 1995; Burrows 2003) were comparable to values reported for other temperate and tropical forests (Cyr and Pace 1993; Coley and Barone 1996). Herbivory potentially alters nutrient cycling patterns by diverting resources from the detrital pathway into a grazing pathway. Herbivores can also interfere with internal nutrient cycling processes because nutrients in leaf tissue removed by grazers are not available for resorption during senescence (Risley and Crossley 1988; Feller 2002). Leaf damage further increases nutrient losses via leaching (Feller et al. 1999). Mangroves also are attacked by wood-feeding herbivores that prune branches and twigs from trees, which alter the quantity and quality of leaf litter and nutrient cycling processes in mangrove ecosystems (Feller and Mathis 1997; Feller and McKee 1999; Feller 2002).

Nutrient enrichment experiments, which have been used to determine patterns of nutrient limitation in mangrove forests and other coastal ecosystems, have reported dramatic increases in primary productivity in response to nutrient enrichment (Feller 1995; Downing et al. 1999; Lovelock et al. 2004). However, nutrient availability is not necessarily uniform and can shift from N to P limitation along tree height gradients across intertidal landscapes (Boto and Wellington 1983; Chen and Twilley 1999; Feller et al. 2003). Other studies have shown that nutrient enrichment also influences community structure and trophic interactions (Feller 1995; Feller et al. 2007; Valiela et al. 2004). Nutrient enrichment is predicted to cause an increase or decrease in primary consumption depending on feeding mode of the herbivore, which, in turn, may affect the interactions between herbivores and their natural enemies (Coley et al. 1985; Bazzaz et al. 1987; Price 1991; Hunter

and Price 1992). In addition, the top-down forces exerted by natural enemies may increase along with nutrient enrichment (Stiling and Rossi 1997; Fraser 1998; Fraser and Grime 1998; Forkner and Hunter 2000) and may be more sensitive to landscape heterogeneity than herbivory (Thies et al. 2003). Thus, landscape variables along with demography, behavior, and feeding mode of herbivores and their natural enemies may result in approaches to primary consumption that are independent of, or interact with, plant chemistry (Clay and Andersen 1996; Polis et al. 1997; Wiens et al. 1997; Forrester et al. 1999; Hochuli 2001; Stiling and Moon 2005).

In this study, we investigated how forest structure and nutrient availability influenced herbivory, differentiated as folivory, loss of yield, and tissue mining, of *R. mangle* in a long-term fertilization experiment at Twin Cays, Belize. This experiment previously revealed a unique switching from N to P limitation of mangrove growth from the tall fringing stands along the shore to the inland dwarf forests (Feller et al. 2003). Trees in the dwarf zone responded to fertilization with P (+P), trees along the fringe to fertilization with N (+N), and trees in a transition zone between the dwarf and fringe zones to both +N and +P, applied separately (Table 1). Here, we tested the hypotheses that: (1) herbivory would vary across the mangrove landscape as a function of heterogeneity in forest structure and nutrient availability, and (2) trees supplemented with a limiting nutrient would experience increased levels of herbivory.

Materials and methods

Study site

Twin Cays is an intertidal, peat-based, 92-ha archipelago, 12 km off shore (16°50′N, 88°06′W) where it receives no terrigenous inputs of freshwater or sediments (Macintyre et al. 2004). Since 1980, these islands have been the primary study site for the Smithsonian Marine Field Station on nearby Carrie Bow Cay (Rützler et al. 2004). The forests

Table 1 Summary of *Rhizophora mangle* growth at Twin Cays, Belize, measured as shoot elongation[a] (cm/year) in three zones (dwarf, transition, fringe) in response to fertilization with N (+*N*) as urea, P (+*P*) as triple superphosphate, or control (no fertilizer added)

Nutrient treatment	Dwarf (cm/year)	Transition (cm/year)	Fringe (cm/year)
Control	2.8 ± 0.6	3.8 ± 0.8	5.6 ± 1.4
+N	7.4 ± 2.8	37.6 ± 12.0	28.2 ± 11.2
+P	73.6 ± 16.6	78.6 ± 36.2	6.0 ± 1.0

[a] Measurements are based on annual increases of individual shoots after 2 years of treatment (from Feller et al. 2003)

are dominated by *R. mangle* L. (red mangrove), *Avicennia germinans* L. (black mangrove), and *Laguncularia racemosa* (L.) Gaertn.f. (white mangrove). Tree diversity is very low, but the habitat structure is heterogeneous and characterized by complex gradients in hydrology and tree height that include a narrow seaward fringe of pure stands of uniformly tall (5–6 m) *R. mangle*, varying in width from 5 to 20 m wide, which occurs in the low intertidal around the periphery of the islands. Tree height decreases rapidly to landward through a 5- to 30-m-wide, mixed scrubby transition zone (2–4 m tall) where *R. mangle* is dominant, but *A. germinans* and *L. racemosa* are intermixed. Further inland, the hinterlands of Twin Cays are dominated by old-growth stands of low stature (≤1.5 m) *R. mangle* trees, hereafter referred to as the "dwarf zone" (Rodriguez and Feller 2004). Hydrology varied along this gradient with the dwarf zone completely inundated or waterlogged over a tidal cycle so that the soil was less flushed at low tide than the transition or fringe zones (McKee et al., in press).

Experimental design

In January 1995, we selected *R. mangle* trees for experimental manipulation at three sites on two of the largest islands of the Twin Cays archipelago. These sites were along the main channels in areas with uninterrupted shoreline, similar forest structure and hydrology, and with enough space to accommodate a replicate of the experimental array. Three transects, 25–50 m long and 10 m apart, were oriented perpendicular to the shoreline at each site. The 10-m intervals were left between transects as buffer zones against possible lateral migration of fertilizers. Transects were subdivided into fringe, transition, and dwarf zones based on tree height as described above.

The fertilization experiment, which is described in detail in Feller et al. (2003), was a two-way ANOVA with three levels of the nutrient treatment (control, +N, +P) and three levels of zone (fringe, transition, dwarf), blocked at the three sites. In each zone, three replicate trees were selected with nine per transect (each spanning the three zones) and 27 per site, for a total of 81 trees sampled. The three nutrient treatment levels were +N as urea (NH_4, 45:0:0), +P as triple superphosphate (P_2O_5, 0:45:0), and control (no nutrient enrichment). Trees were fertilized twice a year at 6-month intervals from January 1995 up to and including January 2003. These methods were based on previous studies where the addition of the limiting nutrient caused dramatic growth increases by the experimental tree as well as other trees within a ∼2-m radius of where the fertilizer was added (Feller 1995; Feller et al. 1999, 2003). We also measured tree height and leaf area index (LAI) of each experimental tree in January 2002. To calculate LAI (m^2 leaf area/m^2 ground), we multiplied the total number of

leaf-bearing shoots in 1 m × 1-m plots from ground level to the tops of the fertilized trees by the mean number of leaves/shoot ($n = 30$ shoots) and mean area/leaf ($n = 75$) of intact leaves.

Herbivory measurements

To quantify the effects of nutrient enrichment and zone on primary consumption, we measured three types of herbivory: (1) leaf-mass consumption (hereafter, folivory), (2) loss of yield, and (3) the frequency of tissue miners. The folivores were insects and crabs that injured or fed directly on expanded leaves, causing holes, marginal bites, scrapes, and mines. To quantify short-term folivory, we measured rates of leaf damage on each of the 81 trees over a 1-month (January–February 1998) and a 4-month (September–December 1998) interval. We selected ten fully mature leaves per tree in penapical positions with no pre-existing damage at the start (time$_0$) of each time interval. Digital images of individual leaves were recorded 1 month later (time$_1$) or 4 months later (time$_2$). The percent leaf area damaged was determined from the digitized images using image analysis software (SigmaScan Pro4). Because these short-term rates of folivory were at or near zero, we also measured the damage that accumulated over the entire lifetime of a leaf, which was approximately 18 months, based on 48 dwarf trees at Twin Cays monitored over a 3-year period (Feller 1995). For this method, we collected and recorded digital images of ten senescing leaves in basal position, five to six nodes proximal to an apical bud from the outer part of the canopy of each experimental tree in August 1999, October 2001, and January 2002. We calculated the percent leaf area damaged and determined the species of folivores responsible for the damage based on experience from extensive collections, observations, and rearings to characterize the feeding pattern of each species. Values for January 2002 were multiplied by the LAI of each tree to estimate a spatial level of damage (m^2 leaf area damaged/m^2 ground area). To determine the relative age (old or young) at which leaves are most susceptible to folivores, we also measured damage on all leaves from the apical to basal positions on a shoot. We collected and photographed ten leaves per leaf position, from the apical leaf (youngest leaf in position 1) to the basal leaf (oldest leaf in position 6), from a sunlit position in the top of the canopy. We used these digital images to measure damage and to determine the herbivores species that caused the damage.

Measures of the holes, scrapes, and mines caused by folivores did not account for injury that resulted in premature leaf abscission or in a failure of the *R. mangle* canopy to achieve its expected yield of leaf area, or "loss of yield" (Pedigo et al. 1986). This term, which is often used to refer

to insect-caused reduction in various crop plants (Petersen and Higley 2000), is also relevant to natural systems to describe a similar reduction in the expected yield. In *R. mangle*, loss of yield was caused mainly by a bud moth (Pyralidae: *Ecdytolopha* sp.), a specialist of unopened apical buds (Onuf et al. 1977; Feller 1995). Its direct feeding was small and inconspicuous and occurred within an unopened apical bud. However, the injury to the plant caused three types of loss of yield: (1) aborted leaves, (2) smaller and misshapen leaves, and (3) dead buds. To determine the effect of *Ecdytolopha* sp. injury on leaf size, we compared mature leaves that developed from attacked buds with mature leaves from non-attacked buds on the same stem ($n = 150$ pairs). To upscale estimates from the leaf level to the canopy, we measured bud moth damage in 1 m × 1-m plots from ground level to the tops of the fertilized trees. Inside each plot, we inspected each leaf-bearing shoot and counted the number of misshapen leaves, aborted leaves, and dead buds. To estimate the number of aborted leaves, we counted the empty leaf nodes between the basal leaves and the apical bud. We combined these data with LAI to estimate the loss of yield per tree caused by *Ecdytolopha* sp.

We also used the 1 m × 1-m plots to measure densities of the other common herbivores in the experimental trees. To count the mobile and furtive mangrove tree crabs (Sesarminae: *Aratus pisonii*), two people carefully approached the plot from opposite directions and counted all *A. pisonii* on prop roots, boles, branches, and twigs within the plots. For densities of two microlepidopteran tissue miners, which are host-taxon- and tissue-specific specialists on *R. mangle* leaves and stems (Gracillariidae: *Marmara* spp.), we counted their mines within each plot. Estimates of canopy LAI were used to standardize density values to leaf area across the tree height gradient. We used tree height data to estimate densities per cubic meter.

To determine if nutrient enrichment and zone affected higher trophic levels, we examined predation and parasitism of the *R. mangle* leaf miner (*Marmara* sp.). In January 2002, we collected samples of 30 mined leaves within a 2-m radius around each tree and examined each mine microscopically to determine if the miner was successful, parasitized, or depredated. Successful miners were indicated by the presence of a crescent-shaped exit hole in the mine or by a live, unparasitized larva. For the parasitoids, which included two species of wasps, the larvae, pupae, or exuviae were visible inside the body of the leaf miner. Predators (i.e., ants, spiders, *A. pisonii*) left distinct marks when they ripped open mines to remove leaf miner larvae.

To determine what scale of heterogeneity at Twin Cays affected herbivory, we also compared damage levels with tree height, LAI, and water depth. For leaf-level effects, we compared damage levels with the C, N, and P values, C:N,

C:P, and N:P ratios, and leaf mass per area [LMA; biomass (g)/leaf area (cm^2)], based on samples of ten fully mature green leaves from penapical stem positions from a sunlit portion of the canopy of each tree.

Statistics

Our data were grouped by nutrient treatment (control, +N, +P) × zone (fringe, transition, dwarf), in three blocks to look for differences in herbivory measurements in this experiment and were analyzed as a factorial ANOVA (fixed effects model) in a randomized complete block experimental design, using SigmaStat 3.1 (Systat Software 2004). We used repeated measures ANOVA to compare folivory levels over 3 years and to compare leaves of different ages on the same tree. When an ANOVA found a significant effect, we used the Holm–Sidak test to examine pairwise differences within and among the treatment levels. Normality assumption was tested with the Kolmogorov–Smirnov test, and equal variance assumption was tested with the Levene median test. For heterogeneous variances, continuous data were transformed using logarithms and non-continuous data (counts) using the square root. Pearson's correlation coefficients were calculated to test the strengths of the relationships between herbivory and leaf-level and landscape variables.

Results

Monthly rates of folivory to individual *R. mangle* leaves were very low and ranged from 0 to 0.4% of the total leaf area. Over 1- and 4-month intervals, we found no differences in rates of damage either by nutrient treatment or by position along the tree height gradient (ANOVA, $P > 0.05$). However, the damage that accumulated over the entire lifetime of a leaf was considerably higher and ranged from approximately 3 to 10% of the leaf area across three separate time intervals (Table 2). Although there were no significant differences among nutrient treatments during any of these years, damage did vary significantly among years and zones. The values measured in 1999 were slightly but significantly lower than in 2001 or 2002. Regardless of year, there was a significant zone effect with the lowest levels consistently in the dwarf trees where leaves sustained less than half the damage of leaves from fringe and transition-zone trees (repeated measures ANOVA, $F_{2,79} = 9.643$, $P < 0.001$). At the leaf level, folivory correlated significantly with LMA (Pearson's coefficient $r = 0.329$, $P < 0.01$), but not with N, P, or C:N, C:P, N:P ratios ($P > 0.5$). For measures of landscape complexity, folivory showed a weak but significant negative correlation with water depth (Pearson's coefficient $r = -0.250$, $P < 0.05$), but not with tree height or LAI ($P > 0.05$).

Table 2 Folivore damage that accumulated over the leaf lifetime for fertilized *R. mangle* by zone and nutrient treatment measured in 1999, 2001, and 2002. Leaves were sampled by nutrient enrichment[a] (control, +N, +P) and zone[b] (fringe, transition, dwarf), replicated in three blocks at Twin Cays, Belize. For abbreviations, see Table 1

Zone	Nutrient treatment	Leaf area damaged (% ± 1 SE)		
		1999	2001	2002
Fringe	Control	6.67 ± 1.38	9.08 ± 1.44	7.89 ± 1.19
	+N	6.86 ± 1.46	9.78 ± 1.71	8.84 ± 1.01
	+P	6.48 ± 1.40	10.29 ± 1.99	9.53 ± 1.07
Transition	Control	5.65 ± 0.71	7.60 ± 1.39	7.76 ± 1.46
	+N	7.32 ± 1.54	8.66 ± 2.15	10.23 ± 1.25
	+P	5.85 ± 1.16	6.63 ± 0.86	6.53 ± 0.69
Dwarf	Control	3.16 ± 0.78	3.87 ± 1.28	5.53 ± 0.52
	+N	2.67 ± 0.80	3.54 ± 0.77	3.04 ± 0.70
	+P	2.69 ± 0.72	4.62 ± 0.84	5.37 ± 1.10

[a] $n = 27$ trees per nutrient treatment

[b] $n = 27$ trees per zone

When damage was divided with respect to the causative herbivores, the mangrove tree crab *A. pisonii* was found to be responsible for significantly more of the damage than all other folivores combined (Table 3; Mann–Whitney rank sum test, $P < 0.001$). Although *A. pisonii* densities were low, there were more crabs in the fringe (0.10 ± 0.05 crabs/m^3, mean ± 1 SE) than in the transition (0.05 ± 0.04 crabs/m^3) or dwarf (0.03 ± 0.02 crabs/m^3) zones. Despite its low density, *A. pisonii*'s distinctive patterns of scraping damage on both leaf surfaces accounted for approximately 80–96% of the total folivory across the forest. The leaf lifetime

damage by *A. pisonii* averaged over 3 years also varied significantly by zone (ANOVA, $F_{2, 80} = 23.740$, $P < 0.001$). The highest values (~9%) were in the fringe and lowest (~3%) were in the dwarf zone (Holm–Sidak pairwise contrasts, dwarf vs. fringe, $t = 6.493$, $P < 0.0001$; dwarf vs. transition, $t = 5.244$, $P < 0.0001$; fringe vs. transition $P > 0.05$). Repeated measures ANOVA results indicated a significant interaction of leaf age and zone on folivory by *A. pisonii* ($F_{10, 335} = 5.024$, $P < 0.0001$; Fig. 1). The oldest leaves on a shoot suffered significantly more damage than did the younger leaves in the fringe and transition zones where 84–98% of the leaf lifetime crab damage occurred on the fifth and older leaf positions. A small fraction of the total damage occurred on leaves in the fourth or younger positions. However, in the dwarf zone where crab occurrence and feeding were very low, the damage pattern accumulated linearly from the youngest to the oldest leaves. Despite significant differences in N% and C:N ratios from young to old leaves that varied by nutrient treatment and zone (leaf nutrient data from Feller et al. 2003), there were no consistent relationships with *A. pisonii* damage.

Marmara sp., an undescribed leaf miner, mined 1–2% of the leaves in the canopy and damaged <1% of the leaf area (Table 3). Although the numbers were low, the transition zone had a significantly higher frequency of leaf mines with approximately twice as many as the dwarf or fringe zones, and slightly but significantly higher levels of damage in the +N trees. Parasites and predators killed ~89.2 ± 0.8% of the leaf miner larvae, but there were no differences in levels of mortality by zone or nutrient treatment. The other folivore category, which included damage by caterpillars (e.g., *Megalopyge dyeri* Hopp and *Oiketicus kirbii* Guilding) and

Table 3 Folivory as percent leaf area damaged and loss of yield for fertilized *R. mangle* by herbivore species, zone, and nutrient treatment measured in 2002. Leaves were sampled by nutrient enrichment[a] (control, +N, +P) and zone[b] (dwarf, fringe, transition), replicated in three blocks at Twin Cays, Belize. For abbreviations, see Table 1

Zone	Nutrient treatment	Leaf area damaged (% ± 1 SE)			Loss of yield due to *Ecdytolopha* sp. (% ± 1 SE)	
		Aratus pisonii	*Marmara* sp.	Other folivores	Smaller + aborted leaves	Dead apical buds
Fringe	Control	7.67 ± 1.30	<0.01 ± 0.00	0.22 ± 0.09	4.84 ± 0.98	9.56 ± 4.07
	+N	7.39 ± 1.04	0.02 ± 0.01	1.44 ± 0.65	5.87 ± 1.00	10.52 ± 2.80
	+P	8.94 ± 1.16	0.04 ± 0.04	0.54 ± 0.16	4.12 ± 0.78	6.35 ± 1.21
Transition	Control	6.88 ± 1.62	0.22 ± 0.21	0.66 ± 0.30	15.92 ± 7.66	20.75 ± 9.51
	+N	8.12 ± 1.20	0.92 ± 0.01	1.20 ± 0.47	10.32 ± 2.45	8.79 ± 2.14
	+P	4.67 ± 1.09	0.08 ± 0.08	1.78 ± 0.77	9.36 ± 2.16	15.48 ± 3.32
Dwarf	Control	3.99 ± 0.45	0.11 ± 0.09	1.43 ± 0.57	3.12 ± 0.80	4.48 ± 1.84
	+N	2.81 ± 0.66	<0.01 ± 0.00	0.22 ± 0.08	3.13 ± 0.49	4.06 ± 0.10
	+P	4.32 ± 1.28	<0.01 ± 0.00	1.05 ± 0.37	3.73 ± 0.68	6.90 ± 1.89

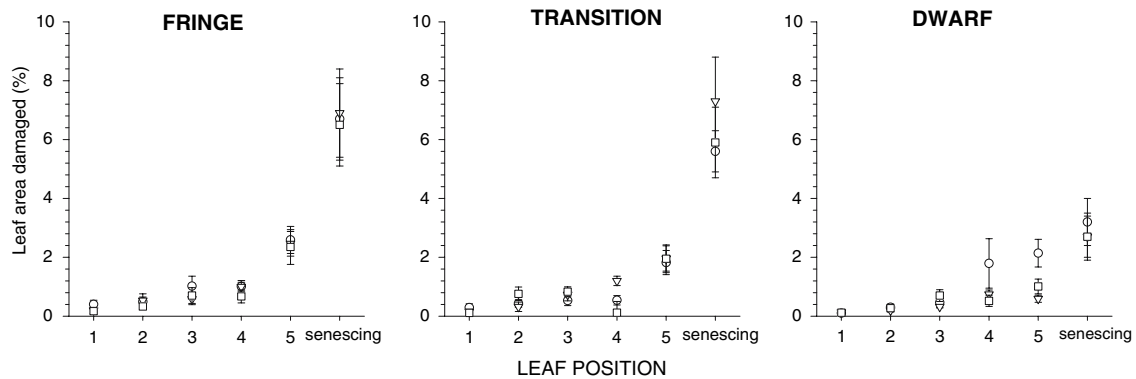[a] $n = 27$ trees per nutrient treatment

[b] $n = 27$ trees per zone

Fig. 1 Percent leaf area damaged by *Aratus pisonii*, the mangrove tree crab, from youngest (position 1) to oldest (senescing) *Rhizophora mangle* leaves on shoots from trees by nutrient enrichment [control, fertilization with N (+N), fertilization with P (+P)] and zone along a tree height gradient (fringe, transition, dwarf). Data are from 2002. Values are means ± 1 SE. $n = 27$ trees per nutrient treatment, $n = 27$ trees per zone

transients such as crickets and katydids, was responsible for 4–31% of the total leaf area damaged (Table 3). However, the pattern was variable with slightly more damage in the +P trees (ANOVA, $F_{2,73} = 3.761$. $P = 0.028$), and no difference among zones ($P > 0.05$).

The above estimates of herbivory were based on the percent leaf area damaged. However, when the damage by these folivores was scaled to area based on LAI [i.e., leaf area damaged (m^2)/ground area (m^2)] to account for differences in tree size and responses to nutrient enrichment, there was a significant interaction between nutrient enrichment and zone ($F_{2,70} = 6.620$, $P < 0.001$; Fig. 2a). For control trees, there was a dramatic gradient in damage along the tree height gradient with fringe = transition > dwarf. Although +N was not different from the controls, damage levels in the +P dwarf trees increased by five- to sevenfold and were similar to levels experienced by the fringe trees. At the canopy level, the leaf P of the fertilized trees correlated significantly with folivory (Pearson's coefficient $r = 0.621$, $P < 0.00001$).

Loss of yield (i.e., reduction in leaf biomass yield because of injury sustained inside the apical bud by *Ecdytolopha* sp.) was another major form of herbivory of the leafy part of the *R. mangle* canopy (Table 3). Zone had a significant effect on loss of yield due to reduced leaf size and aborted leaves ($F_{2,79} = 10.013$, $P < 0.001$) and dead apical buds ($F_{2,79} = 4.552$, $P < 0.014$). Values were higher in the transition than in the fringe ($P = 0.025$) or the dwarf zone ($P = 0.017$). The proportions of dead apical buds were higher in the fringe and transition zones than in the dwarf zone, but values did not vary by nutrient treatment ($P > 0.05$). There was no difference in %N of leaves from undamaged ($0.89 ± 0.05\%$) versus *Ecdytolopha*-damaged buds ($0.84 ± 0.04\%$).

In contrast to the folivores and the bud moth, there was a significant interaction between nutrient treatment and zone on the proportion of stems attacked by a microlepidopteran tissue-mining *Marmara* sp. that feeds within the periderm of *R. mangle* stems ($F_{4,70} = 12.886$, $P < 0.001$; Fig. 2b). Response to nutrient treatment by this herbivore closely mirrored growth response by *R. mangle*. There was no difference in the proportions of stems with *Marmara* sp. mines in control trees among the three zones ($P > 0.05$). The +P treatment caused a dramatic increase in the incidence of this *Marmara* sp. in the dwarf and transition zones (where P was limiting), but had no effect on fringe trees. On the other hand, +N caused a similarly large increase in mines in the fringe and transition zones (where N was limiting), but had no effect on trees in the dwarf zone.

Discussion

Although notorious for their floristic homogeneity, mangrove forests often exhibit extreme structural and biogeochemical heterogeneity along intertidal gradients (Lugo and Snedaker 1974; Alongi et al. 1992; McKee et al. 2002; Feller et al. 2003). In this study, we found multiple mechanisms through which landscape heterogeneity and nutrient enrichment influenced trophic interactions between *R. mangle* and its herbivores. Similar to other ecological processes, herbivore damage revealed a complex pattern of responses that suggested both nutrient availability and position within the mangrove landscape modified herbivore dynamics, depending on behavior, mode of feeding, and the scale at which measurements were made. Insects and crabs comprised a functional group of foliage-feeding herbivores on *R. mangle* that included both generalist and specialist species. Over the short term (1 and 4 months), we found no difference in the percent leaf area damaged by this suite of herbivores, either by nutrient treatment or position along the tree height gradient. This contrasts with long-term
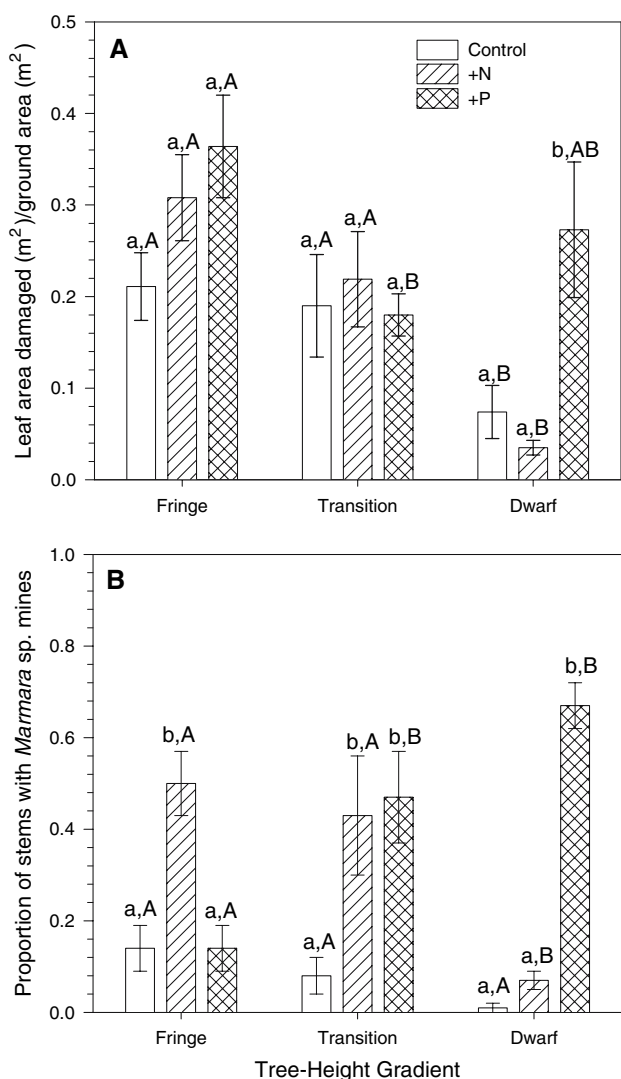
Fig. 2 a Estimate of leaf damage (m^2) by leaf mass consumers per square meter ground area in the canopy. **b** Proportions of *R. mangle* shoots with a periderm-mining microlepidopteran, *Marmara* sp., in the canopy of each of the fertilized *R. mangle* trees by nutrient enrichment (control, +N, +P) and zone along a tree height gradient (fringe, transition, dwarf). Data are from 2002. Values are means ± 1 SE. Within a zone, the *same lowercase letter* indicates that treatment means are not significantly different; among zones, the *same uppercase letter* indicates that treatment means are not significantly different ($P < 0.05$) using a two-way ANOVA and pairwise comparisons. $n = 27$ trees per nutrient treatment, $n = 27$ trees per zone

damage (leaf lifetime) of 3–10% of the leaf area where fringe and transition trees lost more than twice the percent leaf area as dwarf trees regardless of the fertilizer treatment, which is consistent with previous reports from mangroves (Farnsworth and Ellison 1991; Feller 1995; Feller and Mathis 1997). This range of damage is also similar to values reported for other forests (Landsberg and Ohmart 1989; Coley and Barone 1996). However, due to the >25-fold increase in growth caused by +P in the dwarf trees (Feller et al. 2003), the small percentage leaf area damaged (i.e.,

5.4%) experienced by these trees in our 2002 sample (Table 2) represented a huge increase in the actual amount of leaf area damaged on a spatial scale (Fig. 2a). Nutrient ratios, such as N:P, C:N, and C:P ratios, are generally considered important indices of the availability of nutrients and the palatability of plant tissue to herbivores (e.g., Schade et al. 2003). Despite significant differences in chemical content and nutrient ratios of leaves in response to the nutrient treatments, these variables explained very little of the percent leaf area damaged for either the short- or long-term rates. Yet, when folivory was upscaled from the percent leaf damage to damage per square meter ground area, leaf P concentrations correlated significantly with the amount of damage.

To explain the patterns of herbivory that we observed, it was instructive to consider feeding strategies and species-specific behaviors of the herbivores. At Twin Cays, the dominant foliage feeder on *R. mangle* is the mangrove tree crab, *A. pisonii*. This omnivore is a common mangrove resident throughout the Caribbean where it feeds on mangrove leaves, detritus, and insects (Warner 1967). Analysis of stomach contents showed that its diet was primarily *R. mangle* leaves with a tiny fraction of animal and detrital material (Erickson et al. 2003). While occasional consumption of prey by omnivores has been viewed as a feeding strategy to offset the mismatch of their relatively low C:N with the high C:N of their host plants (Denno and Fagan 2003), it is not clear how *A. pisonii* balances its consumption of plant and animal tissue to meet its N requirements. When feeding on leaves, it causes distinctive scrapings to leaf surfaces (Beever et al. 1979; Feller 1995; Erickson et al. 2003). Although our nutrient enrichment treatment had no detectable effect on the percentage of damage by *A. pisonii*, we found many more crabs and crab damage in the fringe and transitions zones than in the dwarf zone. These results suggest that life history traits such as feeding behavior, predator avoidance, and demographics of *A. pisonii* were more likely dependent on landscape differences related to hydrology than on differences in nutrient availability per se. For example, these crabs and their feeding damage may have aggregated in the fringe zone because of its proximity to the shoreline, both as a requirement for ovigerous females that need to deposit their eggs on the outgoing tide and as a source for the planktonic larvae of *A. pisonii* in the incoming tide (Warner 1967; Beever et al. 1979). In addition, these tree climbing crabs are vulnerable to desiccation and must periodically descend the canopy to wet their gills (Warner 1967). Thus, the shaded conditions under the mostly closed canopy in the fringe and transition zones may have provided more protection from drying out than the open canopy that characterized the dwarf forests in the interior of Twin Cays. Similarly, the fringe and transition zones may also have provided more protection from

predation for exophytic herbivores such as *A. pisonii*, which are particularly susceptible to top-down effects (Cornell et al. 1998). We also found that *A. pisonii* fed preferentially on the oldest leaves in the canopy, which contrasts with findings from other tropical forests where daily rates of damage were 5–25 times higher on young leaves than on mature leaves (Coley and Barone 1996), presumably due to their higher nutritive values. Although N% and C:N ratios indicated that older *R. mangle* leaves had much lower nutritional value than younger leaves (Feller et al. 2003), the basal position may have been preferred by *A. pisonii* because it provided a better shelter and a shadier perch, which has been shown to modify the distributions of organisms and influence herbivory on some host plants (Fukui 2001).

R. mangle also hosted at least four undescribed microlepidopteran species of tissue miners in the genus *Marmara* (D. R. Davis, personal communication), all of which were tiny and fed endophytically (Feller 1995; McKeon and Feller 2004). These cryptic herbivores have been generally overlooked even though they are widespread in the Caribbean. We have collected these four *Marmara* spp. in Belize, Panama, Mexico, Puerto Rico and the Dominican Republic (I. C. Feller, unpublished data). Here, we tracked the leaf-mining and the periderm-mining *Marmara* spp. to determine how zone and nutrient availability affected their population densities and feeding damage. Damage by the leaf miner was negligible except for +N trees in the transition zone where values were still less than 1% of the leaf area. Although predation and parasitism caused almost 90% mortality of the leaf-miner larvae, there was also no evidence that nutrient enrichment affected the frequency of attack by its natural enemies. In contrast, the bottom-up effects of nutrient enrichment dramatically increased the frequency of the periderm miner in each zone, and its occurrence mirrored the growth responses by the trees to fertilization (Feller et al. 2003). Specifically, in the dwarf zone, +P caused more than a sevenfold increase in the frequency of mines. In the fringe, +N caused a fivefold increase. Moreover, in the transition zone, both +N and +P caused a fivefold increase. Unlike the foliage-feeding herbivores on *R. mangle*, the foraging strategy of the periderm-mining *Marmara* sp. supported our hypothesis that +N and +P affected primary consumption differentially depending on position along the tree height gradient and nutrient limitation. *Marmara*'s preference for vigorously growing stems is also consistent with Price's (1991) prediction that many specialized herbivores feed preferentially on the more vigorous plants or plant modules in a population. The feeding stages of *Marmara* spp. are sap feeders within living tissue (Wagner et al. 2000). The *R. mangle* periderm where this species of *Marmara* feeds is live tissue found on vigorously growing trees (Gill and Tomlinson 1969). In contrast, this species is not able to feed in the suberized bark of the slow-growing dwarf and fringe trees (Feller 1995). In our fertilization experiment at Twin Cays, shoot elongation and the number of new shoots increased dramatically when trees were fertilized with +P in the dwarf zone, with +N and +P in the transition zone, and +N in the fringe zone (Feller et al. 2003). Nutrient enrichment stimulated the production of shoots with thin, living periderm, which provided an abundant food source for the periderm-mining *Marmara*. Thus, our results showed that the periderm miner was controlled by nutrient availability while the leaf miner was more likely controlled by natural enemies. Similar results have been found in other systems where the relative importance of bottom-up and top-down effects varied depending on the feeding mode of the herbivore (Moon and Stiling 2002).

Loss of yield, which was the direct consequence of bud damage by the bud moth *Ecdytolopha* sp., was an important but complicated form of herbivory to quantify and compare with the more straightforward damage caused by other folivores. Nevertheless, this indirect form of herbivory leading to a combination of reduced leaf size, aborted leaves, and dead apical buds, resulted in a substantial loss of 10–36% of the leaf area in the canopy, which is similar to levels of bud damage reported by Onuf et al. (1977) for *R. mangle* in Florida (USA) and by Burrows (2003) for *Rhizophora stylosa* in Queensland (Australia). Although not influenced by nutrient treatment, loss of yield was particularly high in the transition zone where *Ecdytolopha* sp. killed more than 20% of all apical buds in the canopy. The reasons for the spatial variation in distribution of *Ecdytolopha* sp. across the mangrove landscape are not clear. However, the dense, scrubby vegetation in the transition zone may have provided this small moth with more protection than the more open forests in the fringe or dwarf zones. Because twigs with dead apical buds were no longer capable of producing new leaves or forming new growing points (Gill and Tomlinson 1969), the proportion of dead buds represents a large loss in future leaf production. Thus, the damage that resulted from this bud moth feeding represented a greater reduction of leaf biomass from the *R. mangle* canopy than that due to all folivores combined.

To summarize, the purpose of this study was to use a long-term fertilization experiment to determine the impact of nutrient enrichment and spatial heterogeneity in forest structure on trophic interactions between *R. mangle* and its herbivores. We predicted that herbivory would increase with structural complexity and a positive growth response to nutrient enrichment. Previous studies showed that nutrient enrichment had enormous impacts on primary producers that varied by zone along a tree height gradient (McKee et al. 2002; Feller et al. 2003). However, this effect did not uniformly cascade to the next trophic level. Rather, the

relative importance of each factor depended on the herbivore and the spatial scale at which measurements were made (Wiens 1989). Similarly to Goranson et al. (2004), our data suggest that different herbivore species measure plant quality in different ways. Reduction in leaf area through loss of yield resulting from bud damage by *Ecdytolopha* sp. was greater than damage by all folivores combined at Twin Cays, but spatial variation in habitat quality for this species was not related to nutrient enrichment. Similarly, location within the mangrove and herbivore behavior appeared to control the distribution and damage by the dominant folivore, *A. pisonii*, in a way unrelated to leaf nutritive quality per site. The periderm-mining *Marmara* sp. was the only herbivore species where the mechanisms governing its distribution were clearly related to nutrient availability at all scales examined. In contrast, its leaf-mining sister species was more likely controlled by natural enemies. Our data for this mangrove ecosystem indicated that herbivores' responses to nutrient enrichment also depended on habitat heterogeneity coupled with feeding strategies and species-specific behavior.

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