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SEEDLING SURVIVORSHIP, GROWTH, AND RESPONSE TO DISTURBANCE IN BELIZEAN MANGAL[1]

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Species zonation patterns across tidal gradients in mangrove forests are formed by successful seedling establishment and maintained by replacement of adults by conspecific seedlings. These two processes rarely have been examined experimentally in neotropical mangal. We studied survivorship and growth of seedlings of two species of mangrove, *Rhizophora mangle* L. and *Avicennia germinans* (L.) Stearn, across a tidal gradient in Belize, Central America. Propagules of each species were planted in common gardens at tidal elevations corresponding to lowest low water (LLW), mean water (MW), and highest high water (HHW). Sixty-nine percent of *Rhizophora* seedlings planted at MW and 56% of those planted at LLW survived 1 year. Forty-seven percent of MW *Avicennia* seedlings also survived 1 year. No individuals of either species survived at HHW, and neither did any LLW *Avicennia* seedlings. Among the surviving *Rhizophora* seedlings, LLW seedlings grew more rapidly in terms of height, diameter, leaf production, and biomass than did MW seedlings. Insect herbivory was twice as high on MW seedlings as on LLW *Rhizophora* seedlings. We also examined the response of established *Rhizophora* seedlings to experimental removal of the adult *Rhizophora* canopy. Seedlings in canopy removal areas had higher survivorship, grew twice as fast, produced more leaves, and had less than half the herbivory of seedlings growing beneath an intact canopy. These results provide insights into underlying causes and maintenance of zonation in Caribbean mangrove forests.

Mangrove forests, or mangal, are characterized by one or more species of salt-tolerant trees that form distinct monospecific zones along tropical protected coastlines (Davis, 1940; Lugo and Snedaker, 1974; Chapman, 1976; Tomlinson, 1986). On neotropical coastlines, mature stands of the red mangrove *Rhizophora mangle* L. (Rhizophoraceae) extend from the lowest reaches of the intertidal to the highest reaches of the tides, with maximum density between lowest low water (LLW) and mean water (MW). Mature *Avicennia germinans* (L.) Stearn (Avicenniaceae), the black mangrove, dominate the regions between MW and high water (HW). The white mangrove (*Laguncularia racemosa* [L.] Gaertn., Combretaceae) and the buttonwood (*Conocarpus erectus* L., Combretaceae) predominate from HW to highest high water (HHW) (Davis, 1940; Lugo and Snedaker, 1974; Chapman, 1976; Rabinowitz, 1978b; taxonomy follows Tomlinson, 1986).

Species zonation in mangal has been correlated with land-building properties of 'pioneer' mangroves and subsequent autogenic species-by-species replacement in the higher intertidal (Davis, 1940; Cintrón et al., 1978), tidal flow and geomorphology (Thom, 1967, 1975), and/or environmental conditions that change predictably with tidal elevation. The latter include soil salinity (Morrow and Nickerson, 1973; Naidoo, 1985; López-Portillo and Ezcurra, 1989), anoxia and waterlogging (Kuraishi et al., 1985; Naidoo, 1985; Thibodeau and Nickerson, 1986; McKee and Mendelssohn, 1987; López-Portillo and Ezcurra, 1989), soil sulfide levels (Hart, 1959; Nickerson and Thibodeau, 1985; McKee, Mendelssohn, and Hester, 1988), and nutrient availability (Boto and Wellington, 1984). Mangrove roots themselves modify soil sulfide levels, redox potentials (McKee, Mendelssohn, and Hester, 1988), and salinity (Passioura, Ball, and Knight, 1992), and burrowing crabs modify soil nutrient and oxidation levels around mangrove roots (Smith et al., 1991). Other investigators have proposed that biotic interactions such as interspecific competition (Ball, 1980), tidal sorting of propagules (Rabinowitz, 1978a, b, c), light available to seedlings (Smith, 1987a), and differential seedling predation (Smith, 1987c; Smith et al., 1989) control mangrove zonation. Explanations of zonation patterns based on land-building and edaphic factors predict that each species will establish and grow successfully only in a specific tidal zone, while explanations based on biotic interactions predict that species may establish across an entire tidal gradient, but grow successfully only in one tidal zone. We contrasted these alternative predictions by planting mangrove seedlings of different species in different tidal zones and observing their survivorship and subsequent growth.

Mangrove zonation patterns are *established* initially as new propagules colonize available substrate at the leading edge of the mangal, and as species replacement occurs at higher tidal elevations in a predictable sequence (Lugo, 1980). Rabinowitz (1978a, b, c) showed experimentally that mangrove zonation along the Pacific coast of Panama could be established by tidal sorting: the different depths at which the viviparous propagules of each species would strand. Rabinowitz found that the ≈20-cm-long propagules of *Rhizophora* stranded in deep water, while the smaller propagules of *Laguncularia* and *Avicennia* floated further into shore and normally stranded above MW. Jiménez and Sauter (1991) also found tidal sorting ex-

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plained zonation patterns on the Pacific coast of Costa Rica, but zonation of mangroves in Australian mangal does not appear to be related to propagule size (Tomlinson, 1986).

Smith and his colleagues have demonstrated experimentally that zonation patterns in Australian mangal are more related to differences in predation pressure in different tidal zones than to differential light availability across a tidal gradient (Smith, 1987b, c; Smith et al., 1989; Osborne and Smith, 1990). The role(s) of other herbivores, such as insects, in propagule colonization and establishment has been explored only in Australia (Robertson, Giddens, and Smith, 1990), despite repeated observations that neotropical insect foliovores consume up to 30% of seedling leaf tissue (Farnsworth and Ellison, 1991, in press; Feller, 1993). Foliovores may be especially important in regions such as the Caribbean where propagule predation rates are significantly lower than in Australasian mangal (Smith et al., 1989).

For zonation to be *maintained* in mangal, adults must be replaced by conspecifics following small-scale, localized disturbance. However, there are no studies of the response of mangroves to disturbance (Roth, 1992), despite intense interest in 'gap dynamics' in temperate and tropical forest research (reviewed in Pickett and White, 1985; Denslow, 1987). Part of the reason for the paucity of studies on mangal regeneration and the maintenance of zonation has been the general perception that mangal is a 'steady-state' as opposed to 'successional' ecosystem (Lugo, 1980). In addition, mangroves often lack a significant understory of either conspecifics or heterospecifics (Janzen, 1985; Corlett, 1986; Lugo, 1986; Snedaker and Lahmann, 1988), which would be required for detailed studies of regeneration dynamics. Rabinowitz (1978c) found that seedlings of *Rhizophora* could persist for >1 year in the understory, but that seedling cohorts of *Avicennia, Laguncularia,* and *Pelliciera rhizophorae* Planch & Triana (Theaceae) rarely survived more than 6 months beneath intact conspecific or heterospecific adults. We have observed similar patterns of *Rhizophora, Avicennia,* and *Laguncularia* seedling survivorship in Belize (E. J. Farnsworth and A. M. Ellison, unpublished data).

Here, we report results of experiments examining factors affecting both establishment and maintenance of zonation in Belizean mangal. We studied survivorship and early seedling growth of *Rhizophora mangle* and *Avicennia germinans* planted into three tidal zones, and the impact of insect herbivory on these seedlings. We also examined the regeneration of suppressed *Rhizophora* seedlings following experimental, small-scale disturbance to the adult canopy. This is the first set of manipulative experiments on mangrove seedling growth across a tidal gradient in the Caribbean region. Along with the experiments of Rabinowitz (1978a, b, c) on the Pacific coast of Panama, and those of Jiménez and Sauter (1991) in western Costa Rica, these experiments sketch the beginnings of a more complete picture of the causes and maintenance of species patterning in neotropical mangal.

SITE DESCRIPTION

We studied mangrove seedlings in the Placencia Lagoon on the western shore of the Placencia Peninsula, Stann Creek District, Belize, Central America. A map and detailed description of this site is given by Farnsworth and Ellison (1991). This lagoon is shallow (<1.5 m depth) and brackish, with salinities ranging from 12 to 34 ppt (Ellison and Farnsworth, 1992). Tidal amplitude in the lagoon is ≈30 cm, the range found throughout coastal Belize (Kjerfve, Rützler, and Kierspe, 1982). Placencia Lagoon lies within the tropical moist transition-to-subtropical moist life zone (Holdridge, 1967; Hartshorn et al., 1984) and receives annually 2,000–2,700 mm of rainfall (Hartshorn et al., 1984).

Four mangrove species occur in the lagoon, in distinct zones correlated with tidal height (Farnsworth and Ellison, 1991). From LLW to MW, *Rhizophora mangle* forms a 20- to 200-m-wide monospecific stand of trees 0.5–3 m tall. From MW to HHW, the community is a mixture of *Avicennia germinans, Conocarpus erectus,* and scattered *Laguncularia racemosa* and *Rhizophora.* Above HHW, the peninsula's vegetation is dominated by the palmetto *Paurotis wrightii* (Griseb. & Wendl.) Britt. In the parlance of Lugo and Snedaker (1974), this mangal is a 'fringe mangrove' forest. The soils underlying this mangal are of the Turneffe and Shipstern series (Flores, 1952): a littoral complex of organic peat and swamp/muck soils, and sandy soils derived from dune sands, coral rubble, and upland quartz sands (Hartshorn et al., 1984).

MATERIALS AND METHODS

Establishment—In open areas (no adult canopy) within each of three tidal zones—LLW, MW, HHW—we established four 50 × 50-cm quadrats: two *Rhizophora* monospecific stands and two *Avicennia* stands. Newly fallen propagules were collected on 12 January 1988, and 16 propagules were planted into each quadrat in 4 × 4 arrays; the minimum linear distance between each seedling was 10 cm. Treatment sample sizes were 32 seedlings/species/tidal zone. Because of the lack of tidal benchmarks, we distinguished tidal zones by duration and frequency of inundation. Seedlings in the LLW zone were exposed only at ebb tides during full and new moons. Seedlings at MW were exposed twice daily at low tide, while seedlings at HHW were flooded only during full and new moon flood tides. Quadrats were fenced with plastic mesh screening to prevent seedling predation by grapsid crabs. We monitored changes in seedling height (±1 mm from ground level to the base of the topmost leaf pair) and stem diameter (±0.1 mm at the cotyledonal scar) at ten irregular intervals between 12 January and 19 December 1988. We also counted the number of leaves and number of leaf scars at each sampling date to obtain a measure of leaf production and turnover rate. Leaf area and loss of leaf tissue to insect herbivory were estimated at final harvest with transparent overlays divided into 25-mm^2 squares (Farnsworth and Ellison, 1991). This technique gives results within 2% (on average) of those obtained with a desktop leaf area meter (Farnsworth and Ellison, in press). On 17 December 1988, all seedlings were harvested, sun-dried for 1 week, and weighed (±0.1 g).

Regeneration following disturbance—To examine regeneration of established *Rhizophora* seedlings growing under a canopy of 3–5-m-tall mature adults, we removed

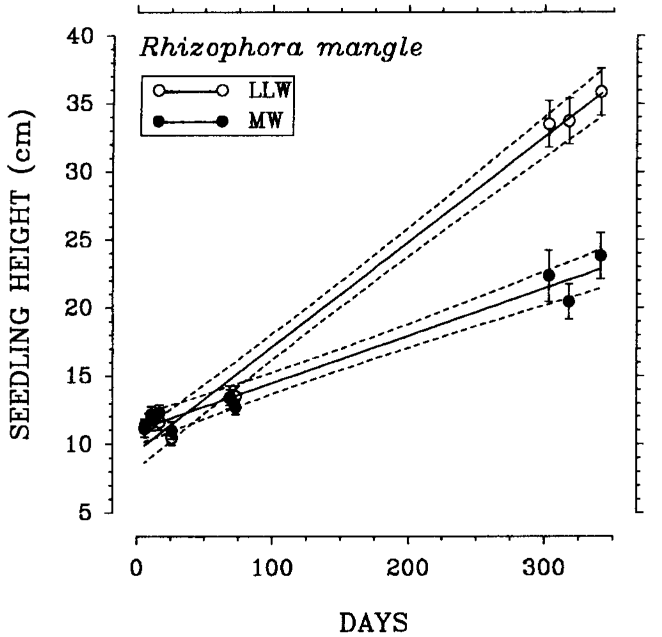

Fig. 2. Height growth of *Rhizophora* seedlings growing at LLW and MW. Values shown are $\bar{X} \pm 1$ SD. Solid lines are best-fit model I linear regessions; dotted lines are 95% confidence bands for the regression lines.

6.5 (6.7) ± 1.98 mm. Total leaf production over the year was significantly higher ($P = 0.004$) for LLW *Rhizophora* seedlings (13 [13] ± 3.6 leaves) than for MW seedlings (11 [11] ± 3.5 leaves). However, at the final harvest, seedlings in both zones had similar number of leaves remaining (LLW seedlings: 7 [7] ± 2.6; MW seedlings: 8 [7] ± 3.5; $P = 0.456$). Thus, leaf turnover rate was more rapid at LLW than at MW. Between planting and harvest 1 year later, *Avicennia* seedlings growing at MW increased in height from 6.9 (6.3) ± 2.59 cm to 9.7 (10.0) ±1.67 cm, increased in diameter from 2.9 (2.5) ± 1.9 mm to 3.5 (3.2) ± 0.94 mm, and produced 9 (9) ± 1.7 leaves. Individual HW *Rhizophora* and *Avicennia* seedlings and LLW *Avicennia* seedlings did not show significant increases in height or diameter prior to death.

Consonant with their greater height, LLW *Rhizophora* seedlings were significantly heavier at harvest than MW *Rhizophora* seedlings (LLW seedlings: 21.6 [22.0] ± 9.83 g; MW seedlings: 14.2 [12.2] ± 5.81 g; $P = 0.023$). Relative allocation of biomass to leaves, stems, and roots also differed between *Rhizophora* seedlings in these two zones (Fig. 3). Compared to surviving MW seedlings, LLW seedlings allocated significantly more biomass to stems ($P = 0.105$) and roots ($P = 0.034$) and less biomass to leaves ($P < 0.001$). These differences in biomass allocation patterns reflect actual differences, not epiphenomena of different numbers or sizes of leaves in the different habitats. Seedlings in both zones had ≈7 leaves at harvest (see above), and these leaves did not differ in absolute biomass (LLW seedlings: 3.9 [4.0] ± 1.94 g; MW seedlings: 3.8 [3.4] ± 1.97 g; $P = 0.860$). Surviving (MW) *Avicennia* seedlings were an order of magnitude lighter than MW *Rhizophora* seedlings, with a mass at harvest of 1.1 (0.9) ± 0.59 g. Biomass allocation by *Avicennia* to leaves, stems, and roots is shown in Fig. 3; *Avicennia* seedlings allocated proportionately more biomass to stems than did *Rhizophora* seedlings.

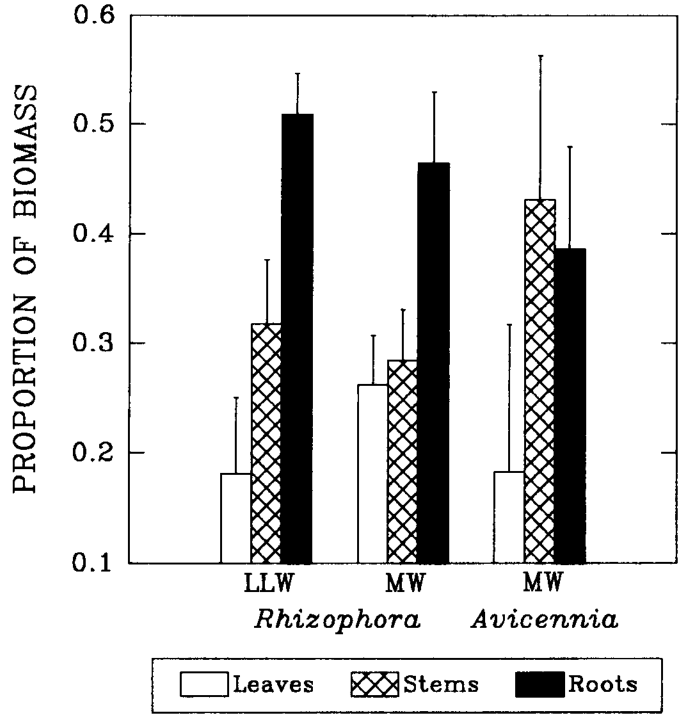

Fig. 3. Proportion ($\bar{X} \pm$ SD) of final dry biomass in roots, stems, and leaves by LLW and MW *Rhizophora* seedlings, and MW *Avicennia* seedlings.

Insect herbivory determined at final harvest was significantly greater ($P < 0.001$, parametric ANOVA on angular-transformed data) on the slower-growing MW *Rhizophora* seedlings (7.1 ± 10.7% of leaf tissue removed) than on the more rapidly growing LLW seedlings (3.7 ± 6.2% of leaf tissue removed). To assess the effects of herbivory on *Rhizophora* seedling growth over the year, we examined the relationship between relative change in stem volume (= [final volume − initial volume]/initial volume) and total fraction of leaf tissue lost per seedling (= [Σ_1^N leaf area lost to herbivores]/[Σ_1^N leaf area], where N = the number of leaves per seedling). Because we did not have a value for initial (at time of planting) seedling dry mass, we used stem volume (= $\pi \cdot$seedling height$\cdot$[stem diameter/2]^2) as a surrogate for mass. At the final harvest, seedling dry mass was reasonably well predicted by linear regression on stem volume (dry mass = 8.661 ± 0.543$\cdot$ stem volume; $r^2 = 0.669$, $P < 0.001$). There was a significant negative relationship between the fraction of leaf tissue eaten by herbivores and the seedlings' changes in stem volume (Kendall's rank correlation coefficient $\tau = -0.303$, $N = 36$ seedlings, $P < 0.01$; Fig. 4). Insects consumed 11.1 ± 32.99% of the leaf tissue of MW *Avicennia* seedlings. As with *Rhizophora*, there was a negative relationship between insect herbivory and change in stem volume. However, this relationship was not significant for *Avicennia* ($\tau = -0.156$, $N = 14$ seedlings, $P > 0.10$).

Regeneration after disturbance—Survivorship of seedlings after 1 year was lower among seedlings under intact canopy (78%) than in canopy removal plots (90%). Prior

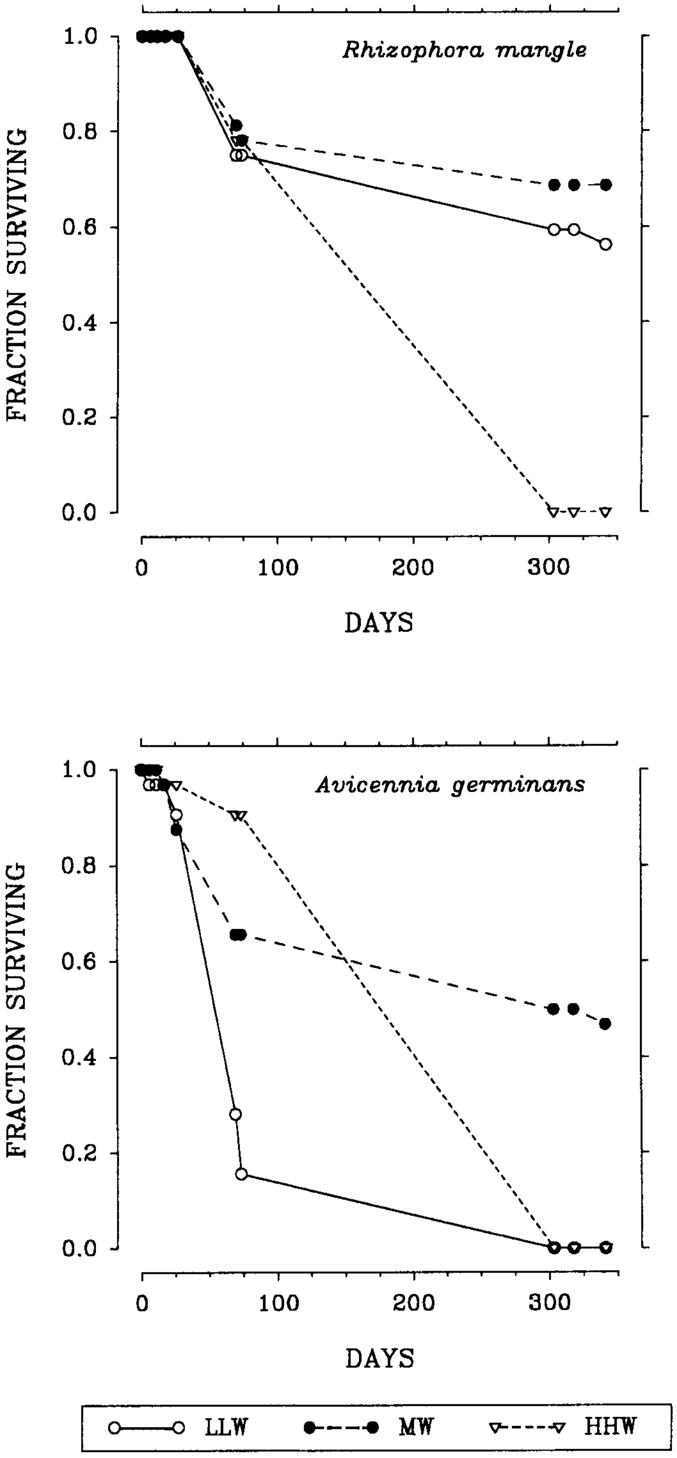

Fig. 1. Survivorship curves of *Rhizophora* and *Avicennia* seedlings planted in common gardens in three tidal zones.

the adult canopy in three 3 × 3-m quadrats in the MW zone. This size canopy opening is created by the death or fall of one to two trees in this mangal (A. M. Ellison and E. J. Farnsworth, personal observation). All branches and foliage above 1 m were cut with a machete on 21 March 1988. All cut plant material was removed from the quadrats to minimize potential nutrient enrichment of the quadrat resulting from litter decomposition. Two additional 3 × 3-m quadrats were established as controls. These control quadrats were within 50 m of the canopy removal quadrats, and had similar densities of established seedlings in the understory. The canopies over the control quadrats were left intact. In both canopy removal and canopy control quadrats, we tagged all the established seedlings, and followed them for 1 year as described above for the transplant experiments. The average distance between seedlings was 26.0 ± 22.06 (SD) cm in the canopy control quadrats and 20.3 ± 18.25 cm in the canopy removal quadrats. There were no differences in initial seedling densities between treatments ($P = 0.103$, ANOVA) or quadrats within treatments ($P = 0.141$, ANOVA), both of which were ≈½ the density of the seedlings in the common gardens used in the establishment experiments. Leaf scars were not counted on these seedlings, because secondary thickening and a history of slow growth obscured them and made counts unreliable (cf. Duke and Pinzón M., 1992). All seedlings in the canopy removal and control quadrats were harvested on 17 December 1988, sun-dried for 1 week, and weighed (±0.1 g). The absence of an understory of *Avicennia* seedlings beneath mature *Avicennia* trees precluded a similar experiment with this species.

Statistical analyses—We used distribution-free (nonparametric) statistics for most analyses because the data generally were heteroscedastic and transformations did not equalize or normalize variances. Therefore, in addition to means and standard deviations, we report medians and quartiles in the results. Unless otherwise noted in the results, we used the Mann-Whitney U test for pairwise comparisons, and Kruskal-Wallis one-way nonparametric ANOVA for multiple comparisons across single treatments. Analyses were performed using Systat *ver.* 5.01 (Wilkinson, 1990) or S-Plus for DOS *ver.* 2.0 (Becker, Chambers, and Wilks, 1988) on an IBM workstation. Details of statistical analyses are presented in the results below.

RESULTS

Establishment and growth—Survivorship of both *Rhizophora* and *Avicennia* seedlings was highest in the MW zone (Fig. 1). Of the three *Rhizophora* seedling populations, no HHW seedlings, 56% of the LLW seedlings, and 69% of the MW seedlings survived the year. After 1 year, 47% of the *Avicennia* seedlings remained alive at MW, while none of the *Avicennia* seedlings survived in either LLW or HHW gardens. Based on the Mantel-Haenszel log-rank test for censored survivorship data (Pyke and Thompson, 1986), mortality rates differed significantly among all three populations of each species (*Rhizophora*: $\chi^2_2 = 35.5$, $P = 1.92 \times 10^{-8}$; *Avicennia*: $\chi^2_2 = 23.5$, $P = 8.03 \times 10^{-6}$).

Despite their lower survivorship, LLW *Rhizophora* seedlings increased in height at twice the rate of MW *Rhizophora* seedlings (Fig. 2). Increases in stem diameter followed a similar pattern: LLW *Rhizophora* seedlings grew from a mean of 3.9 (median = 4.0) ± 0.99 (SD) mm at planting to 9.1 (9.2) ± 2.09 mm at harvest, and MW *Rhizophora* seedlings grew from 3.3 (3.0) ± 0.85 mm to

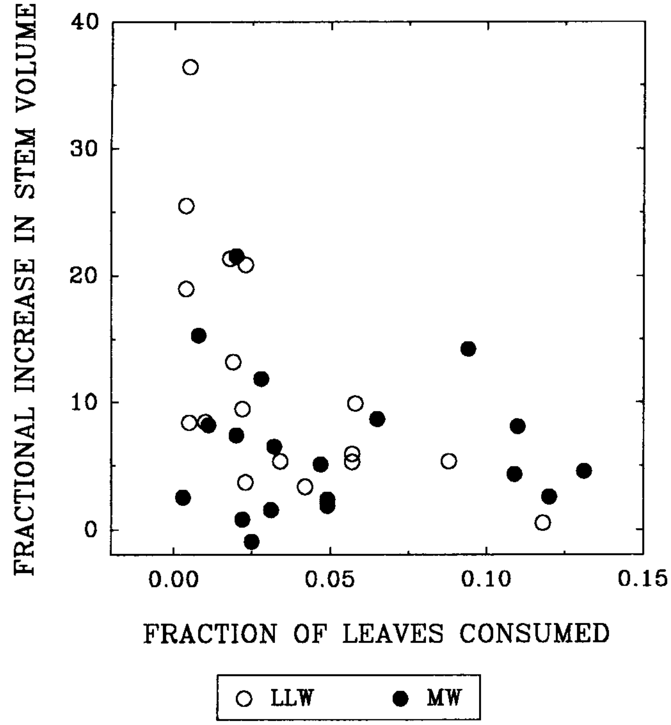

Fig. 4. Relationship between the fraction of *Rhizophora* leaves consumed by herbivores and the annual increase in seedling stem volume. Note that LLW *Rhizophora* seedlings grew more rapidly and suffered less herbivory than MW seedlings. No relationship was found for *Avicennia,* so those data are not plotted. See text for statistics.

to canopy removal, there were no significant differences among quadrats in understory seedling height (Control: 29.79 [27.50] ± 9.73 cm; Removal: 31.97 [29.40] ± 12.14 cm, $P = 0.234$) or number of leaves (Control: 5 [5] ± 2.1; Removal: 5 [4] ± 2.1, $P = 0.189$). Initial mean diameter was slightly larger among seedlings in removal quadrats (Control: 4.56 [4.00] ± 1.91 mm; Removal: 5.82 [5.30] ± 2.18 mm, $P < 0.001$).

After 1 year, seedlings in the removal quadrats had produced significantly more leaves ($P = 0.003$) and were significantly heavier (total dry mass = roots + shoots) ($P = 0.040$) than seedlings in the control quadrats (Fig. 5). The apparent significant difference in diameter between seedlings in control and seedling quadrats ($P = 0.001$; Fig. 5) was, however, an artifact of the difference in initial seedling diameters. When the latter were taken into account by examining the relative change in stem diameters, the difference disappeared ($P = 0.384$; Fig. 5). In contrast, although the final absolute seedling heights were not significantly different because of the extremely high variance among seedlings ($P = 0.10$; Fig. 5), the relative change in height between seedlings in the two treatments was significantly different ($P = 0.009$; Fig. 5). Seedlings in removal quadrats increased in height at twice the rate of their counterparts beneath the intact canopy.

Biomass allocation patterns also differed between seedlings in the two treatments (Fig. 6). Allocation of biomass to roots did not differ between treatments ($P = 0.384$). Seedlings in the control quadrats allocated proportionately more biomass to stems ($P = 0.022$) and less to leaves ($P = 0.010$) than did seedlings in canopy removal quadrats. The latter result is due to the significantly greater leaf production ($P = 0.003$) of seedlings in the canopy removal quadrats (5 [5] ± 2.5 leaves at harvest) relative to seedlings beneath intact canopy (4 [4] ± 1.7 leaves at harvest).

The percent of leaf tissue lost to insect herbivores also differed between the two treatments. Herbivores removed an average of 10.6 ± 0.8% of leaf area of seedlings in canopy removal quadrats ($N = 459$ leaves), and 23.5 ± 1.8% of leaf area of seedlings beneath the intact canopy ($N = 208$ leaves) ($P < 0.001$, parametric ANOVA on angular-transformed data).

DISCUSSION

Establishment and maintenance of species zonation patterns in Belizean mangal result from differential seedling survivorship, growth, and response to disturbance among mangrove species. Seaward expansion of mangrove forests occurs in the lower intertidal, and only *Rhizophora* seedlings establish in the LLW zone (Fig. 1). Growth rate (Fig. 2) and leaf production are most rapid at LLW. Compared to MW *Rhizophora* seedlings, it appears that LLW seedlings are allocating significantly more biomass to roots (possibly for anchoring in submerged conditions) and stems (possibly to place leaves above water) (Fig. 3). *Rhizophora* seedlings growing at MW suffered twice the herbivory of LLW seedlings, contributing to the observed lower growth rates of the former. Patterns of herbivory in this experiment are consistent with previous mangal-wide surveys (Farnsworth and Ellison, 1991). Given lower herbivory rates on, and higher growth rates of LLW *Rhizophora,* together with the inability of *Avicennia* to establish at LLW, it is not surprising that *Rhizophora* predominates in this zone in Belizean mangal.

At MW, the situation is more complex. Mixed species stands of adult mangroves, common above MW, occur in part because both *Avicennia* and *Rhizophora* can establish successfully in this zone. Both *Rhizophora* and *Avicennia* grow well at MW, and relative abundances of adults in this part of the mangal may be influenced by interspecific competition (Ball, 1980). Experimental work on interspecific competitive interactions among mangroves is sorely needed in both the neotropics and paleotropics. Insect herbivory, which negatively impacts seedling growth (Fig. 4), also may influence the outcome of competitive interactions between *Avicennia* and *Rhizophora.* Such indirect effects of insect herbivores on plant competitive dynamics have been observed in salt marshes (Ellison, 1991) and old-fields (Bentley and Whittaker, 1979; Whittaker, 1979). The existence of significant levels of insect herbivory in mangal has been pointed out only recently (Feller and Mathis, 1988; Farnsworth and Ellison, 1991, in press; Feller, 1993), and the role of insect herbivores in neotropical mangrove community structure has not been investigated experimentally.

Species zonation in Belizean mangal is maintained in part by the lack of a heterospecific understory beneath the *Rhizophora* canopy, which could replace the existing species following disturbance. We found that suppressed *Rhizophora* seedlings respond to disturbance (canopy removal) with rapid stem elongation and expansion (Fig.

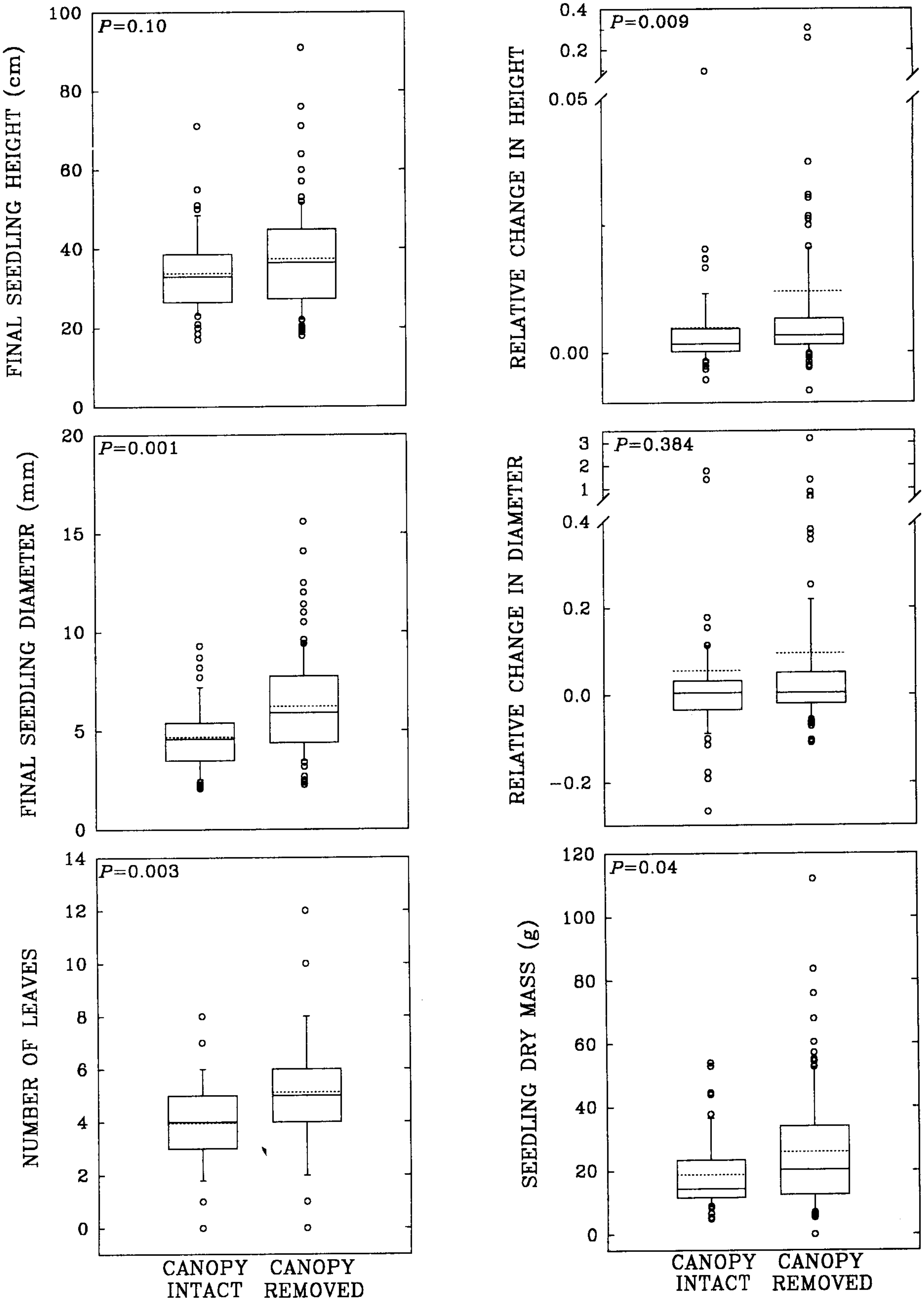

Fig. 5. Growth responses of *Rhizophora* seedlings to experimental removal of the adult canopy. On each box-plot, the median is indicated by the solid horizontal line in the center of the box, the mean by the dotted line, and upper and lower quartiles by the top and bottom of the box, respectively. The whiskers extend to the data points at the 10th and 90th percentiles; individual data points outside these deciles are shown by individual circles. Treatments are indicated on the x-axis. Results of Kruskal-Wallis nonparametric ANOVA examining treatment effects for each variable are shown in the upper left corner of each frame.

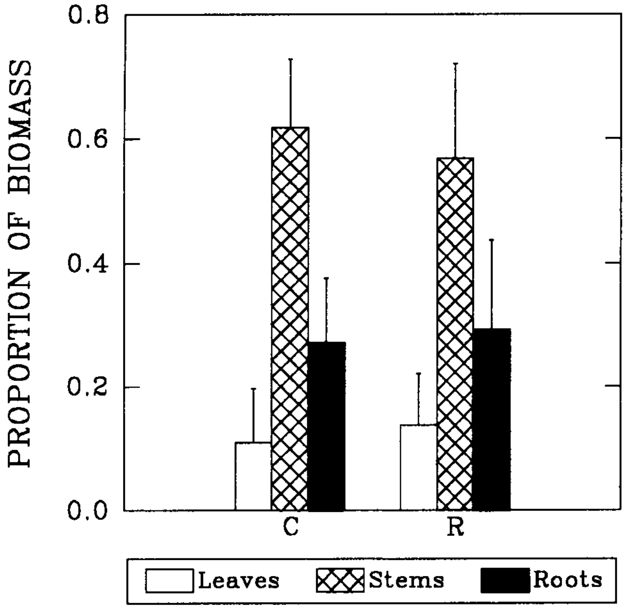

Fig. 6. Proportion ($\bar{X} \pm$ SD) of final dry biomass in roots, stems, and leaves by *Rhizophora* seedlings beneath intact canopy (C) and in the canopy removal (R) quadrats.

5), and increased biomass allocation to leaves (Fig. 6). This observed growth response of seedlings to canopy removal could result from responses to increased light, increased soil nutrients resulting from decomposition of roots (leaf and stem litter were removed; see Materials and Methods), and/or the interaction of light and nutrients. Phosphorus has been found to be the primary nutrient limiting *Rhizophora* growth at or above MW in Belize (Feller, 1993) and Australia (Boto and Wellington, 1983). We have no data on mineralization of P released from decomposing roots, and such data have never been collected from any mangal. Data from mangroves in Australia (Boto and Wellington, 1983) and Taiwan (Chou and Bi, 1990) indicate that foliar P content is highly correlated with soil P, but root and stem P contents are significantly lower than leaf P content and appear to be uncorrelated with soil P (Chou and Bi, 1990). Because we removed leaf and stem litter from our canopy removal quadrats, we suspect that we minimized potential fertilization effects attributable to litter decomposition, and that the growth response that we observed was primarily a response to increased light availability. The observed rapid response of suppressed mangrove seedlings to increased light is consistent with expectations derived from studies of early successional understory species in other tropical and temperate forests (e.g., Bazzaz, 1979; Bazzaz and Pickett, 1980; Pickett and White, 1985; Denslow, 1987). Tomlinson (1986) observed that *Rhizophora* possesses life-history traits characteristic of both early- and late-successional species; such phenotypic plasticity likely contributes to the relatively high abundance of *Rhizophora* in the understory of Belizean mangal and in mangal elsewhere in the neotropics (Rabinowitz, 1978c).

Seedlings of other mangrove species may appear in the *Rhizophora* understory in seasonal flushes, but these heterospecific cohorts do not appear to survive >6 months beneath intact *Rhizophora* canopy in Belize (E. J. Farnsworth and A. M. Ellison, unpublished data) or Panama (Rabinowitz, 1978c). Given the apparent low frequency of natural disturbance in Central American mangal, including the lack of regular hurricanes that make landfall on the Central American mainland south of 18°N latitude (Roth, 1992), and the discordance in timing between the hurricane season (August–October) and the dispersal of *Avicennia* and *Laguncularia* propagules (November–December; E. J. Farnsworth and A. M. Ellison, unpublished data) it is unlikely that a mature *Rhizophora* stand would be replaced autogenically by *Avicennia* or *Laguncularia* (cf. Lugo, 1980).

That neither *Rhizophora* nor *Avicennia* can recruit successfully to HHW makes adult tree distributions at this tidal elevation somewhat puzzling. Occasional *Avicennia* individuals are observed in the higher reaches of the mangal; these individuals may reflect establishment events that occurred when such areas were at lower elevation (cf. Davis, 1940; Thom, 1967). Adult *Avicennia* individuals predominate from MW to HHW, and adult *Laguncularia* and *Conocarpus* predominate at the upper margins of the mangal. *Avicennia* propagules can clearly establish and grow at MW in open areas. However, that *Avicennia* seedlings can clearly germinate, but do not persist, beneath adult mangrove canopies at or above MW (Rabinowitz, 1978c; E. J. Farnsworth and A. M. Ellison, unpublished data) implies that *Avicennia* may be a true gap-specialist, dependent on chance disturbance for successful establishment. Maintenance of an adult *Avicennia* zone likely depends more on its inferred competitive superiority under conditions of fluctuating salinity relative to *Rhizophora* (Ball, 1980) than on replacement by conspecific seedlings. Our current studies of *Avicennia* and *Laguncularia* seedling establishment and growth should provide information about processes affecting species zonation at the upper edge of the mangal.

Although we did not measure soil edaphic conditions (due to logistical constraints at the field site), our observations of survivorship and growth of *Avicennia* and *Rhizophora* accord with correlative studies of mangrove growth as a function of edaphic factors that vary in predictable ways across tidal gradients (e.g., Chapman, 1976; Patterson and Mendelssohn, 1991). Tidal inundation and waterlogging is normally greatest and available oxygen (redox potential) is lowest at LLW. *Rhizophora* is tolerant of these conditions, while *Avicennia* is not (e.g., Naidoo, 1985; López-Portillo and Ezcurra, 1989). Soil salinity usually declines with elevation, although local areas of high salinity, such as salt pans, can occur near HHW, and *Avicennia* is known to be more tolerant of high salinity than *Rhizophora* (Walsh, 1974; Cintrón et al., 1978; Ball, 1988). The general patterning of species in Belizean mangal, and their behavior when transplanted, is reminiscent of similar situations in temperate-zone salt marshes: the lower elevational limit of a species is determined by edaphic or physiological factors, while the upper elevational limit is determined by biotic interactions, notably competition (Bertness and Ellison, 1987) and herbivory (Ellison, 1987, 1991). Future experimental investigations on mangrove establishment should focus on the interactions among edaphic conditions, plant ecophysiology, competition, and herbivory.

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