Population Ecology

Propagule size and predispersal damage by insects affect establishment and early growth of mangrove seedlings

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Abstract Variation in rates of seedling recruitment, growth, and survival can strongly influence the rate and course of forest regeneration following disturbance. Using a combination of field sampling and shadehouse experiments, we investigated the influence of propagule size and predispersal insect damage on the establishment and early growth of the three common mangrove species on the Caribbean coast of Panama: *Avicennia germinans*, *Laguncularia racemosa*, and *Rhizophora mangle*. In our field samples, all three species exhibited considerable intraspecific variation in mature propagule size, and suffered moderate to high levels of predispersal attack by larval insects. Rates of insect attack were largely independent of propagule size both within and among trees. Our experimental studies using undamaged mature propagules showed that, for all three species, seedlings established at high rates regardless of propagule size. However, propagule size did have a marked effect on early seedling growth: seedlings that developed from larger propagules grew more rapidly. Predispersal insect infestations that had destroyed or removed a substantial amount of tissue, particularly if that tissue was meristematic or conductive, reduced the establishment of propagules of all three species. The effect of sublethal tissue damage or loss on the subsequent growth of established seedlings varied among the three mangrove species. For *Avicennia*, the growth response was graded: for a propagule of a given size, the more tissue lost, the slower the growth of the seedling. For *Laguncularia*, the response to insect attack appeared to be all-or-none. If the boring insect penetrated the outer spongy seed coat and reached the developing embryo, it usually caused sufficient damage to prevent a seedling from developing. On the other hand, if the insect damaged but did not penetrate the seed coat, a completely healthy seedling developed and its growth rate was indistinguishable from a seedling developing from an undamaged propagule of the same size. Similar to *Avicennia*, if an infestation did not completely girdle a *Rhizophora* seedling, it survived, but grew at a reduced rate. In summary, our experiments demonstrated that natural levels of variation in propagule size and predispersal damage by insects translate into significant differences in seedling performance in terms of establishment and/or early growth. Such differences are sufficiently large that they could influence the intensity and outcome of competitive interactions during forest regeneration.

Introduction

Seedling establishment and early growth are critical phases in the life history of a plant. Typically, a very small proportion of the propagules dispersed from a parent plant survive to establish as seedlings, and many of these die soon after establishing (Harper and White 1974; Harper 1977). Under certain conditions, such early mortality can determine the density of adult plants (Andersen 1989; Crawley 1989, 1992; Louda 1989). The growth rates of individuals that do manage to survive this early period can be quite variable, even among members of the same cohort. Differences in early growth can have a marked impact on demographic features such as the age at first reproduction and lifetime reproductive output, and on the outcome of biotic interactions, especially competition (Black 1958; Scheiber 1967; Weiner 1985, 1990). In the course of regeneration following disturbance, the asymmetrical interactions among plants of different size can strongly influence the chance of an individual growing into the adult canopy (e.g. Uhl et al. 1988; Brokaw and Scheiner 1989; Poulson and Platt 1996; Brokaw and Busing 2000).

As part of our ongoing study of regeneration following lightning disturbance in mangrove forests on the Caribbean coast of Panama, we have investigated a number of factors that potentially influence the establishment and early growth of mangrove seedlings. Factors know to affect these processes include: flooding depth and period (Rabinowitz 1978; Jimenez and Sauter 1991; McGuinness 1997a; Delgado et al. 2001), soil characteristics (Jimenez and Sauter 1991; McKee 1995a), desiccation stress (Jimenez and Sauter 1991; McKee 1995a; McGuinness 1997a), and predation by crabs (Smith 1987; Smith et al. 1989; McKee 1995b; McGuinness 1997b; Sousa and Mitchell 1999; Delgado et al. 2001; Clarke and Kerrigan 2002). Two less well-studied factors that may influence the success of dispersing propagules and young seedlings are propagule size and predispersal damage by insects (Onuf et al. 1977; Robertson et al. 1990; Minchinton and Dalby-Ball 2001). We have observed considerable intraspecific variation in both these characteristics at our study sites. One would predict that the greater nutritional resources within larger propagules should result in a higher rate of seedling establishment and support more rapid early growth. Loss of tissue to predispersal insect attack could reduce nutritional reserves or damage the embryo, resulting in reduced rates of seedling establishment and growth. The study reported here assessed the influences of propagule size and level of predispersal insect damage on seedling establishment and early growth, and thus their potential to affect patterns of mangrove forest regeneration. We employed (1) sampling studies to document natural levels of intraspecific variation in propagule size and predispersal rates of attack by insects, and (2) shadehouse experiments to assess the influence of these factors on the establishment and early growth of seedlings. These studies were conducted with each of the three common mangrove tree species in our study forests.

Materials and methods

Study area and species

The study was conducted in mainland mangrove forests near the Smithsonian Tropical Research Institute's Galeta Marine Laboratory (9°24′18″N, 79°51′48.5″W) at Punta Galeta on the Caribbean coast of Panama, approximately 8 km northeast of the city of Colón (see Fig. 1 in Sousa and Mitchell 1999).

Three tree species (hereafter, referred to by their generic names) comprise the canopy of the study forests: *Avicennia germinans* (Avicenniaceae), *Laguncularia racemosa* (Combretaceae), and *Rhizophora mangle* (Rhizophoraceae). In these forests, as elsewhere (Davis [1940](#); Schaeffer-Novelli et al. [1990](#); McKee [1995](#)a; Imbert and Menard [1997](#); Sherman et al. [2000](#)), these species are distributed differentially with distance from the water's edge, forming several zones of differing canopy composition along the tidal gradient, as described in Sousa and Mitchell ([1999](#)).

All three species disperse their propagules during the rainy season (May to late December), but have fairly distinctive dispersal periods within the season (Rabinowitz [1978](#); Duke and Pinzón [1993](#); W. Sousa and B. Mitchell, personal observation). The propagules of all three species are dispersed by water, but differ in the duration and pattern of floating, and time to establishment as rooted seedlings. Dispersing propagules are transported across the forest floor by runoff following rainfall and by tidal action.

The size and shape of the three species' propagules differ markedly (see drawings in Rabinowitz [1978](#) and Tomlinson [1986](#)). *Rhizophora* has the largest propagules, averaging 223 mm in length and 17.5 g fresh weight. The species is viviparous; the dispersing hypocotyl is rod-like in shape with pointed ends, one being the plumule (embryonic shoot), and the other, the radicle. *Avicennia* propagules have a flattened ovoid shape with a short stylar beak, and average 19 mm in length and 1.0 g fresh weight. *Laguncularia* propagules have a flattened, obovoid shape and are the smallest of the three, averaging 20 mm in length and 0.6 g fresh weight. Due to the lack of propagule dormancy and waterlogged, anoxic soil conditions, these species do not develop propagule banks in the soil. As a consequence, the demography of juvenile mangroves is characterized by annual cohorts of seedlings that establish across the forest floor (W. Sousa, unpublished data).

Sampling studies

Collection of samples

For each of the three canopy species in our study area we quantified natural variation in propagule size, rate of predispersal insect attack, and level of insect damage. Samples of dispersing propagules were collected in plastic tarpaulins (1.5 m×2.1 m), suspended 0.5 m off the ground, under the canopies of individual trees. For each mangrove species, three to six actively fruiting trees were haphazardly selected for sampling within one forest stand at each of several sites within the study area (Table [1](#)). These sites were separated from each other by 0.8–2.5 km. The type of stand in which a particular species was sampled contained most of the adult trees of the target species within the study area (W. Sousa, unpublished data). *Avicennia* propagules were sampled in upper intertidal stands in which this species comprised more than 95% of the canopy trees. *Laguncularia* propagules were sampled in low to mid intertidal, mixed-species stands of *Rhizophora* and *Laguncularia*, with the latter constituting 51–74% of canopy trees. *Rhizophora* propagules were sampled in low intertidal stands of similar mixed-species composition, in which 40% of the canopy trees were *Rhizophora*.

Table 1. Propagule sampling design. Entries include the sites (BM, MN, PL, or PE) at which each species was sampled, the number of trees sampled at each site (in parentheses), sampling periods, and ranges of sample sizes

Design element	*Avicennia*	*Laguncularia*	*Rhizophora*
	BM (5), MN (5), PL (5)	BM (5), PE (5), PL (6)	1994: BM (3), PL (5)

Sites sampled			1999: BM (6), PL (4)
Sampling period(s)	12–19 July 1994	15 Sept–27 Oct 1994	6 Sept–20 Oct 1994
			25 Sept–12 Oct 1999
Range of propagule numbers collected per tree or per site[a]	36–458	94–1176	1994: 33–34
			1999: 33–44

[a]Values for *Avicennia* and *Laguncularia* are for tarpaulin collections beneath individual trees. For *Rhizophora*, tarpaulin collections from individual trees within a site were pooled

Propagule sampling periods and sample sizes per tree or site are summarized in Table 1. Captured propagules were collected from the tarpaulins every few days to minimize their likelihood of being washed or blown off. For *Avicennia* and *Laguncularia*, this sampling program allowed an analysis of variation in propagule size and rates of insect attack within and among individual adult trees, and among different sites. However, as *Rhizophora* trees produce far fewer propagules than either *Avicennia* or *Laguncularia* (Table 1), the numbers we caught per tarpaulin during our 1994 sampling were inadequate for a meaningful analysis of variation in propagule size and rate of insect attack among individual *Rhizophora* trees. Therefore, we pooled the tarpaulin samples within a site and limited our analysis to an examination of variation in these characteristics between sites. Since our sample sizes were modest, we decided to evaluate the generality of the 1994 patterns by resampling dispersing *Rhizophora* propagules in the same two sites in 1999. In addition to providing a replicate measure of intersite variation in propagule size distributions and insect attack rates, the 1999 samples afforded a measure of temporal variation in these variables.

In the laboratory, the length of each propagule in a sample was measured to the nearest mm. Propagule length is highly correlated with propagule fresh weight for all three species (*Avicennia*: $R^2=0.95$, $n=100$, $P<0.001$; *Laguncularia*: $R^2=0.85$, $n=100$, $P<0.001$; *Rhizophora*: $R^2=0.94$, $n=60$, $P<0.001$). For *Avicennia* and *Laguncularia*, 30 individuals, randomly selected from each tarpaulin collection, were inspected for insect damage by dissection. Each propagule was assigned to one of four levels of insect damage, characterized differently for the two species (Table 2). *Avicennia* propagules were attacked by larvae of a weevil (*Stenobaris* sp., Curculionidae), pyralid moth (Pyralidae), and agromyzid fly (*Phytoliriomyza* sp., Agromyzidae), which often burrowed into and fed extensively throughout the fleshy cotyledons, sometimes damaging the embryonic axis. *Laguncularia* propagules were attacked by larvae of a noctuid moth (Noctuidae).

Table 2. Categories of predispersal insect damage to *Avicennia* and *Laguncularia* propagules

Level/type of damage	Description
Avicennia	
None	No sign of insect attack
Low	$\leq$5% of embryo consumed
Medium	6–25% of embryo consumed
High	>25% of embryo consumed, often with damage to plumule
Laguncularia	
None	No sign of insect attack

External only	Seed coat bored into, but not penetrated; no damage to living tissue
Minor internal	Seed coat penetrated, cotyledons partially consumed, but minor or no damage to other tissues
Major internal	Seed coat penetrated, colyledons, plumule and radicle partially or completely consumed

For *Rhizophora*, because sample sizes were substantially smaller, all collected individuals were inspected for insect damage. The only insect found infesting *Rhizophora* propagules was the scolytid beetle, *Coccotrypes rhizophorae*, formerly known as *Poecilips rhizophorae* (Browne 1961; Woodruff 1970; Onuf et al. 1977; Rabinowitz 1977; Wood 1982; Farnsworth and Ellison 1997), which often caused extensive damage to the interior of the propagule. *Rhizophora* propagules were dichotomously scored for the presence or absence of active beetle infestations.

Statistical analyses

For *Avicennia* and *Laguncularia*, variation in mean propagule length among sites and among replicate trees within sites was examined with nested ANOVA. Replicate trees were treated as a nested factor within site; both were considered random factors. In both analyses, the dependent variable was propagule length. There was modest heterogeneity in variances among samples (Cochran's C, $P<0.05$ for both species) that was not improved by transformation; however, large sample sizes help insure that the analysis is robust (Underwood 1997, pp 192–194). For each species, the average proportion of propagules from an individual tree that were attacked by insects was compared among sites with one-way ANOVA. Variances of the untransformed proportions were homogeneous for both species (Cochran's C, $P>0.5$). Tukey HSD tests were used for a posteriori comparisons in all analyses.

For *Rhizophora*, the mean lengths of propagules were compared between sites and years with two-way ANOVA; both factors were considered random variables. Variances of the untransformed lengths were homogeneous (Cochran's C, $P>0.05$). Counts of beetle-infested and uninfested propagules in pooled samples of propagules from tarpaulins within each site and sample year were organized as a multidimensional contingency table. Using log-linear analysis, we tested for the effects of year, site, and their interaction on the rate of infestation.

The relationship between propagule size and the likelihood of predispersal insect attack was examined in two ways. First, for *Avicennia* and *Laguncularia*, we tested for a correlation between the average length of propagules in a tarpaulin collection and the proportion that had been attacked. Second, for each of the three species, we used paired *t*-tests to compare the mean length of infested and uninfested propagules within collections from individual trees (or sites and years in the case of *Rhizophora*); trees with fewer than five propagules in either the infested or uninfested class were excluded from the analysis.

Experimental shadehouse studies of seedling establishment and growth

Effect of propagule size

We evaluated the influence of propagule size on seedling establishment and early growth for each mangrove species with a series of shadehouse experiments. The procedure was similar for each species. Undamaged, insect-free propagules of 4 or 5 different length/weight classes (Table 3) were planted in peat pots (5.7 cm diameter, 5.7 cm deep) that were filled with soil collected from a mixed species stand

containing adults of all three mangrove species. One propagule was planted in each pot; *Avicennia* and *Laguncularia* propagules were laid flat on the soil surface, while *Rhizophora* propagules were planted upright with the radicle end inserted 4–5 cm into the soil. Propagules used in this and the following experiment on insect damage were drawn from large pooled collections of propagules that had recently dropped from canopy trees in the same forest stands in which our propagule sampling study was conducted. This insured that the source of propagules did not vary among treatments and that the propagules were in an early stage of development, not yet having developed roots or an expanded shoot with leaves. The pericarp had fallen off the *Avicennia* propagules prior to planting, as typically occurs soon after they drop from the parent tree, but their cotyledons remained tightly closed. The rolled cotyledons and other embryonic tissues of *Laguncularia* propagules were fully enclosed within the seed coat when the propagules were planted. *Rhizophora* propagules had a tightly closed stipule and no roots.

Table 3. Design of shadehouse experiments examining the effects of propagule size and insect damage on seedling establishment and growth. For the propagule size experiments we report the range of propagule lengths and fresh weights for each size-class. For the insect damage experiments, we report the mean length (SE) of propagules in each attack/damage class

	Avicennia		*Laguncularia*		*Rhizophora*	
Propagule size experiment						
Size-class	Range:					
	Length (mm)	Fresh weight (g)	Length (mm)	Fresh weight (g)	Length (mm)	Fresh weight (g)
Extra small (XS)	12–18	0.17–0.40				
Small (S)	15–20	0.51–0.82	15–17	0.25–0.37	110–138	3.60–8.04
Medium (M)	19–23	1.00–1.47	19–21	0.58–0.60	160–188	9.27–12.85
Large (L)	25–34	1.99–3.46	23–25	0.71–0.79	210–238	15.09–20.00
Extra large (XL)	34–42	3.96–5.85	27–29	0.83–0.86	260–288	21.51–26.53
Replicates per class	20		10		15[a]	
Planting date	31 July 1994		14 Sept 1995		9 Sept 1994	
Harvest date	31 Oct 1994		8 Jan 1996		26 Dec 1994	
Experiment duration (days)	92		116		108	
Insect damage experiment						
Attack/damage-class	Mean (SE):					
	Length (mm)		Length (mm)		Length (mm)	
Unattacked/no damage	26.3 (0.39)		23.2 (0.44)		224.8 (0.44)	
Attacked/damage undetermined			23.2 (0.44)		225.6 (0.46)	
Attacked/low damage	26.7 (0.36)					
Attacked/medium damage	24.5 (0.33)					
Attacked/high damage	25.7 (0.37)					
Test of equal mean lengths	$F_{3, 128}=2.33$, $P=0.077$		intentionally size-matched		$t=0.09$, $df=86$, $P=0.926$	

Replicates per class	33	27	44[b]
Planting date	1 Aug 1994	14 Sept 1995	4 Sept. 1994
Harvest date	3 Nov 1994	8 Jan 1996	26 Dec. 1994
Experiment duration (days)	94	116	113

[a] Three propagules, one each in the S, M, and L size-classes, developed beetle infestations and were excluded from the analysis

[b] Beetle infestations developed in six of the control propagules, so the final number of infested propagules was 50 and uninfested was 38

The potted propagules were arranged in slotted plastic plant trays that were placed in fiberglass troughs; size-classes were randomly intermingled within a tray. Each trough contained 3–4 cm of standing brackish water, so the lower halves of the peat pots were constantly immersed. Salinity was maintained at 10–15 ppt, comparable to the average salinity of interstitial water in the top 15 cm of low and mid-intertidal soils during the rainy season (W. Sousa, unpublished data). The troughs were positioned beneath a 2 m high, translucent fiberglass awning, which was open on all sides. This shadehouse was located in an open, shade-free site; light levels (PAR) under the awning averaged 71% of ambient.

The three species were tested in separate experimental trials initiated between the end of July and the middle of September (Table 3), a period mid-way through the rainy season, when seedlings of the three species are naturally establishing in our study area. The timing of these trials differed by species, dictated by temporal differences in their production and release of mature propagules. Because our study focused exclusively on intraspecific effects of variation in propagule size, there was no need for the species' experimental trials to run concurrently. In fact, it was more appropriate to conduct the trials at times when each of the species' seedlings naturally establish. We monitored the propagules' success at developing into upright seedlings, and then measured their subsequent growth. Data for *Avicennia* and *Rhizophora* come from trials conducted in 1994. A comparable trial with *Laguncularia* propagules was initiated in mid-November of that year, but shortly after being planted all of the propagules were killed by several days of unusually hot, dry weather that marked an early onset of the dry season. Consequently, we repeated the experiment for this species in the following year, but with an earlier start date in mid-September.

All stages of seedling establishment (i.e. anchoring of roots and elongation of shoot) were easily observed for *Avicennia* and *Laguncularia* propagules. However, because the radicle ends of *Rhizophora* propagules were buried in soil, we could not directly observe the production and growth of roots. Therefore, for this species, seedling establishment was defined as the flushing of leaves. We measured seedling height (or shoot length for *Rhizophora*, see below) and branch lengths (if present), and counted the number of fully expanded leaves at weekly or bi-weekly intervals. Dry weights of entire seedlings or parts thereof (i.e. root and shoot) were measured at the end of the experiment.

Effect of insect damage

We compared rates of seedling establishment and early growth for propagules of similar size that had suffered different degrees of insect damage. Our definition of damage varied with the species of propagule. In the case of *Avicennia*, the morphology of its propagule allowed us to non-destructively

examine the degree to which insects had damaged internal tissues. Consequently, for this species we were able to compare the performance of propagules representing each of the four levels of damage distinguished in the field survey (Table 2). However, for *Rhizophora* and *Laguncularia*, without destructively dissecting the propagule, it is only possible to observe the external signs of insect attack, so we compared the performance of propagules that had been attacked with those that had not. Attacked *Rhizophora* propagules had active beetle infestations, evidenced by the presence of recently dug burrow openings (~1 mm diameter) and associated dangling plumes of rust-colored frass. *Laguncularia* propagules that had been attacked by moth larvae had conspicuous holes (~1 mm diameter) in their seed coats; in some, but not all cases, frass was visible at the burrow opening.

Planting techniques and timing, growth conditions, and measurements made of propagule and seedling performance were nearly identical to those of the propagule size study. Details of experimental design are presented in Table 3. Seedling establishment and growth were monitored weekly. For *Avicennia* and *Rhizophora*, propagules assigned to each attack/damage class fell within specific ranges of length (21–33 mm and 165–280 mm, respectively), and mean initial propagule lengths ($\log_{10} (X+1)$ transformed to homogenize variances, Cochran's C, $P>0.05$) did not differ among attack/damage classes (Table 3). For *Laguncularia*, the size-distributions of attacked and unattacked propagules were identical because we were able to match each attacked propagule with an unattacked one of equal length. In the experimental trials for *Avicennia* and *Laguncularia*, replicate pots of the different damage classes were randomly intermingled within trays. For *Rhizophora*, trays of infested and uninfested control propagules were maintained in separate, adjacent troughs, which were isolated from each other by a wall of fine fiberglass screening. This prevented dispersing female beetles from attacking uninfested propagules.

Statistical analyses

We tested for differences in rates of seedling establishment and growth as a function of propagule size or level of insect damage/attack. Depending on the species, as detailed above, there were 4–5 levels of the size factor and 2–4 levels of insect damage/attack. Analyses of seedling establishment rates employed chi-square tests (with Yates correction for 2×2 tables) to compare the frequencies of propagules that did or did not successfully establish as rooted, upright seedlings at different levels of the independent variable. In the growth analyses, we used one-way ANOVA or *t*-tests to compare mean indices of growth among levels of the independent variable. When necessary, dependent variables were $\log_{10} (X+1)$ transformed to homogenize variances (Cochran's C, $P>0.05$), or Welch's approximate *t*-test for unequal variances was employed. Tukey HSD tests were used for a posteriori comparisons in all ANOVA analyses.

The growth indices we compared varied slightly depending on the species and experiment. For *Avicennia* and *Laguncularia* in the propagule size experiment, we tested for treatment effects on final main stem height (measured from the soil surface), leaf number, and the final dry weights of the entire seedling, its shoot, and roots. Because the initial heights of *Rhizophora* seedlings varied with the length of the planted hypocotyl, we measured growth of this species as the final length, leaf number, and dry weight of the shoot, rather than the entire seedling. We found it difficult to free *Rhizophora* roots from the soil without damaging them, so did not measure their weight. Branches were produced by some *Avicennia* seedlings, but by neither of the other species' seedlings over the time course of our experiment. Therefore, for *Avicennia*, we also compared the final total stem length (main stem height plus branch lengths) of seedlings among treatments. We evaluated the same seedling growth indices in the insect damage study,

except that only the dry weight of aboveground tissues was measured.

Results

Natural patterns: variation in propagule size

All three mangroves exhibited considerable intraspecific variation in the size of mature propagules. This variation occurred at a range of spatial scales. Within a collection from a single tree, mature propagule lengths varied as much as 3.5-fold for *Avicennia* and 2.8-fold for *Laguncularia*. The lengths of *Rhizophora* propagules in a pooled collection from a single site varied as much as 2.9-fold.

At larger spatial scales, the mean length of *Avicennia* propagules (Fig. 1) varied significantly among trees within a site ($F_{12, 2319}$=1.21, $P<0.001$), but not among sites ($F_{2, 12}$=0.43, $P=0.658$). The mean length of *Laguncularia* propagules (Fig. 1) varied significantly at both of these larger scales (trees within site: $F_{13, 3688}$=72.48, $P<0.001$; among sites: $F_{2, 13}$=4.88, $P=0.026$). The mean lengths of *Rhizophora* propagules did not differ between sites in 1994, but propagules from the PL site were significantly larger than those from the BM site in 1999 (Fig. 2; Site × Year interaction: $F_{1, 140}$=4.42, $P=0.037$).
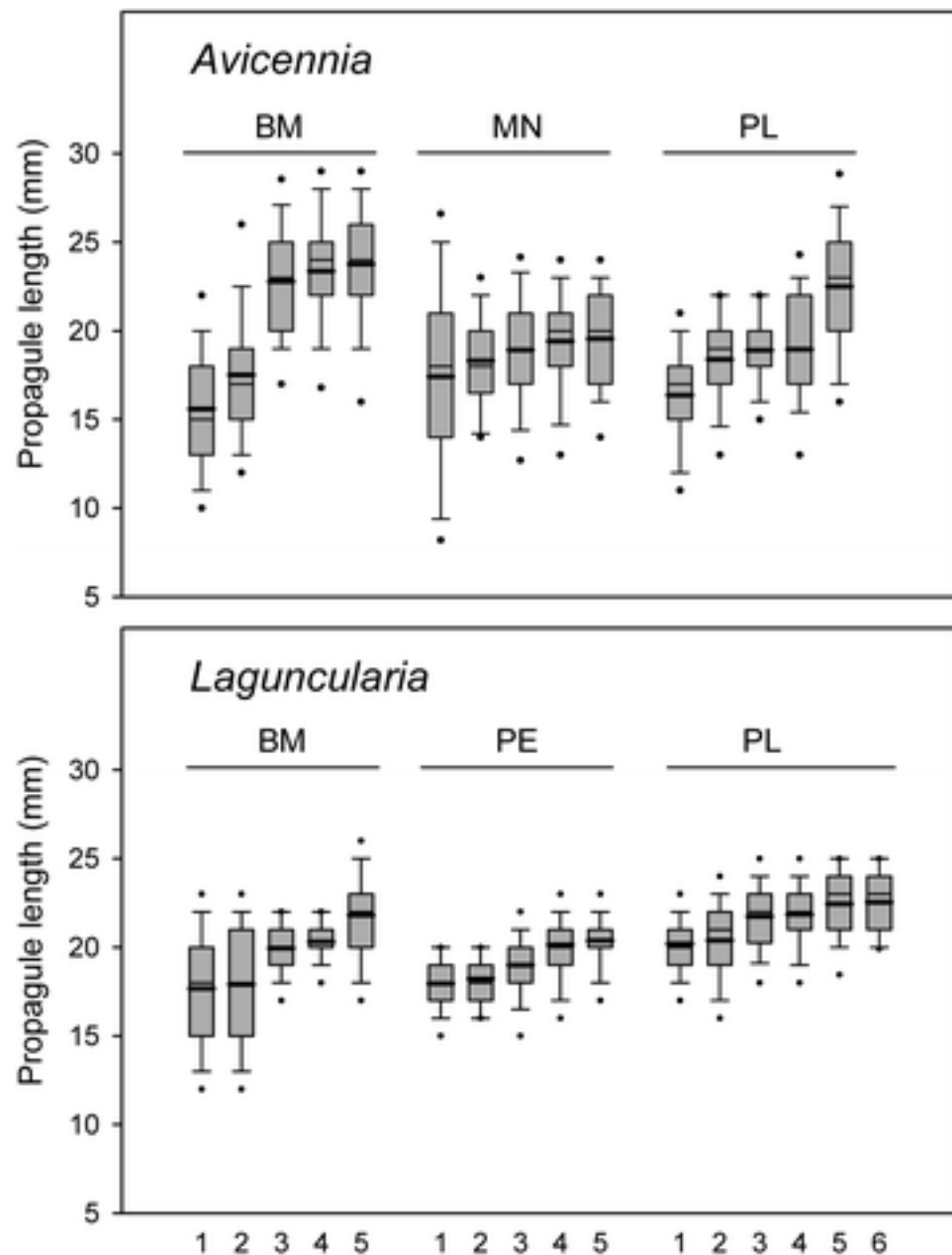
Replicate tree

Fig. 1. Size-distributions of *Avicennia* and *Laguncularia* propagules falling from individual trees within different sites (*BM*, *MN*, *PL*, *PE*). Box boundaries show 25th and 75th percentiles; *thin and thick lines* inside box mark median (50th percentile) and mean, respectively. *Whiskers* represent 10th and 90th percentiles, and *points* indicate 5th and 95th percentiles
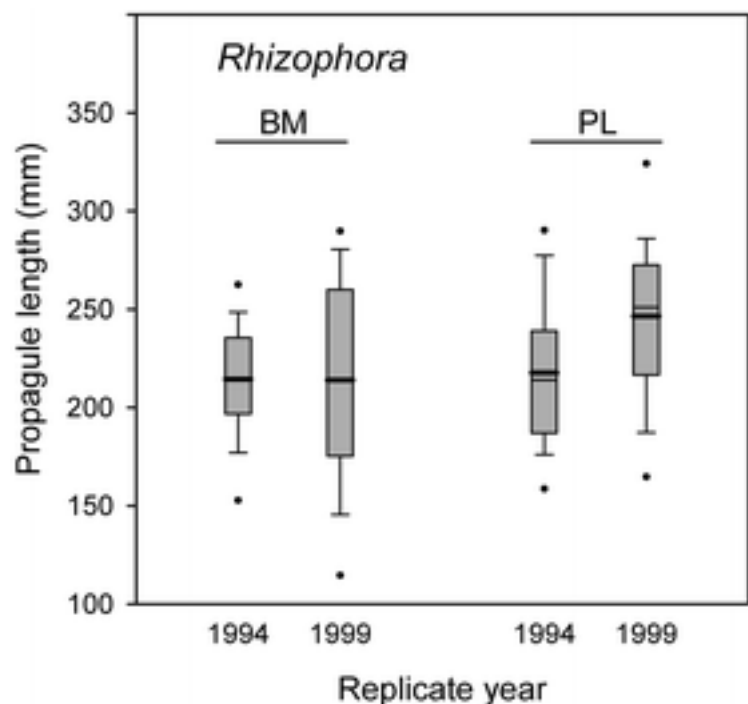

Fig. 2. Size-distributions of pooled samples of *Rhizophora* propagules falling from 3–6 trees in each of two sites (*BM*, *PL*) in 2 different years (1994, 1999). Box plot characteristics as in Fig. 1

Natural patterns: variation in predispersal insect attack and damage

Rates of predispersal insect attack on *Avicennia* propagules were quite high, ranging from 46.7–100.0% (median =90.0%) for collections from individual trees (Fig. 3). Mean attack rates differed among sites ($F_{2, 12}$=4.27, *P*=0.040), with collections from the BM site exhibiting lower rates on average than those from the MN and PL sites, which did not differ (Tukey HSD test, *P*>0.05). *Laguncularia* propagules were attacked at lower rates than *Avicennia*. The per tree rates ranged from 3.3–56.7% (median =33.3%) for collections from individual trees (Fig. 3). Mean attack rates did not differ among sites ($F_{2, 13}$=1.51, *P*=0.347). Overall rates of beetle infestation in *Rhizophora* propagules did not differ between the two sampling periods (1994: 14 out of 67, or 20.9%; 1999: 17 out of 77, or 22.1%; G to remove Year × Beetle interaction from best fit model =0.11, *df*=1, *P*=0.741). However, beetle infestations were more frequent in propagules falling from trees in the PL site (1994: 8 out of 33, or 24.2%; 1999: 12 out of 33, or 36.4%) than the BM site (1994: 6 out of 34, or 17.6%; 1999: 5 out of 44, or 11.4%) in both years (G to remove Site × Beetle interaction from best fit model =5.65, *df*=1, *P*=0.017; G to remove Year × Site × Beetle interaction =1.66, *df*=1, *P*=0.197).
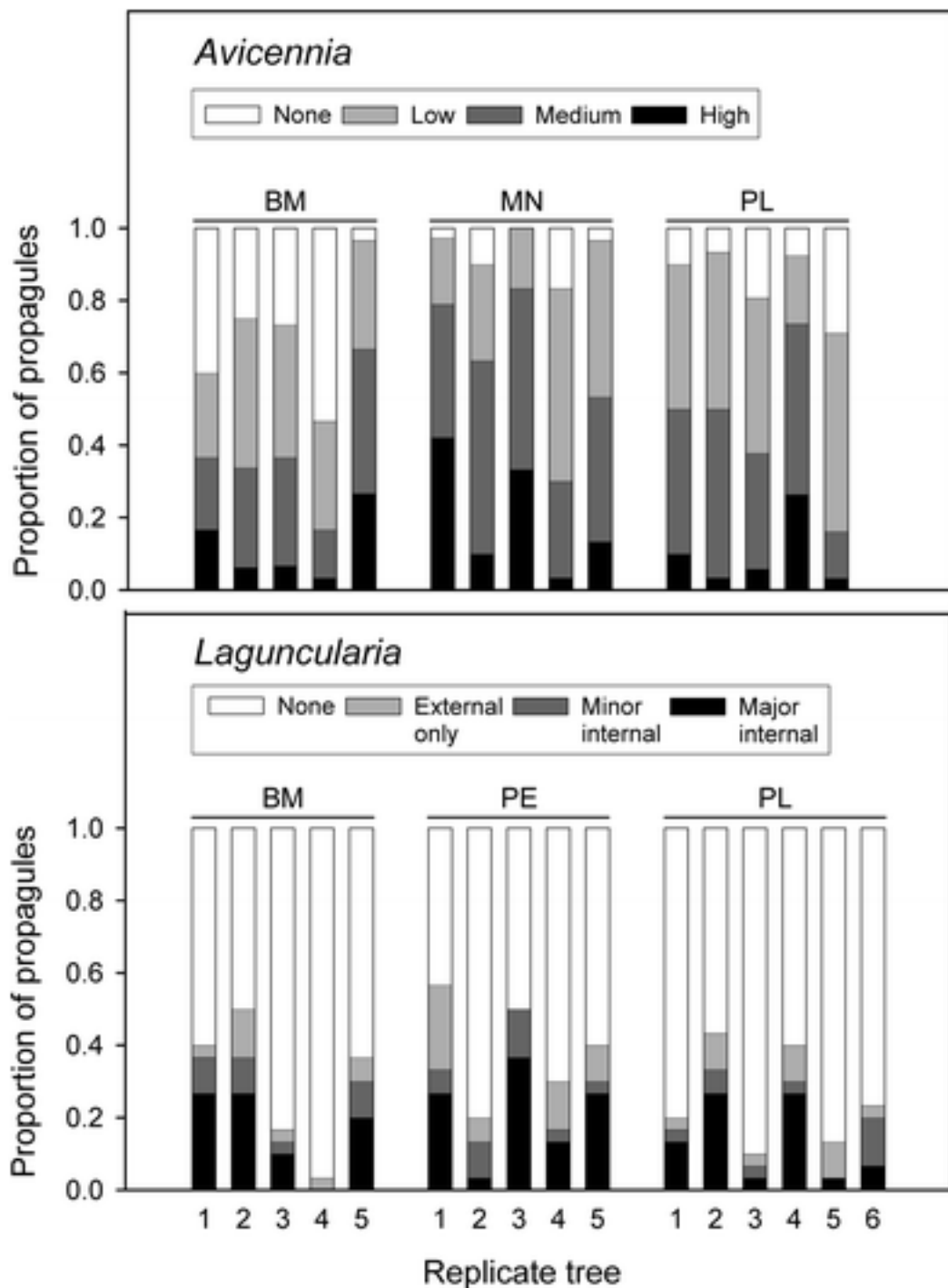
Fig. 3. Proportions of *Avicennia* and *Laguncularia* propagules suffering different degrees of predispersal insect damage in collections shown in Fig. 1. See Table 2 for definitions of damage categories. Box plot characteristics as in Fig. 1

We found little relationship between propagule size and rate of insect attack. The proportion attacked showed no relationship with the average length of propagules released from an individual tree, either for *Avicennia* ($r=-0.236$, $df=13$, two-tailed $P>0.20$) or *Laguncularia* ($r=-0.473$, $df=14$, $P>0.05$). Comparing the mean lengths of infested and uninfested propagules within collections from individual trees (or sites and years in the case of *Rhizophora*), *Avicennia* propagules that had been attacked were slightly larger on average (by 1.4 mm) than those that had not been attacked ($t=2.63$, $df=6$, $P=0.039$). No such difference was detected for *Laguncularia* ($t=0.14$, $df=12$, $P=0.894$) or *Rhizophora* ($t=0.95$, $df=3$; $P=0.411$).

Experimental studies: effects of propagule size

All *Avicennia* propagules, regardless of size, successfully established as rooted, upright seedlings that survived for the duration of the experiment. Larger propagules developed into taller seedlings (Fig. 4; final seedling height: $F_{4, 95}=177.89$, $P<0.001$) of greater total dry weight ($F_{4, 95}=475.58$, $P<0.001$) than smaller propagules. Seedlings developing from larger propagules also produced more leaves (Table 4). Only seedlings that developed from propagules in the two largest size-classes produced branches, averaging 0.6 and 1.4 branches per plant grown from large and extra large propagules (Table 3), respectively. The average summed lengths of branches for these two groups were 0.71 cm and 3.18 cm, respectively. This combined enhancement of main stem growth and branch production resulted in a highly significant positive effect of propagule size on final total stem length ($F_{4, 95}=185.96$, $P<0.001$). Root and shoot dry weights also increased with propagule size, with no change in their ratio (Table 4).
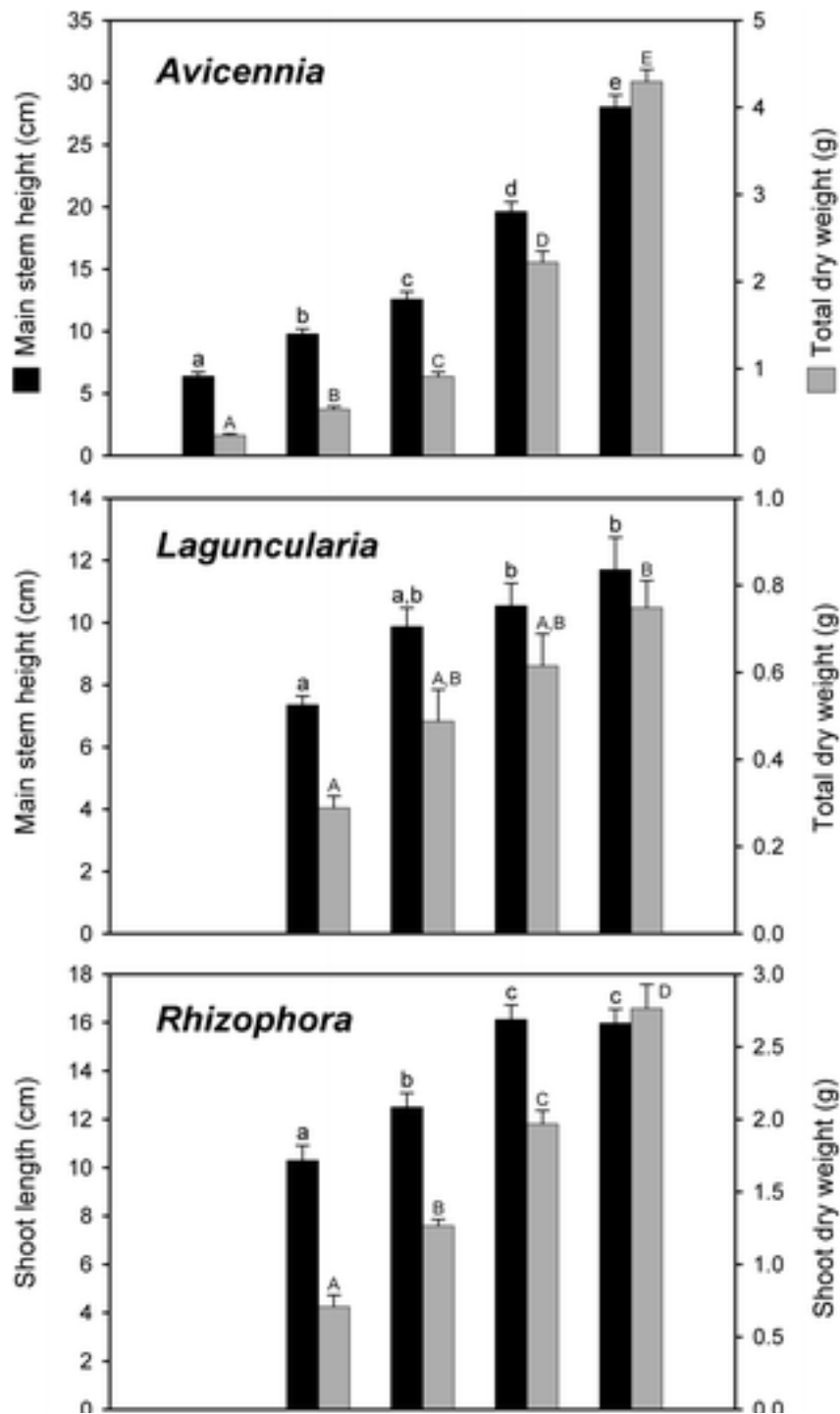
XS   S   M   L   XL

Propagule size

Fig. 4. Effects of propagule size on final seedling size and dry weight for each of the three study species. See Table 3 for definitions of propagule size-classes. Letters above bars summarize the results of a posteriori Tukey HSD tests; means marked with different letters are significantly different at *P*<0.05. *Lower and upper case letters* indicate results for seedling size and dry weight, respectively

Table 4. Effects of propagule size and insect damage on various indices of seedling growth and morphology. Mean values (SE) are presented for each size or damage-class; these are compared with one-way ANOVA or *t*-tests. When necessary, data were $\log_{10}(X+1)$ transformed to homogenize variances. Superscript letters summarize results of a posteriori Tukey HSD tests: means marked with different letters are significantly different at *P*<0.05

Experiment: *Species*	Size or damage class					*F* or *t*	*df*	*P*
Propagule size	XS	S	M	L	XL			
Avicennia								
Leaf number	4.20[a] (0.25)	4.80[a] (0.23)	4.80[a] (0.23)	7.60[b] (0.49)	10.90[c] (0.90)	41.46	4, 95	<0.001
Shoot dry wt (g)	0.14[a] (0.01)	0.33[b] (0.02)	0.56[c] (0.03)	1.32[d] (0.07)	2.54[e] (0.10)	456.39	4, 95	<0.001
Root dry wt (g)	0.09[a] (0.01)	0.20[b] (0.02)	0.35[c] (0.02)	0.90[d] (0.06)	1.76[e] (0.08)	304.57	4, 95	<0.001
Root/shoot ratio	0.66 (0.04)	0.62 (0.02)	0.64 (0.03)	0.67 (0.03)	0.70 (0.03)	1.20	4, 95	0.315
Laguncularia								
Leaf number		2.80 (0.49)	3.75 (0.45)	3.33 (0.33)	3.67 (0.33)	0.93	3, 24	0.440
Shoot dry wt (g)		0.17[a] (0.01)	0.32[a,b] (0.05)	0.41[b,c] (0.05)	0.51[c] (0.05)	8.80	3, 24	<0.001
Root dry wt (g)		0.11[a] (0.02)	0.16[a,b] (0.03)	0.20[a,b] (0.03)	0.24[b] (0.01)	3.49	3, 24	0.031
Root/shoot ratio		0.65 (0.08)	0.50 (0.03)	0.49 (0.03)	0.47 (0.03)	1.42	3, 23*	0.262
Rhizophora								
Leaf number		4.00[a] (0.0)	4.57[a] (0.25)	5.43[b] (0.25)	6.13[c] (0.13)	25.41	3, 53	<0.001
Insect damage	none/not attacked	low	medium	high	attacked			
Avicennia								

Leaf number	6.32^a (0.26)	6.06^{a,b} (0.18)	5.52^{b,c} (0.21)	5.24^c (0.18)		4.85	3, 122	0.003
Laguncularia								
Leaf number	3.54 (0.17)				3.33 (0.33)	0.61	31	0.549
Rhizophora								
Leaf number	5.79 (0.10)				4.00 (0.62)	2.86**	6.3	0.027

*One extreme outlier removed

**Welch's approximate *t* for unequal variances

Propagule size had very similar effects on *Laguncularia* establishment and growth. It did not affect the proportion of propagules that established as rooted, upright seedlings (χ^2=4.76, *df*=3, *P*=0.190), however, the average establishment rate of *Laguncularia* propagules (70.0%) was somewhat lower than that of *Avicennia* propagules (100.0%). Final seedling height and total dry weight increased with propagule size (Fig. 4; height: $F_{3, 24}$=5.86, *P*=0.004; total dry weight: $F_{3, 24}$=7.22, *P*=0.001), as did root and shoot dry weights, with no change in their ratio (Table 4). In contrast to *Avicennia*, the mean number of leaves that flushed during the experimental period did not vary significantly between seedlings that developed from propagules of different initial size (Table 4).

All *Rhizophora* propagules, regardless of size, successfully rooted, grew a shoot and flushed leaves. Similar to the other two species, larger propagules produced longer shoots (Fig. 4; $F_{3, 53}$=21.14, *P*<0.001) of greater dry weight ($F_{3, 53}$=81.76, *P*<0.001). Like *Avicennia*, shoots developing from larger propagules produced more leaves (Table 4).

Experimental studies: effects of insect damage

The establishment of *Avicennia* seedlings was significantly reduced by insect damage to the propagule (χ^2=12.38, *df*=3, *P*=0.006), but only if such damage was high (see Table 2 for definitions). Percent establishment for propagules suffering>25% tissue loss was 87.9%, whereas it was 100.0% for propagules with less damage. Tissue loss of $\leq$5% (Low damage) had no effect on seedling growth. As damage increased above this threshold, greater tissue loss resulted in slower seedling growth (Fig. 5), as reflected in smaller mean seedling heights ($F_{3, 122}$=8.15, *P*<0.001) and shoot dry weights ($F_{3, 122}$=18.87, *P*<0.001) at the end of the experiment. The relationship of insect damage to total stem length ($F_{3, 122}$=8.82, *P*<0.001) was nearly identical to that for seedling height alone, since only 6.3% (8 out of 126) of seedlings produced branches. *Avicennia* seedlings developing from propagules that suffered greater insect damage produced fewer leaves (Table 4).
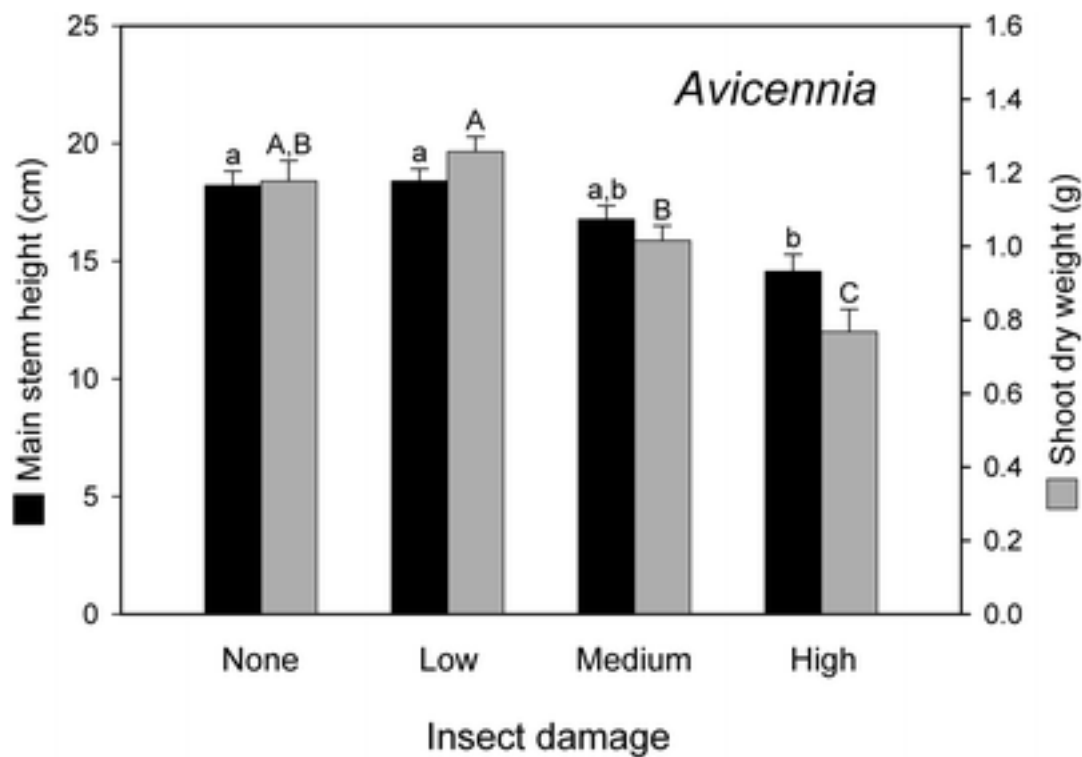
Fig. 5. Effects of different levels of predispersal insect damage to *Avicennia* propagules on final main stem height and dry weight of seedlings. See Table 2 for definitions of damage categories. Results of a posteriori Tukey HSD tests indicated as in Fig. 4

The rates at which *Laguncularia* propagules established as rooted, upright seedlings were markedly different for those that had been attacked by insects (9 out of 27, or 33.0%) and those that had not (25 out of 27, or 92.6%; Yates corrected χ^2=17.87, *df*=1, *P*<0.001). All of the established seedlings survived

until the end of the experiment, with the exception of one that developed from an unattacked propagule but died for an unknown reason by day 28. This individual was excluded from our analysis of seedling growth. The nine seedlings that developed from propagules that had external signs of attack by moth larvae (holes into their seed coats) grew no differently than the 24 that developed from undamaged control propagules (Fig. 6; final height: *t*=0.22, *df*=31, *P*=0.830; final shoot dry weight: *t*=0.79, *df*=31, *P*=0.438). Leaf number also did not differ between the two groups (Table 4). Paired *t*-tests comparing growth of seven of the seedlings that developed from attacked propagules with their size-matched controls (controls for the other two had died) also failed to detect differences (final height: *t*=0.31, *df*=6, *P*=0.767; final shoot dry weight: *t*=0.96, *df*=6, *P*=0.375; leaf number: *t*=2.12, *df*=6, *P*=0.078). Thus the effects of insect attacks on *Laguncularia* propagules were dichotomous: either the propagule was killed or a healthy seedling developed. If the insect penetrates the seed coat and feeds on the embryo, the propagule usually does not survive and fails to develop into a seedling. However, superficial damage to the seed coat has no effect on seedling development or growth. The 33.0% establishment rate of insect-attacked seeds is consistent with the sampling observation that on average, 31.5% (range of site means: 28.8–34.6%) of the *Laguncularia* propagules collected from a tarpaulin that exhibited external signs of insect attack were found to be free of internal damage when dissected.
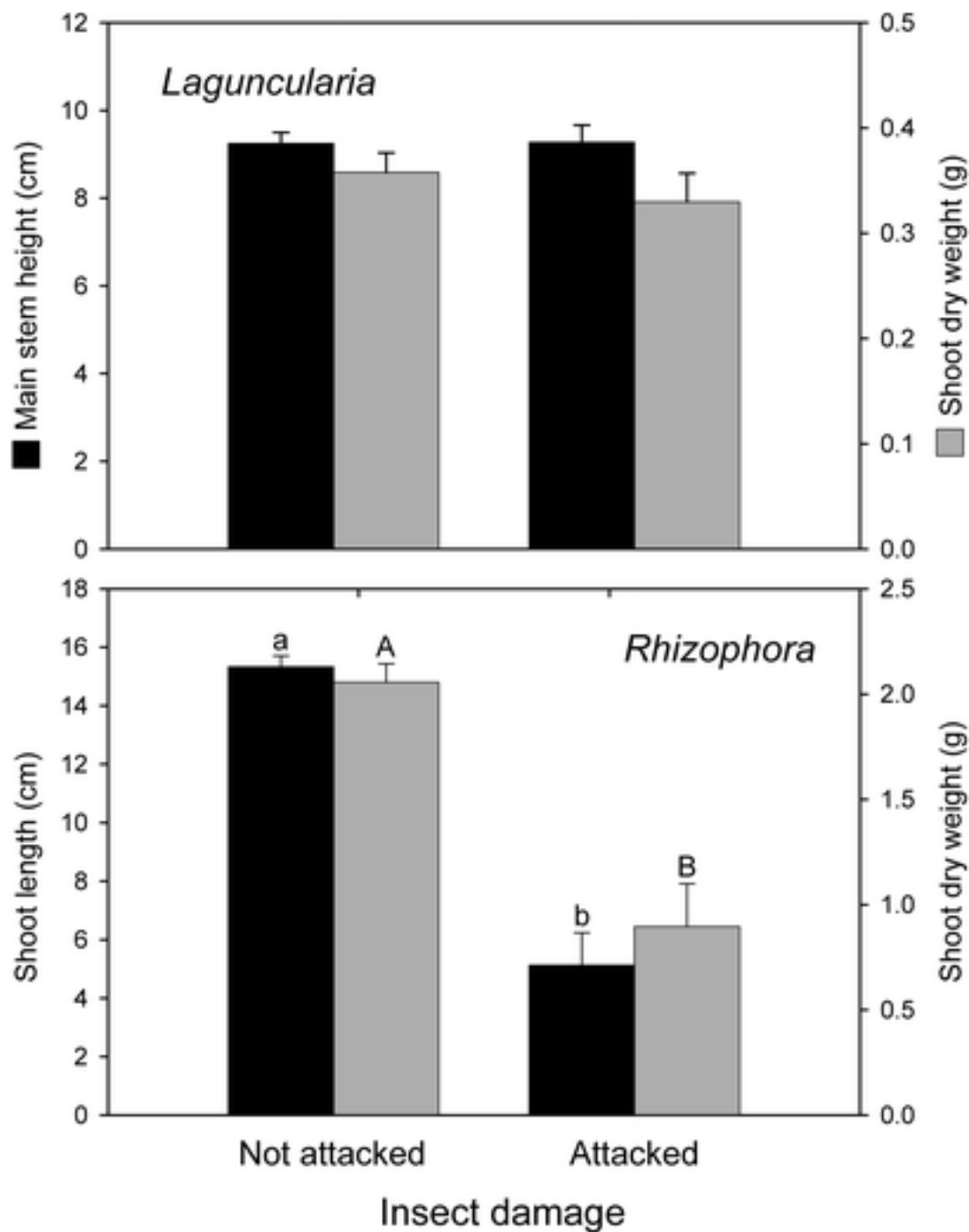
Fig. 6. Comparison of growth indices for seedlings developing from *Laguncularia* (main stem height and shoot dry weight) or *Rhizophora* (shoot length and dry weight) propagules that had or had not suffered predispersal insect attack. Neither growth index differed between the two groups for those *Laguncularia* propagules that successfully established as seedlings (see text). Significant differences in growth indices between the two groups of *Rhizophora* propagules as detected by *t*-test (see text) are indicated with *lower and upper case letters* as in Fig. 4

Rhizophora propagules with beetle infestations suffered 86.0% mortality (43 killed out of 50), and only 20.0% (10 out of 50) flushed leaves. In contrast, all 38 of the uninfected controls survived and established as leafed seedlings. These differences in survival and leaf flushing rates were highly significant (survival: Yates corrected $\chi^2=60.51$, $df=1$, $P<0.001$; leaf flushing: Yates corrected $\chi^2=52.55$,

df=1, *P*<0.001). By the end of the experiment, the shoots of beetle-free seedlings were three times as long and weighed more than twice as much as the shoots of surviving seedlings that harbored beetles (Fig. 6; final shoot length: *t*=10.32, *df*=43, *P*<0.001; final shoot dry weight: *t*=5.27, *df*=43, *P*<0.001). Shoots that grew from beetle-free propagules also produced more leaves (Table 4). These differences in growth responses were not attributable to any initial difference in propagule size between the seven surviving beetle infested seedlings and the 38 control seedlings (length: *t*=0.60, *df*=43, *P*=0.550; fresh weight: *t*=0.11, *df*=43, *P*=0.915).

Discussion

We found that each of the three canopy mangrove species in our study area exhibited considerable intraspecific variation in propagule size. Depending on the species, this variation was present among the progeny of individual trees, trees within a site, or sites separated by 0.8–2.5 km. Despite Harper et al.'s (1970) prediction that seed size should be a canalized trait that varies little within a species, intraspecific variation in seed size, of similar or greater magnitude to that which we observed, has been demonstrated in numerous subsequent studies. Such variation occurs over a wide range of spatial scales: within plants, among plants, and among populations (Wulff 1973, 1986a; Schaal 1980; Howe and Richter 1982; Stanton 1984; Winn 1988; Moegenburg 1996; Vaughton and Ramsey 1997, 1998; Eriksson 1999).

What are the consequences of this intraspecific variation in propagule size for the establishment and early growth of seedlings? Propagule size did not affect seedling establishment rates or root/shoot ratios for any of the three mangrove species we studied. However, for all three species, larger propagules developed into taller seedlings of greater dry weight. In the cases of *Avicennia* and *Rhizophora*, these larger seedlings also had more leaves than those that developed from smaller propagules. The latter result, that larger seedlings develop from larger propagules, appears quite general (Howe and Richter 1982; Stanton 1984; Wulff 1986b; Moegenburg 1996; Vaughton and Ramsey 1998; Eriksson 1999). However, the effect of propagule size on seedling establishment is more variable; in some cases there is little or no effect, as in our study (Wulff 1986b; Vaughton and Ramsey 1998; Eriksson 1999), but in others, seedling emergence rates are higher for larger propagules (Stanton 1984; Winn 1988).

Although we have not directly investigated the effect of propagule size on the competitive success of mangrove seedlings under field conditions, new seedlings commonly recruit as dense annual cohorts on the forest floor (W. Sousa, unpublished data). Such seedlings experience a highly competitive environment where an early size advantage could make a large difference to their fates. In an ongoing experiment that examines intra- and interspecific competition among mangrove seedlings in light gap and understory environments, we have observed strongly asymmetrical, size-dependent effects of competition: as density increases, taller individuals exhibit higher growth and survival than smaller ones (W. Sousa, unpublished data). Therefore, propagule size, through its influence on seedling performance, could affect the rate and course of regeneration following disturbance.

Herbivorous insects commonly damage or kill large numbers of seeds prior to their dispersal from the parent plant (Andersen 1988; Crawley 1989, 1992; Louda 1989). The rates of predispersal insect attack on propagules that we observed (median per sample rates: *Avicennia*—90.0%, *Laguncularia*—33.0%, *Rhizophora*—20.5%) fall within the wide range of values (0–100%) reported by previous surveys of such rates in different populations and/or species of mangroves (Onuf et al. 1977; Robertson et al. 1990; Clarke 1992; Farnsworth and Ellison 1997; Minchinton and Dalby-Ball 2001; Krauss and Allen 2003).

Rhizophora mangle is the only one of our three study species for which there are previous estimates of predispersal insect damage. Onuf et al. (1977) monitored rates of attack by the same species of scolytid beetle, *Coccotrypes rhizophorae*, on propagules produced in two stands on the fringe of small near-shore islands on the Atlantic coast of Florida, USA. These *Rhizophora* stands differed in the rate of nutrient input from guano produced by roosting birds. The percentage of propagules infested with beetles increased over the period of observation (June–October), reaching 100% at the high nutrient site and 43.2% at the low nutrient site. The lower rates of *Coccotrypes* infestation that we observed could be ascribed to any of the myriad differences between our study areas. Among other differences, we sampled *Rhizophora* propagules inside a mainland forest rather than on the fringe of a small island, and the trees we sampled were about 16.5 m tall as compared to the 4–5 m maximum height of trees in Onuf et al.'s (1977) study site.

We can only speculate about the possible causes of spatial and temporal intraspecific variation in attack rates that we observed. Several studies have found that the risk of predation by insects or small mammals increases with seed size (Thompson 1987; Reader 1993; Moegenburg 1996; Brewer 2001; but see Eriksson 1999) However, a recent model of the co-evolution of seed size and seed predation (Geritz 1998) predicts an evolutionary stable strategy consisting of a continuous range of seed sizes, with small seeds tending to be attacked more frequently than large seeds. In our system, we observed little or no correlation between rates of insect attack and propagule size. Other unexplored causes for the intraspecific variation we observed in rates of insect attack among trees or sites include differences in rates of propagule development or abscission that might lead to variation in the period that immature propagules are exposed to ovipositing insects (Farnsworth and Ellison 1997), or differences in the concentrations of nitrogen or defensive chemicals in propagule tissues (Onuf et al. 1977).

During the limited time frame of our field sampling, propagules of the three mangrove species exhibited marked differences in rates of predispersal attack by insects. The higher attack rates suffered by *Avicennia* propagules could be related to the fact that their thin pericarp and fleshy cotyledons are relatively easily penetrated by boring insects as compared to the thick spongy seed coat of *Laguncularia*, or the dense, fibrous cortical tissues of *Rhizophora's* hypocotyl. In addition, *Avicennia's* tissues have higher nitrogen concentrations and lower C/N, and lack the potentially defensive phenolic compounds that are present in high concentrations in the other two species (McKee 1995c; W. Sousa, unpublished data). On the other hand, *Avicennia* tissues contain iridoid glycosides (Fauvel et al. 1995) that serve as a defense against generalist herbivores in other systems (Bowers 1992). At the present time, our limited knowledge of the biology of the insect species that feed on mangrove propagules in our study area precludes a rigorous evaluation of these and other alternative explanations for differences in the rates at which propagules of the different mangroves are attacked. It is also important to recognize that absolute and relative rates of insect attack depend not only on properties of the propagules, but also on the abundances of insects, which vary in space and time. For example, as discussed above, rates of *Coccotrypes* attack on *Rhizophora* propagules differed greatly between our sites and those of Onuf et al. (1977) in Florida, where they reached levels comparable to the high rates of insect attack we observed for *Avicennia*.

For all three mangrove species, propagules whose tissues were more heavily damaged or consumed by insects were less likely to establish as seedlings, especially if the embryonic shoot or a substantial amount of conductive tissue was destroyed. Less severely damaged propagules established as seedlings

but grew more slowly than seedlings that developed from undamaged propagules of the same size. The few previous studies of the effects of predispersal insect damage to mangrove propagules on seedling establishment and growth have reported similar effects. Onuf et al. (1977) also found that infestations of *Rhizophora* propagules by the beetle, *Coccotrypes*, strongly inhibited their establishment as leafed seedlings. Robertson et al. (1990) documented a variety of responses to predispersal insect attacks among eight Australian mangrove species. Two of them exhibited reduced seedling establishment and growth in response to insect attack. One species established at lower rates if attacked, but once established, seedlings that developed from attacked propagules grew as well as those from unattacked propagules. The establishment of two other species was unaffected by insect attack, but the seedlings that developed from attacked propagules grew more slowly than those from unattacked propagules. Finally, insect attack had no measurable effect on either the establishment or growth of the remaining two species (see also Krauss and Allen 2003). Both Onuf et al.'s (1977) and Robertson et al.'s (1990) studies compared the performance of insect-attacked and unattacked propagules, without regard to the degree of damage. More recently, Minchinton and Dalby-Ball (2001) examined the effects on seedling establishment and early growth of different levels of predispersal damage to *Avicennia marina* propagules by fly and moth larvae. The number of insect exit holes in the cotyledons (zero, one, two, or three) was used as an index of the degree of damage. Measured in this manner, level of damage had no effect on the rate at which seedlings established, but subsequent growth declined with increasing damage to the cotyledons. These results are quite similar to ours for *Avicennia germinans*. We found that insect damage reduced the establishment of this species, but only when such damage was severe. As in their study, seedling growth steadily declined with increasing damage to the propagule.

The observation that *Avicennia* propagules, with their large cotyledons, can lose a substantial amount of tissue and still establish as viable seedlings is not peculiar to this species. Similar responses have been documented in large-seeded, rainforest tree species (Dalling et al. 1997; Mack 1998; Dalling and Harms 1999). In these studies, 50% or more of the cotyledonary mass was experimentally removed with little or no effect on seedling establishment or growth. In such cases, large cotyledons or endosperm provide an effective mechanism for tolerating herbivore damage (Rosenthal and Kotanen 1994).

In summary, we found that each of the common species of mangroves on the Caribbean coast of Panama exhibited substantial intraspecific variation in the sizes of mature, abscised propagules and in the rates at which they had been attacked by insect herbivores prior to abscission. Both characteristics varied over a range of spatial scales from individual trees to forest stands separated by 0.8–2.5 km. Our shadehouse experiments demonstrated that natural variation in both these propagule characteristics translates into significant differences in seedling performance in terms of establishment and/or early growth, which could influence forest dynamics. The failure of badly damaged propagules to establish as seedlings could potentially determine the density of adult trees if the supply of propagules is limiting (Andersen 1989; Crawley 1989, 1992; Louda 1989). However, even when propagules are not in short supply, the more subtle effects of propagule size and sublethal insect damage on seedling growth are sufficiently large that they could influence the rate and outcome of competition for regeneration microsites or the tolerance of seedlings to additional herbivory.

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