The effect of seed predators on plant distributions: is there a general pattern in mangroves?

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Selective crab predation has been hypothesized to maintain mangrove forest zonation by preventing the establishment of certain species' seedlings at particular tidal elevations. Support for this hypothesis consists of observations that the propagules of some mangrove species are consumed at a rate that is inversely related to the species' relative abundance in the adult canopy. In addition, one previous study found that rates of crab predation were lower in large light gaps than in small ones. We conducted a mensurative field experiment to assay rates of crab predation on dispersing propagules of the dominant mangrove species (*Avicennia germinans*, *Laguncularia racemosa*, and *Rhizophora mangle*) in our study forests at Punta Galeta on the Caribbean coast of Panama. The experiment specifically examined whether rates of crab predation varied 1) with species of propagule, 2) with changes in stand composition along the tidal gradient, and 3) inside versus outside of light gaps. Lightning-created canopy gaps are the primary sites of tree regeneration in these and other tall-stature mangrove forests.

Propagules of the three mangrove species were tethered inside and in the understory surrounding nine light gaps, with representatives in each of the major stand types that occur along the intertidal gradient. Fates of propagules were monitored over a four-wk period. Rates of propagule predation varied spatially, with highest rates of removal occurring in lower intertidal *R. mangle*/*L. racemosa* stands, where the large herbivorous crabs, *Ucides cordatus* and *Goniopsis cruentata* are common. In mid- and upper intertidal stands, dominated by *A. germinans* or *L. racemosa*, where detritivorous *Uca* spp. are abundant but larger herbivorous crabs are rare, few propagules were consumed. The propagules of *A. germinans* were preyed upon more heavily than those of the other two species; rates of predation on *R. mangle* and *L. racemosa* propagules did not differ. Light environment (i.e. inside versus outside a gap) had no significant effect on the rate of propagule predation. The enhanced survival of juvenile mangroves in light gaps that we have observed is probably due to other factors such as higher light and nutrient availability, and in some situations, lower insect herbivory.

Only the propagules of *A. germinans* experienced a pattern of predation consistent with the dominance-predation model: they were consumed at higher rates in the low intertidal where adults of the species are rare, and at lower rates in high intertidal areas where the species dominates the canopy. This suggests that predation on mangrove propagules by herbivorous crabs could influence the species composition of low intertidal forests by differentially reducing the recruitment of *A. germinans*. On the other hand, rates of crab predation on *A. germinans* propagules seem insufficient to prevent *A. germinans* from establishing in low intertidal areas. In opposition to the dominance-predation hypothesis, crab predation cannot account for the distribution patterns of *R. mangle* or *L. racemosa* whose propagules were preyed on most heavily in lower intertidal areas where these species are very abundant. Our results, together with those of two earlier studies, indicate that predation by crabs on dispersing propagules is not a general explanation for the zonation of tree species along tidal gradients in mangrove forests.

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In almost every natural ecosystem, one observes species of the same ecological guild (sensu Root 1967) differentially distributed along an environmental gradient. In some cases, distributions are sufficiently disjunct that the species live in more or less distinct zones running perpendicular to the gradient. Such zonation is a characteristic feature of communities of rocky seashores, salt marshes, mangroves, riverbanks, lake shores, hill slopes, and mountain sides. Throughout the history of ecology, investigations of the underlying causes of these patterns have yielded tremendous insight to the relative and interacting roles of abiotic and biotic factors in organizing natural assemblages of plants and animals (e.g. Connell 1961, 1975, Whittaker 1967, Lubchenco 1980, Grace and Wetzel 1981, Louda 1982, 1983, 1989, Silander and Antonovics 1982, Gurevitch 1986, Grace 1987, Bertness and Ellison 1987, Bertness 1991a, b). Setting aside the reality of multiple causation, the four main univariate hypotheses for differential distribution of species along environmental gradients are (1) physiological specialization to different portions of the gradient, (2) differential dispersal of propagules along the gradient, (3) altered relative, interspecific competitive abilities with position on the gradient, and (4) changing predation pressure among species along the gradient (Louda 1989).

Studies of terrestrial plant distributions have focused primarily on physiological specialization and competitive displacement mechanisms, paying less attention to the roles of differential predation and propagule dispersal. In fact, Louda (1989) concluded that there was too little experimental evidence to assert that differential predation pressure commonly controls the distributions of terrestrial angiosperms along environmental gradients. She singled out Smith et al.'s (1989) experimental investigation of seed predation by crabs in mangrove forests as the first to demonstrate that seed predators can control the distributions of trees along a gradient. In this and earlier studies, Smith and co-workers assayed rates of crab predation on mangrove propagules at sites in Australia, Malaysia, Florida, and Panama (Smith 1987a, b, 1988, 1992, Smith et al. 1989). Rates of propagule consumption by crabs differed among mangrove species, and often varied spatially within a forest. In a number of cases, a species suffered higher rates of predation in forest stands where conspecifics were rare or absent, and survived better where conspecifics dominated the canopy. These observations inspired the general hypothesis that selective crab predation maintains characteristic patterns of mangrove tree zonation by preventing the establishment of certain species' seedlings at particular tidal elevations. Hereafter, we refer to this hypothesis as the dominance-predation model (Smith et al. 1989).

Since the publication of Smith et al. (1989) and Louda (1989), the dominance-predation model of mangrove zonation has been independently tested in two

investigations, one in Belize (McKee 1995a) and the other in northern Australia (McGuinness 1997a). The results of these studies provide little support for the model. McKee concluded that propagules of only one of the three species at her study site suffered patterns of predation that were consistent with the model. McGuinness found no significant relationship between the degree of conspecific dominance of the canopy and rates of propagule predation. In fact, Smith et al. (1989) pointed out that some of their own results from Florida and Panama did not support their model, and attributed these exceptions to geographic variation in the composition of the guild of crabs that consume mangrove propagules. McGuinness' findings challenge this interpretation since the assemblage of herbivorous crabs at his study sites in northern Australia is very similar in composition to that at Smith's Indo-west Pacific sites, yet the spatial patterns of seed predation with respect to canopy composition were different. Thus, the generality of differential seed predation as an explanation for mangrove zonation along intertidal gradients is in some doubt, and differences in the composition of the consumer guild do not seem a sufficient explanation for the failure of the model in these two systems.

In this paper, we present the results of a third independent test of the dominance-predation model for mangrove zonation; this time, on the Caribbean coast of Panama. This study is part of our larger investigation of patterns and mechanisms of mangrove forest regeneration in the study area. We conducted a mensurative factorial experiment (sensu Hurlbert 1984) to assay rates of predation by crabs on dispersing propagules of the three dominant tree species: *Avicennia germinans* (L.), *Laguncularia racemosa* (L.), and *Rhizophora mangle* (L.). The study, conducted between July and September of 1993, addressed the following questions: how do rates of crab predation on mangrove propagules vary 1) with species of propagule, 2) with changes in stand composition along the tidal gradient, and 3) inside versus outside of light gaps? The investigation of these questions simultaneously yielded information necessary for evaluating the role of crabs in structuring the study forests and for testing the generality of patterns observed in Smith's studies described above. If the dominance-predation model holds, we expected lower predation on a given species in stands dominated by conspecifics, and higher levels of predation outside those stands. Question 3, concerning the comparison of predation rates in different light environments, was motivated by the finding of Osborne and Smith (1990) in an Australian mangrove forest that crabs consumed fewer *Avicennia marina* propagules in large light gaps than in small ones. In our study site, as in tall-stature, mangrove forests of Australia and Florida, lightning-created canopy gaps are a common form of disturbance and the primary sites of canopy tree

Fig. 1. Map of the study area at Punta Galeta, Panama indicating the locations where mangrove propagules were tethered. See Table 1 for key to light gap codes and gap descriptions. In the large bottom panel that details the study area, light gray shading indicates mangrove forest, dark gray shading indicates upland forest and developed areas. The four-pointed star in the upper right panel is at 9°25′N, 79°50′W.
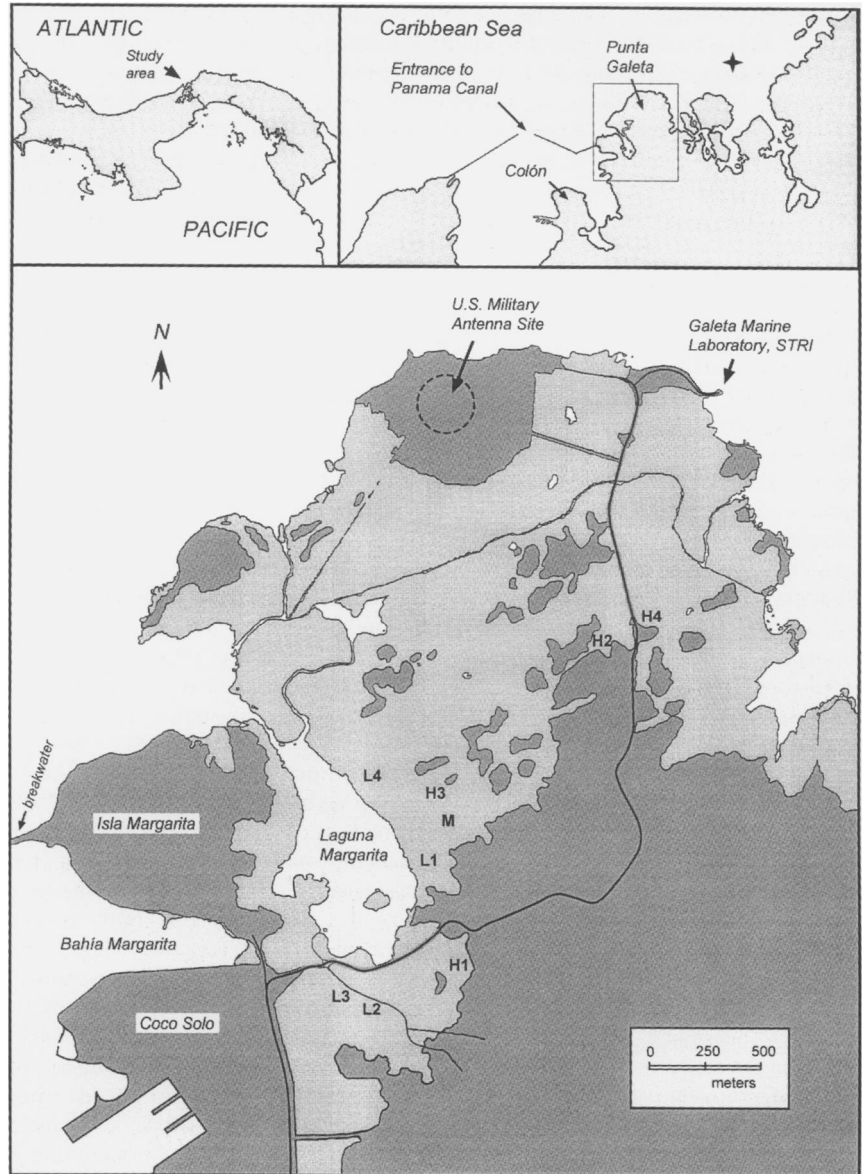
regeneration (Smith 1992, Smith et al. 1994, W. Sousa and B. Mitchell unpubl.). A number of studies in temperate and tropical forests have documented differences in rates of seed predation inside versus outside light gaps (see Discussion). We wished to evaluate whether the higher densities of juvenile trees in gaps at our study sites could be explained by a lower rate of crab predation on propagules that disperse into this microhabitat.

Methods

Study site 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 (Fig. 1). These are some of the same forests in which Rabinowitz (1978a, b, c) conducted her experimental studies of mangrove seedling growth and survival. Punta San Blas, Smith et al.'s (1989) study site in Panama, lies on the Caribbean coast about 100 km east of Punta Galeta.

Our study focused on the three tree species that dominate the canopy of the study forests: *Avicennia germinans*, *Laguncularia racemosa*, and *Rhizophora mangle*. As has been described for other locations (Davis 1940, Schaeffer-Novelli et al. 1990, McKee 1995b, Imbert and Ménard 1997), these species are

distributed differentially with distance from the seaward edge of the forest, but their distributions overlap to varying degrees (W. Sousa and B. Mitchell unpubl.). Typically, within 10–20 m of its seaward edge, the forest is monopolized by *R. mangle*. The composition then changes to a more even mixture of *R. mangle* and *L. racemosa*, which extends landward for another 40–180 m before adult *A. germinans* join the canopy. In another 30–70 m, *R. mangle* drops out. Above that point, in most areas, *A. germinans* gradually monopolizes the canopy. *L. racemosa* may disappear completely from the canopy 20–40 m above the upper limit of *R. mangle*, or it may occur only as scattered individuals. Variations on this general pattern are common, however. In some locations, the distribution of *L. racemosa* is bimodal; it occurs mixed with *R. mangle* at lower elevations, then becomes uncommon at mid to upper levels where *A. germinans* dominates, then increases in abundance again immediately adjacent to the upland edge, where it can form a monospecific band. At some sites, where for whatever reason *A. germinans* has not monopolized the higher elevation forests, *L. racemosa* can do so, growing in sizeable pure stands.

All three species disperse their propagules during the rainy season, which runs roughly from May to late December. More than 90% of the 200–400 cm of rainfall Punta Galeta receives annually occurs during these months (Cubit et al. 1988, 1989, Duke et al. 1997). Within the rainy season, the dispersal periods of the species overlap to differing degrees (Rabinowitz 1978a, Duke and Pinzón 1993, W. Sousa and B. Mitchell pers. obs.). Mature *R. mangle* propagules are dispersed primarily between April and October, with a peak in May to July. *A. germinans* propagules are released only between June and early August; although unrooted, dispersing seedlings of this species can be found on the forest floor into September or October. *L. racemosa* propagules are dispersed from late August to late November. The propagules of all three species are dispersed by water (hydrochory), but differ in the duration and pattern of floating, period of obligate dispersal, and time to establishment as rooted seedlings (Rabinowitz 1978a). Dispersing propagules are transported across the forest floor by runoff following rainfall and by tidal action. The tidal range at our study site is small: the mean daily range at Cristóbal, the regional tidal reference station immediately adjacent to Colón, is only 33.8 cm (U.S. National Ocean Service 1993).

The size and shape of the species' propagules differ markedly (see drawings in Rabinowitz 1978a). *R. mangle* has by far the largest propagules of the three species, with a grand mean length and fresh weight of 216.0 mm (range: 125.0–320.0 mm) and 16.7 g (seed trap samples from 10 trees, 5–12 mature propagules measured per tree). The dispersing hypocotyl is rod-like in shape with pointed ends, one being the plumule. When they drop from the parent tree, *A. germinans*

propagules have a flattened ovoid shape with a short stylar beak, and are considerably smaller than *R. mangle* propagules with a grand mean length and fresh weight of 19.5 mm (range: 12.0–42.0 mm) and 0.9 g (seed trap samples from 15 trees, 36–471 mature propagules measured per tree). *L. racemosa* propagules have a flattened, obovoid shape and are the smallest of the three with a grand mean length and fresh weight of 20.2 mm (range: 12.0–28.0 mm) and 0.5 g (seed trap samples from 16 trees, 94–491 mature propagules measured per tree).

Probably the most important predators on mangrove propagules in the study forests are the relatively large, herbivorous crabs, *Ucides cordatus* L. (Ocypodidae) and *Goniopsis cruentata* Latreille (Grapsidae). Both are very abundant, particularly in lower intertidal areas where *R. mangle* is common (Abele 1976). In fact, the forest floor in these areas is densely populated with the large entrance holes to burrows constructed by *U. cordatus*. These burrows are readily used by other species, including *G. cruentata* (Warner 1969). *U. cordatus* and *G. cruentata* are much less abundant in upper intertidal forests where the crab fauna largely consists of detritivorous *Uca* spp. Some propagules may be consumed by a variety of other crabs that inhabit the study forests (Abele 1976), including the relatively small, but abundant, herbivorous grapsid crab, *Aratus pisonii* (Beever et al. 1979).

Smith et al. (1989) reported that the snails *Cerithidea scalariformis* (Say) and *Melampus coeffeus* (L.) consumed 73% of the *A. germinans* propagules they tethered in four mangrove forests in the Florida Everglades. McKee (1995a) also reported *M. coeffeus* feeding on *A. germinans* propagules in Belize, but only in the interior forest that was dominated by *A. germinans*, and the damage was minor. Several species of snails, including *Cerithidea pliculosa* (Menke) and *Melampus coeffeus*, are common in our study forests, but we have never observed them feeding on mangrove propagules, including those we tethered.

Experimental design

To assess rates of crab predation on propagules of the three mangrove species, we monitored survival of tethered propagules as in previous studies (Smith 1987a, b, 1988, Smith et al. 1989, McKee 1995a, McGuinness 1997a, b, c). In contrast to these studies, in which each propagule was tethered on a separate line, we attached ten mature propagules of a given species to a length of nylon twine, with the points of attachment spaced 15 cm apart. Ends of the nylon twine were tied to prop roots, pneumatophores, or stems of samplings. Each propagule was connected to the main line by a 20-cm piece of monofilament, one end of which was tied to a small, knotted loop on the main line, and the other to

Table 1. Characteristics of light gaps used for propagule predation study. Gap area was estimated geometrically from measurements of eight, center-to-edge radii taken at 45° intervals around the gap. The local species composition of canopy trees was based on a combined census of trees that were killed by the lightning strike that created the gap, and surviving trees that formed the gap's edge.

Gap	Estimated area (m²)	Approx. age (yr)	Tidal height	Local species composition of canopy trees (%)		
				Rhizophora	*Laguncularia*	*Avicennia*
L1	201	2	low	41.3	58.7	0.0
L2	549	2	low	44.1	40.7	15.2
L3	617	2	low	42.4	57.6	0.0
L4	296	2	low	51.4	48.6	0.0
M	622	1	mid	15.1	81.1	3.8
H1	1075	2	high	0.0	100.0	0.0
H2	743	1	high	0.0	100.0	0.0
H3	634	1	high	0.0	0.0	100.0
H4	677	2	high	0.0	17.2	82.8

the propagule. Each species of propagule was tied in a different manner. For *R. mangle*, the monofilament was threaded with a needle through a small hole in the hypocotyl about 2 cm below the plumule, then tied securely around the propagule. For *A. germinans*, the monofilament was placed between the cotyledons and tied in a secure loop around the hypocotyl. For *L. racemosa*, the monofilament was threaded through two small holes in the outer edge of the pericarp, carefully avoiding the enclosed embryo, and then tied securely around the propagule. These attachment methods minimized damage to the propagules; those that were not consumed continued to develop normally, many gained a roothold, and a sizeable proportion became established as upright, leafed seedlings. All lines of a given species had the same distribution of propagule sizes within the following length ranges: *R. mangle* (130.0–260.0 mm), *A. germinans* (17.0–34.0 mm), and *L. racemosa* (20.0–25.0 mm). Propagules used in the experiment were collected either directly from trees, or shortly after they had fallen to the ground (i.e. they had not developed roots, and in the case of *A. germinans*, the cotyledons had not unfolded). All were screened for pre-dispersal insect damage; damaged propagules were discarded.

Nine light gaps were selected as experimental sites, with representatives in each of the major stand types along the intertidal gradient (Table 1). Four (L1–L4) were located in low intertidal, evenly mixed *R. mangle*/*L. racemosa* stands, one (M) was in an intermediate elevation stand that was dominated by *L. racemosa* but also contained *R. mangle* and *A. germinans*, two (H1, H2) were in high intertidal, monospecific stands of *L. racemosa*, and two (H3, H4) were in high intertidal, *A. germinans*-dominated stands. *R. mangle* was absent from all four of the high intertidal sites.

At each experimental gap, three lines of each species' propagules were placed inside the gap and three lines in the understory, outside of the gap edge, for a total of 30 propagules of each species inside and 30 outside of each gap. We tried to evenly distribute the three lines of a given species placed within a gap; no line was closer than 5 m to another, and all lines were positioned > 2 m inside the gap edge. The three lines of each species placed in the surrounding understory were roughly evenly spaced around the outside of the gap and > 7 m from its edge. In each light environment, the lines of *Avicennia* and *Rhizophora* propagules were spatially interspersed. Lines of *Laguncularia* propagules were set out separately, as described below.

Differences in the temporal availability of propagules, described above, necessitated some staggering of the experimental periods for the different species. Lines of *A. germinans* and *R. mangle* propagules were installed in gaps L1, L2, and M on 12 July, in gaps L4 and H1 on 13 July, and in gaps L3, H2, H3, and H4 on 23 July. Lines were monitored at weekly intervals for 4 wk. The 4-wk checks on *A. germinans* and *R. mangle* propagules in the three sets of gaps were made on 9, 10, and 20 August, respectively. About 3 wk later, all tether lines and surviving propagules of these species were removed as lines of tethered *L. racemosa* propagules were installed at each site: gaps L3, L4, and H1 on 27 August, gaps L1, L2, M, and H3 on 30 August, and gaps H2 and H4 on 31 August. These lines were monitored at the same intervals using the same survival criterion as for the other species; final checks on the three sets of gaps were made on 24, 27, and 28 September, respectively, at which time all tethers and surviving propagules were removed. We selected 4 wk as the duration of the study because it is roughly the length of time that propagules are freely dispersing before establishing a firm roothold. In fact, many surviving *A. germinans* propagules, and some *L. racemosa* propagules, had developed into erect seedlings with the first pair of leaves by the last census date, particularly in low intertidal sites. A propagule was considered dead when either: 1) > 50% of the tissue had been consumed, 2) it had been pulled down a crab burrow (none ever reappeared intact at the surface), or 3) for *R. mangle*, if the proximal end of the propagule, including the plumule and cotyledonary ring, had been removed.

Peterson and Black (1994) pointed out that rates of predation on experimentally tethered prey will often differ from those experienced by untethered prey. Mangrove propagules are passively dispersed by tidal currents and runoff from rainfall. Within mature forests that grow in regions where the tidal amplitude is small, as is true for Punta Galeta, dispersing propagules usually meander slowly across the forest floor, often stranding on a variety of natural obstacles (e.g. pneumatophores, logs, etc.), and are easy prey for large crabs. Thus, tethering of mangrove propagules is unlikely to increase their risk of consumption by crabs.

Conversely, the tethers may reduce predation rates by interfering with a predator's handling of prey. *Ucides cordatus* often pulls tethered propagules down into its burrow before consuming them. In our study, some *U. cordatus* may have been prevented from moving a propagule into their burrows by the tether and therefore rejected it rather than consuming it on the surface. The significance of this potential artifact cannot be evaluated without more detailed information on the feeding behavior of this species than is currently available.

While tethering may bias absolute rates of predation, deployment of tethered prey can still be an effective means of comparing relative rates of predation among habitats, provided the artifacts attendant to tethering are consistent in direction and strength across habitats. We have been unable to identify a phenomenon that might generate an interaction between tethering effect and tethering site. McGuinness (1997c) explicitly tested for, and failed to find, an interaction between location and the artifactual effect of tethering on rates of crab predation on mangrove propagules at his study site in northern Australia.

Data analysis

We used three-way factorial ANOVA with three replicates per cell to examine the effects of species of propagule (three levels), light environment (two levels: inside gap versus understory), and light gap (nine levels) on the mean number of propagules per tether line killed during the four-wk experimental period. Species of propagule and light environment are fixed factors, but light gap could be interpreted either as a random or fixed factor. The nine experimental gaps comprised most of the young gaps that were available to us at the time of the experiment. So, on the one hand, they represent a random, or at least haphazard, sample of a larger pool of gaps about which we would like to generalize. On the other hand, their individual characteristics with respect to tidal position and canopy composition form the basis for a specific test of the dominance-predation hypothesis, and therefore we wished to compare the mean rates of propagule preda-

tion among the different gaps. Ideally, light gap would be treated as a nested random factor within a fixed tidal height (or canopy composition) factor, but the gaps we used could not be divided in an even manner between tidal heights, and modest replication precluded discarding data to achieve a balanced design. Analysis of unbalanced, multi-factorial designs is difficult and controversial (Underwood 1997: 380–384). As a compromise solution, we performed two three-way analyses, one with light gap as a fixed factor, and the other with light gap as a random factor. The number of propagules killed per line was $\sqrt{(n + \frac{1}{2})}$ transformed before analysis to homogenize cell variances (Cochran's $C = 0.0889$, $P > 0.05$). Tukey's HSD test was used for a posteriori comparisons of treatment means.

Results

Rates of removal of tethered propagules differed significantly among mangrove species and among light gaps, but did not differ between gap and understory environments (Table 2). There were no significant interactions among these factors. The results were consistent regardless of whether light gap was treated as a fixed or random factor, as were the differences detected by a posteriori multiple comparisons of treatment means (results for Model I reported here). Rates of mortality were highest at sites in low intertidal, *R. mangle/L. racemosa* stands, and were very low in upper intertidal forests irrespective of which species, *A. germinans* or *L. racemosa*, dominated the canopy (Fig. 2). Propagules tethered at the mid-intertidal gap (M) were killed at intermediate rates.

Propagules of *Avicennia* were preyed on more heavily (Fig. 3A) than those of either *R. mangle* or *L. racemosa*. *R. mangle* and *L. racemosa* propagules did not differ in their rates of mortality. This pattern was consistent at different tidal elevations (Fig. 3B), but all three species suffered much greater losses in low intertidal areas. In these four low sites, *A. germinans* propagules experienced roughly 50% higher mortality than propagules of the other two species.

Although we did not directly observe the crabs *Ucides cordatus* or *Goniopsis cruentata* consuming tethered propagules, *G. cruentata* is known to feed on young mangrove shoots and *R. mangle* propagules (Hartnoll 1965, Smith et al. 1989, McKee 1995a), and we observed 16 instances (seven *R. mangle*, eight *A. germinans*, and one *L. racemosa*) in which a propagule, still attached to its tether, had been pulled down a *Ucides* burrow. Upon inspection, most of these had been partially eaten, and by the next census all had disappeared from their tether lines. McKee (1995a) observed the same phenomenon in Belize.

Variation in rates of propagule loss from replicate tether lines within a site was large, even in low inter-

Table 2. Results of three-way ANOVA examining the influence of species of propagule (Species), light environment (Light: inside gap vs understory), and light gap (Gap) on the mean number of propagules per tether line that were killed by crabs during the four-wk experiment. The analysis was conducted twice, first as a Model I ANOVA with all three factors fixed, then as a mixed Model III ANOVA with Species and Light fixed, but Gap random. Model designations as in Zar (1996). Data were $\sqrt{(N+\frac{1}{2})}$ transformed prior to analysis. Model I: $r^2 = 0.613$; Model III: $r^2 = 0.501$.

Source of variation	SS	df	MS	Model I		Model III	
				F	P	$F\dagger$	$P\dagger$
Species	2.846	2	1.423	4.380	0.015	4.40	0.014
Light	0.403	1	0.403	1.239	0.268	0.643	0.446
Gap	35.282	8	4.410	13.575	0.000	13.629	0.000
Species × Light	1.861	2	0.931	2.865	0.061	2.876	0.060
Species × Gap	6.420	16	0.401	1.235	0.254	–	–
Light × Gap	5.008	8	0.626	1.927	0.063	1.934	0.059
Species × Light × Gap	3.797	16	0.237	0.730	0.758	–	–
Model I Within cell	35.087	108	0.325				
Model III Within cell†	45.303	140	0.324				

$\dagger$ Preliminary tests on the full model failed to reject the null hypotheses that $\sigma^2_{Species \times Gap}$ and $\sigma^2_{Species \times Light \times Gap} = 0$ at $\alpha = 0.25$. These two sources of variation were pooled with the Within cell variation for the final test of the model (see Winer et al. 1991: 377).

tidal areas where rates of crab predation were high. For example, in five of the eight sets of three replicate *A. germinans* lines established at the four low intertidal gaps (i.e. four gaps × two light environments), the difference in the number of propagules consumed on the most heavily versus least heavily attacked lines was five or greater (i.e. > 50% of the total number on a line). In other words, the risk of predation varied substantially on the scale of several meters, probably reflecting the localized foraging activity of individual crabs. This speculation is supported by the observation that over a series of censuses, propagules were often removed sequentially along a single tether line.

Discussion

We found that rates of predation by crabs on mangrove propagules varied strongly with position along the intertidal gradient. Crabs consumed propagules tethered in low intertidal stands co-dominated by *R. mangle* and *L. racemosa* at a much higher rate than those tethered in upper areas of the forest where either *A. germinans* or *L. racemosa* dominated the canopy. As noted earlier, this gradient in predation likely reflects a shift in crab species composition with tidal height, relatively large herbivorous species being common in low intertidal areas and small, detritivorous species comprising most of the higher intertidal crab fauna.
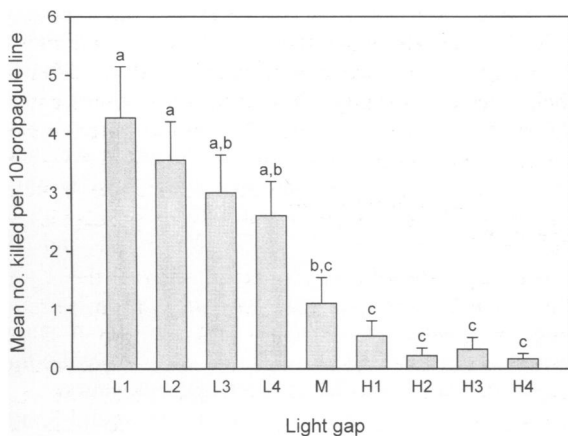

Fig. 2. Effect of light gap location on the mean number of propagules killed per tether line (+ 1 SE; data pooled across species and light environments). The nine light gap locations are ordered left to right from low to high intertidal. See Table 1 for light gap codes and descriptions. Letters above bars summarize the results of an a posteriori Tukey HSD test; means marked with different letters are significantly different at $P < 0.05$.
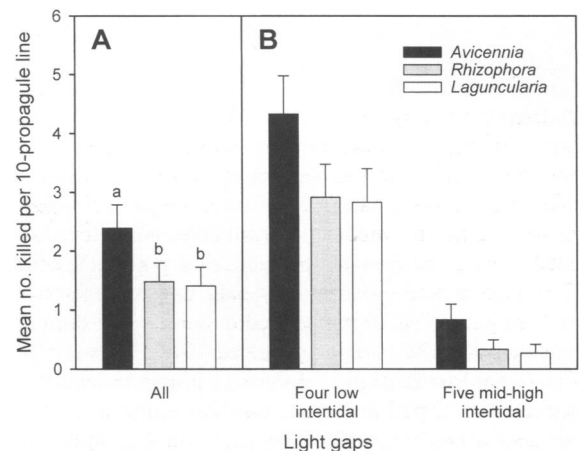

Fig. 3. Effect of mangrove species on the mean number of propagules killed per tether line (+ 1 SE; data pooled across light environments) for all nine light gaps combined (A), and for the four low intertidal versus five mid-high intertidal gaps (B). Letters above bars in panel A summarize the results of an a posteriori Tukey HSD test; means marked with different letters are significantly different at $P < 0.05$.

Table 3. Comparisons of seed predation rates inside versus outside light gaps in various forest types. Two or three categories of microhabitats were compared in each study including gap interior (G), small gap interior (SG), large gap interior (LG), gap edge (GE), general understory interior (U), understory interior beneath fruiting conspecific (UB), and understory interior away from fruiting conspecific (UA). Pattern of predation indicates relationships among mean predation rates measured in the different microhabitats.

Habitat	Location	Seed species	Predators	Pattern of predation	Reference
Deciduous forest	United States (IL)	Prunus serotina Phytolacca americana	Rodents	G = GE > U	Hoppes 1985
Deciduous forest	United States (MN)	Prunus avium	Rodents	G < U	Webb and Willson 1985
Deciduous forest	United States (MN)	Uvalaria grandiflora	Ants and rodents	G = U	Webb and Willson 1985
Rainforest	Mexico (Vera Cruz)	Trichilia mariana	Birds and rodents	GE > G = U	Dirzo and Dominguez 1986
Rainforest	Panama (Barro Colorado Is.)	Faramea occidentalis	Rodents	G = UB > UA	Schupp 1988a
				G > UB = UA	Schupp 1988b
Rainforest	Australia (Queensland)	Endiandra cowleyana Hodgkinsonia frutescens Castanospermum australe Prunus turnerana Litsea leefiana Connarus conchocarpus	Rodents	G = U	Willson 1988
Rainforest	Costa Rica (Heredia)	Welfia georgii	Rodents	G = UB > UA	Schupp and Frost 1989
Mangrove forest	Australia (Queensland)	Avicennia marina	Crabs	SG > LG	Osborne and Smith 1990
Mangrove forest	Panama (Colón)	Avicennia germinans Rhizophora mangle Laguncularia racemosa	Crabs	G = U SG = LG	This study

As in earlier studies by Smith and co-workers (Smith 1987a, b, 1988, Smith et al. 1989), McKee (1995a), and McGuinness (1997a), *Avicennia* propagules suffered higher mortality than those of other species, although predation on propagules of *R. mangle* and *L. racemosa* was substantial. Rates of predation on the latter two species did not differ, as McKee (1995a) also found in Belize. A variety of morphological and chemical differences among these propagules could account for crab preferences. *A. germinans* propagules are fleshier, have a higher nutritive quality, and lower concentrations of total phenolics, gallotannins, and condensed tannins than the other two species (McKee 1995a).

We found no consistent difference in the mortality of propagules tethered inside a gap versus in the surrounding understory. Nor did rates of crab predation on propagules tethered in the four low intertidal gaps (in the zone where herbivorous crabs are abundant) correlate with gap area ($r^2 = 0.388$, $P = 0.612$), contrary to Osborne and Smith's (1990) observation that the rate of predation declined with increasing gap size in an Australian mangrove forest. Therefore, the dense stands of saplings characteristic of lightning-caused canopy gaps in our study area are not the result of propagules recruiting to a spatial refuge from crab predation. Other factors including higher light and nutrient availability, and in some situations, lower insect herbivory, account for the enhanced survival of juvenile mangroves within light gaps (Smith 1987b, c, 1992, Ellison and Farnsworth 1993, W. Sousa and B. Mitchell unpubl.).

Given differences in the composition of the herbivorous crab fauna and in other features of our study systems, it is not particularly surprising that we did not detect the same pattern of propagule predation as a function of light environment that Osborne and Smith (1990) did in Australia. More generally, the risk of seed predation inside versus outside of light gaps does not differ in a consistent way among studies of post-dispersal seed predation in tropical and temperate forests (Table 3). These seemingly idiosyncratic patterns may reflect the species-specific habitat preferences and foraging behaviors of the seed predators in each study system.

Does the dominance-predation model (Smith et al. 1989) explain patterns of mangrove zonation at Punta Galeta, Panama? Our answer is a qualified no, the same conclusion reached by McKee (1995a) for forests comprised of the same three canopy species on Twin Cays archipelago off the coast Belize. Crab predation cannot account for the zonation of *R. mangle*: propagules of this species are most heavily consumed in areas where it is most abundantly represented in the adult canopy. Conversely, *R. mangle* is absent from high intertidal *A. germinans* and *L. racemosa* stands where its propagules would suffer almost no crab predation. Smith et al. (1989) obtained the same result at Punta San Blas, their study site on the Caribbean coast of Panama.

Similarly, the distribution of adult *L. racemosa* at our study sites exhibited no correlation with rates of crab predation on its propagules. This mangrove is consistently abundant in the lower intertidal, mixed with *R. mangle*, where its propagules suffer relatively high mortality due to crabs, but it can also form pure stands far from the water where crab predation on propagules is minimal. Neither Smith et al. (1989) nor McKee (1995a) compared predation rates on *L. racemosa* among stands of different species composition or tidal height.

Only *A. germinans* propagules suffered a pattern of mortality consistent with Smith's dominance-predation model: the impact of crab predation was greatest in low intertidal *R. mangle/L. racemosa* stands where adult *A. germinans* were rare or absent altogether. Crab predation on *A. germinans* propagules cannot, however, explain the absence of this species in high intertidal pure stands of *L. racemosa* since nearly all of the tethered propagules, regardless of species, survived in these stands. Nevertheless, crab predation does reduce the numbers of *A. germinans* seedlings that become established in the low intertidal, and may thereby exert some control over canopy composition in these areas.

The rate of crab predation on *A. germinans* propagules that we measured does not, however, seem sufficient to exclude this species from the low intertidal altogether. Fifty-seven percent (136 out of 240) of the *A. germinans* propagules tethered at the four gaps in low intertidal stands survived the 4-wk period of observation (Fig. 3B), and 34% of these survivors had become established as erect seedlings. When the lines of tethered *A. germinans* were removed, 7 wk after they were installed, 74% of the surviving *A. germinans* propagules ($N = 114$) had developed into erect seedlings. Thus, a sizeable fraction of the tethered *A. germinans* propagules escaped crab predation to become rooted, erect seedlings. This observation, in and of itself, does not negate crab predation as the dominant force controlling low intertidal forest structure because seedlings might continue to suffer high levels of crab predation. We found, however, that the risk of predation by crabs declines sharply once an *A. germinans* propagule has transformed into an upright seedling. During the three-wk period between the last census and the time the tether lines were removed, unestablished propagules suffered 21.1% mortality compared to only 6.5% for established seedlings ($G = 5.43$, $df = 1$, $P = 0.02$, $N = 90$, 46, respectively). McKee (1995a) reported a similar pattern of differential mortality in low intertidal areas at her study site in Belize. Over an 8-d period, 64% ($SE = 8$) of tethered *A. germinans* propagules were consumed as compared to 48% ($SE = 8$) of rooted seedlings that had been transplanted nearby. This difference was not statistically significant, but its direction is consistent with our observation that rooted seedlings are less vulnerable to crabs than dispersing propagules. In Australia, Smith (1987b) compared rates of predation on caged and uncaged *A. marina* seedlings that he transplanted into the plots at two months of age. Uncaged seedlings suffered much higher mortality than caged ones, indicating that crabs readily fed on seedlings. The herbivorous crab fauna at his sites is quite distinct from that in Central America (Smith et al. 1989) and this could account for the higher vulnerability of seedlings.

The absolute rates of propagule predation we measured were generally lower, with one exception, than those reported by McKee (1995a) for Belize and Smith et al. (1989) for Florida and Panama. In part, this could be explained by the timing of the experimental trails relative to the fruiting season of the target species. Our trials were run during peak periods of propagule release for each of the species, and naturally dispersing propagules were abundant in the areas where we placed tether lines. In contrast, McKee's experimental trials were conducted during periods when background densities of naturally dispersing propagules in her study plots were described as "nil". The ready availability of alternative natural prey in our study sites may have lessened the impact of crabs on tethered propagules, as compared to that measured by McKee. As McKee points out, the levels of predation she observed were maximum values. Similarly, Smith et al. (1989) tethered *R. mangle* propagules at Punta San Blas $\approx 6–8$ wk after fruit fall so predation pressure on their experimental propagules may have been accentuated for lack of alternate prey.

The difference in the background abundance of naturally dispersing propagules between McKee's and our studies might also explain why we observed a greater differential in rates of predation on *A. germinans* propagules versus established seedlings. With preferred propagules in short supply, crabs at McKee's site may have shifted to feeding on less preferred seedlings. In our study, propagules were not in short supply, so crabs rarely fed on seedlings.

Variation in rates of propagule predation measured in different studies could also be attributable to differences in the timing of the experiments relative to seasonal variation in crab foraging activity. McKee (1995a) measured large differences in rates of crab

predation on *R. mangle* propagules in different seasons (25% versus 75% rendered non-viable in 9 d, in December and July, respectively), even though background abundances of naturally dispersing propagules were low at both times. In Belizean forests, herbivorous crabs are much more active during July than December to February (K. McKee pers. comm.).

Differences in the density and species composition of propagule predators among the study sites could also account for variation in rates at which tethered propagules are consumed. For example, the rates of predation we measured on *R. mangle* propagules tethered in the low intertidal were much higher than Smith et al. (1989) observed in Florida, where none were eaten at any tidal height. This difference is probably due to the rarity of the large herbivorous crabs, *Ucides cordatus* and *Goniopsis cruentata* in Florida (T. J. Smith III pers. comm. in McKee 1995a). In contrast, Smith et al. (1989) reported substantially higher rates of predation on *A. germinans* propagules at both low and high elevation sites in Florida than we observed at Punta Galeta. In this case, the difference is not explained by differences in crab assemblages, since the diversity and density of herbivorous crabs is lower in Florida, and crab predation accounted for only a modest proportion of the losses at one low intertidal site (Smith et al. 1989). Instead, snails and some unknown water-borne organism, possibly a fish, ate most of the tethered *A. germinans*. Neither of these consumers was important in our study forests.

Another potentially important difference between our study and earlier investigations is in tethering techniques. Smith et al. (1989)and McKee (1995a) tethered propagules individually on 1-m or 0.5-m-long lines, whereas we tethered 10 propagules along approximately 1.35 m of line, each on a separate 20-cm-long lead tied to the main line. In a specific test for an effect of tether length, McGuinness (1997c) found that crabs removed individually tethered *Ceriops tagal* propagules from 100-cm tethers at a higher rate than from 5- or 50-cm-long tethers; rates did not differ between the latter two lengths. Given our multiple propagule tether design, it is difficult to say how this effect of individual tether length bears on the hypothesis that the lower rates of predation we observed were due to our unique tethering scheme. Our tethers were functionally shorter than 1 m, so it is possible that our tethering method differentially interfered with the handling behavior of crabs that retreat to a burrow to feed, as discussed earlier. Several factors, however, would have ameliorated the effect of this bias. First, the density of large crab burrows (> 5 cm diameter) is much higher in our low intertidal sites where the bulk of predation occurred (mean of 2.3 burrows/m^2, total $N = 60$ quadrats taken along three distinct transects, W. Sousa and B. Mitchell unpubl.) than in McGuinness' sites where the artifact was demonstrated (mean of 0.1 burrows/ m^2, McGuinness

1997b). Therefore, the number of burrows nearby our tether lines was greater, reducing the influence of tether length. In addition, the length of time that our propagules were exposed to predators was much longer (4 wk) than in either Smith et al's (4 d) or McKee's (9 d) study. Further, we often observed that over a series of censuses, propagules were removed sequentially along a line, suggesting that individual crabs were not deterred from feeding on the tethered propagules. Finally, *Goniopsis cruentata*, which feeds on propagules aboveground (McKee 1995a), is abundant in our study areas, and should be little affected by the tethers.

Given these considerations, we believe our results are representative of natural predation rates in our study forests. If this is the case, a fair number of *A. germinans* propagules are escaping crab predation in the low intertidal zone, due in large part to the patchy nature of crab foraging. Rates of predation varied considerably among replicate tether lines indicating that there is small-scale, spatial variation in the risk of crab predation across the forest floor. Furthermore, each year, large numbers of dispersing *A. germinans* propagules are being transported into this zone by surface runoff from more landward, monospecific stands of *A. germinans* (W. Sousa and B. Mitchell unpubl.). Therefore, if a low abundance of adult *A. germinans* is a static feature of these areas, then some other biotic or abiotic factor is preventing the establishment of *A. germinans* in the forest canopy. Possible factors include water depth, soil chemistry, interspecific competition, or insect herbivory.

Alternatively, the pattern of zonation could be dynamic rather than static. *A. germinans* may be gradually invading low intertidal forests, at a rate that is partially determined by levels of crab predation on propagules. Two observations support this scenario (W. Sousa and B. Mitchell unpubl.). First, *A. germinans* saplings often outnumber those of *R. mangle* and *L. racemosa* in the understory of low intertidal forests. Second, *A. germinans* seedlings we have experimentally transplanted to these forests survive and grow very well, even better than they do in higher intertidal, pure *A. germinans* stands. Ongoing long-term monitoring studies of forest structure should reveal the static versus dynamic nature of mangrove zonation in our study area.

Apart from the insights this study gives to the processes that structure mangrove forests on the Caribbean coast of Panama, its results, along with those of Smith et al. (1989), McKee (1995a), and McGuinness (1997a), highlight the importance of replicating ecological investigations in different geographical locations. Unfortunately, few ecological studies are ever repeated within the same habitat at different locations, or in the same location at different times, and when they are, editors or reviewers often discourage the publication of what they perceive to be "redundant" results. As a consequence, we often have little sense for how representa-

tive our "classic" examples are, or how robust our generalizations. Smith's early studies in Australia (Smith 1987a, b, 1988) documented spatial patterns of propagule predation by crabs that could maintain existing patterns of mangrove zonation at his study sites. This result naturally attracted the attention of researchers interested in the role that seed predators play in structuring plant communities along environmental gradients, and at the time was heralded as a key demonstration of their importance (Louda 1989). As subsequent investigations have shown, however, Smith's dominance-predation model has not proven to be a general explanation for the zonation of mangrove tree species. Nonetheless, it has served the vital role of a plausible alternative to the classical physiological explanations for such patterns.

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