

Wayne P. Sousa · Swee P. Quek · Betsy J. Mitchell

Regeneration of *Rhizophora mangle* in a Caribbean mangrove forest: interacting effects of canopy disturbance and a stem-boring beetle

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Abstract Current theory predicts that in low-density, seed-limited plant populations, seed predation will be more important than competition in determining the number of individuals that reach maturity. However, when plant density is high, competition for microsites suitable for establishment and growth is expected to have a relatively greater effect. This dichotomous perspective does not account for situations in which the risk of seed predation differs inside versus outside recruitment microsites. We report the results of a field experiment and sampling studies that demonstrate such an interaction between microsite quality and the risk of propagule predation in mangrove forests on the Caribbean coast of Panama, where it appears to play a key role in shaping the demography and dynamics of the mangrove, *Rhizophora mangle*. *Rhizophora*'s water-borne propagules establish wherever they strand, but long-term sampling revealed that only those that do so in or near lightning-created canopy gaps survive and grow to maturity. These microsites afford better growth conditions than the surrounding understory and, as importantly, provide a refuge from predation by the scolytid beetle, *Coccotrypes rhizophorae*. This refuge effect was confirmed with a field experiment in which *Rhizophora* seedlings were planted at different positions relative to gap edges, from 5 m inside to 20 m outside the gap. Mortality due to beetle attack increased linearly from an average of 10% inside a gap to 72% at 20 m into the forest. The interaction between canopy disturbance and propagule predation may be having a large impact on the composition of our study

forests. Being shade-tolerant, *Rhizophora* seedlings that escape or survive beetle attack can persist in the understory for years. However, the high rate of beetle-induced mortality effectively eliminates the contribution of advance regeneration by *Rhizophora* saplings to gap succession. This may explain why the shade-intolerant mangrove, *Laguncularia racemosa*, is able to co-dominate the canopy in low intertidal forests at our study sites.

Keywords Advance regeneration · *Coccotrypes rhizophorae* · Light gap · Panama · Propagule predation

Introduction

Animals feeding on flowers, ovules, and seeds can greatly reduce the numbers and quality of seeds that are available to establish as seedlings (e.g. Janzen 1971; Harper 1977; Fenner 1985; Hendrix 1988; Crawley 1989, 1992; Louda 1989a; Hulme 1993). Under what conditions does this loss of viable propagules lead to a reduction in the density of adult plants? Discussions of this issue in the literature over the past decade (e.g. Andersen 1989, Crawley 1989, 1992; Louda 1989a; Louda and Potvin 1995; Hulme 1996; Maron and Simms 1997) have generated the following predictions. Seed/propagule predation can influence the density of adult plants when or where recruitment is seed-limited, for example, in populations that are chronically at low density or cover, or have recently colonized and are expanding in size. In contrast, seed/propagule predation will have little or no effect when or where plant density or cover is high and recruitment is limited by the availability of microsites for establishment and growth. In this circumstance, intense competition for such sites dictates the eventual number of individuals that reach maturity. A large reduction in propagule availability by predators will not result in lower adult density because those propagules that escape predation will benefit from a compensatory reduction in the intensity of competition they experience in the microsites where they establish. A corollary to

W. P. Sousa (✉) · B. J. Mitchell
Department of Integrative Biology,
University of California,
3060 VLSB, Berkeley, CA 94720, USA
e-mail: wpsousa@socrates.berkeley.edu
Tel.: +1-510-6435782
Fax: +1-510-6436264

S. P. Quek
Museum of Comparative Zoology,
Harvard University,
Cambridge, MA 02138, USA

these predictions is that seed/propagule predation is more likely to affect annual or “fugitive” species that depend on abundant propagules for persistence, than it is longer-lived, “competitive” species.

These predictions concerning the relative roles of propagule predation versus microsite limitation in determining plant population density assume that the suitability of a recruitment microsite is independent of the risk of predation faced by propagules that disperse to it. Anderson (1989, p 310) states this assumption explicitly: “seed predators do not influence the *safeness* of a site”. However, a number of studies have demonstrated that the risk of seed predation can covary with the environmental conditions that determine the quality of a site for plant recruitment and growth (e.g. Hulme 1997; studies listed in Table 3 of Sousa and Mitchell 1999). As reported here, we found a similar interaction, specifically between insect predation on mangrove propagules and the quality of microsites for seedling recruitment and growth. In such cases, the environmental conditions that promote plant recruitment and growth may enhance or diminish the risk of propagule predation, complicating the simple dichotomous predictions described above.

Furthermore, these predictions assume that when adult plants are abundant, they inhibit the recruitment of juveniles. This assumption reflects a historical bias in the studies that have given rise to the prevailing theory. Past work on this question (see above references) has focused predominately on assemblages of relatively small plants that are dominated by shade intolerant species (e.g. annual grasses, short-lived fugitive perennials). However, the situation may be markedly different in mature forests, where the juvenile stages of the canopy tree species exhibit varying degrees of shade tolerance. These juveniles can persist for some years in the understory, “waiting” for nearby disturbances to provide the necessary resources (e.g. light, nutrients) to support their growth into the canopy. If herbivores limit or prevent the accumulation of shade tolerant juvenile stages under the adult canopy, often referred to as a seedling bank or advance regeneration (Grime 1979; Marks and Gardescu 1998), they can have a marked impact on plant populations, albeit in the future, even when the density and cover of adult plants is high, contrary to the foregoing predictions. Due to their greater initial size, previously established seedlings are often at a distinct competitive advantage when a disturbance creates favorable conditions for growth (e.g. Uhl et al. 1988; Brokaw and Scheiner 1989; Poulson and Platt 1996; Brokaw and Busing 2000). By reducing or eliminating their influence on the process of gap regeneration, herbivores can alter the outcome of interspecific competition and hence the composition of the canopy. This scenario is at the heart of a number of theories concerning the role of seed predators in structuring forest assemblages, including their impact on the diversity of tropical rain forests (e.g. Janzen 1970; Connell 1971). What is unique about our study is the degree to which we have been able to link the impact of

propagule predators to the pattern and process of forest regeneration.

The work reported here is part of a broader investigation of the factors influencing patterns of mangrove forest regeneration and zonation at Punta Galeta, on the Caribbean coast of Panama. In this area, lightning strikes are the primary cause of canopy tree mortality, and the light gaps they produce are sites of vigorous regeneration as evidenced by the high density of saplings as compared to the understory (W. Sousa and B. Mitchell, unpublished data). Lightning gaps have been recognized as key sites of regeneration in mangrove forests throughout the tropics (Craighead 1971; Pajmans and Rollet 1977; Odum et al. 1982; Smith 1992; Smith et al. 1994; Sousa and Mitchell 1999; Clarke and Kerrigan 2000; Sherman et al. 2000).

In the course of our studies of the patterns and mechanisms of light gap regeneration, it became apparent that a small, stem-boring, scolytid beetle, *Coccotrypes rhizophorae* (hereafter, referred to as *Coccotrypes*) which infests propagules and young seedlings of the mangrove *Rhizophora mangle* (hereafter, referred to as *Rhizophora*), was potentially having a major effect on the regeneration of this canopy species. Specifically, we observed that *Coccotrypes* attacked and killed a high proportion of the *Rhizophora* seedlings that we had planted as part of a long-term, field experiment designed to measure rates and outcomes of competition among juvenile mangroves in different forest floor environments. This mortality was concentrated in low intertidal sites, where *Rhizophora* typically dominates or co-dominates the canopy, but varied dramatically between microhabitats. Within the first year of this experiment, the details of which will be reported elsewhere, beetles killed 72.6–89.1% of the seedlings planted in three closed-canopy, understory sites, but only 0.9–2.1% in three adjacent light gaps. The juvenile stages of *Rhizophora* are relatively shade-tolerant (Duke and Pinzón-M 1992; Ellison and Farnsworth 1993; Farnsworth and Ellison 1996; Smith and Lee 1999), so their elimination from the understory by *Coccotrypes* would greatly reduce the contribution of this species’ advance regeneration to forest dynamics. Here, we present the results of an experiment designed to quantify variation in the risk of mortality due to beetle attack as a function of a seedling’s position relative to a light gap. This experiment ran for several months, a short period relative to the time course of forest regeneration. To evaluate whether its results meaningfully predicted patterns and processes of stand regeneration over longer periods, we examined multiannual sampling data on the size-structure of *Rhizophora* trees in relatively undisturbed stands and on patterns of natural regeneration in representative light gaps. As we demonstrate, patterns at these larger spatial and temporal scales are entirely consistent with our experimental findings. These complementary lines of evidence strongly suggest that *Coccotrypes* is having a major influence on the dynamics of mangrove forest regeneration following disturbance by lightning.

Materials and methods

Study site

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).

Study species

Mangroves

Three tree species (hereafter, referred to by their generic names) comprise the canopy of the study forests: *Avicennia germinans* (L.) Stearn (Avicenniaceae), *Laguncularia racemosa* (L.) Gaertn. f. (Combretaceae), and *Rhizophora mangle* L. (Rhizophoraceae). In these forests, as elsewhere (Davis 1940; Schaeffer-Novelli et al. 1990; McKee 1995; Imbert and Menard 1997; Sherman et al. 2000), the three species are distributed differentially with distance from the water's edge, but their distributions overlap to varying degrees (W. Sousa and B. Mitchell, unpublished data). In our study forests, several zones of differing canopy composition occur along the tidal gradient. *Rhizophora* forms a pure or nearly pure stand at the seaward fringe. About 10–20 m from the water's edge, *Laguncularia* joins the canopy, forming a nearly even mixture with *Rhizophora* in the low intertidal. *Avicennia* joins the canopy in the mid-intertidal, creating a mixed canopy of the three species, and then gradually monopolizes most upper intertidal stands. *Laguncularia* may disappear completely from the canopy in the upper intertidal, or occur only as scattered individuals or small stands.

Mature *Rhizophora* propagules are dispersed during the rainy season, primarily between April and October (Rabinowitz 1978; Duke and Pinzón 1993; W. Sousa and B. Mitchell, personal observation). *Rhizophora* is fully viviparous (Rabinowitz 1978; Tomlinson 1986); the immature propagule remains attached to the parent for 4–6 months after germination. The mature propagule is large (mean length: 22.3 cm, mean fresh weight: 17.5 g; Sousa et al. 2003) and rod-like in shape, with pointed ends. Propagules are buoyant and dispersed to a limited degree across the flooded forest floor by both runoff following rainfall and tidal action. Marked propagules moved a maximum of 8 m, and on average less than 3 m from the point of release (W. Sousa and B. Mitchell, unpublished data). The combination of a viviparous life history and water-logged, anoxic soil conditions prevents *Rhizophora* from developing a dormant propagule bank in the soil. As a consequence, the demography of its juvenile stages is characterized by annual cohorts of seedlings that establish across the low intertidal forest floor, in both understory and gap environments.

Lightning strikes produce more than 90% of canopy gaps in our study forest. The remaining gaps are created by wind throw or mortality from pathogens or physiological stress. As opposed to the largely individual deaths caused by wind throw and disease, lightning strikes usually kill multiple trees (as many as 65 in one strike). Canopy gaps in our study forest range in size from 68 to 1,075 m², averaging 329 m² ($n=58$, W. Sousa and B. Mitchell, unpublished data). Since 1991, when we began monitoring gap formation, an average of 0.80% (range: 0.20–1.33%) of the canopy of our study areas has been disturbed annually by lightning strikes. At our sites, lightning strikes kill or injure taller trees, but do not damage understory vegetation growing below about 3–4 m, including advance regeneration in the form of suppressed seedlings and saplings. This contrasts with the observation of Sherman et al. (2000) that lightning strikes kill both overstory and understory vegetation in Dominican Republic mangrove forests.

Beetles

This study examined the impact of the herbivorous scolytid beetle, *Coccotrypes rhizophorae* (Tribe Dryocoetini; recently known as *Poecilips rhizophorae*, Wood 1982) on recruitment of *Rhizophora* in our study forests. *Rhizophora* appears to be the exclusive host species of *Coccotrypes* in the Caribbean. The beetle attacks propagules, both pre- and post-dispersal, and newly established seedlings (Browne 1961; Woodruff 1970; Onuf et al. 1977; Farnsworth and Ellison 1997). In two different years, we observed that about 20% of the propagules produced by *Rhizophora* trees in our study forests became infested with beetles prior to abscission (Sousa et al. 2003). *Coccotrypes* can also infest young prop and aerial roots of *Rhizophora* (Atkinson and Peck 1994; I. Feller, personal communication; W. Sousa and S. Quek, personal observation).

Coccotrypes is a small (1.6–3.0 mm long), dark reddish brown scolytid beetle (Fig. 1a, also see Fig. 175 in Wood 1982). Infestation begins when a mated female digs a short burrow into the surface of the hypocotyl or aerial root where she deposits clusters of eggs. Upon hatching, the larvae greatly extend and enlarge the parental tunnel, as they rapidly mature. Mature, mated females emerge to seek a new host. Persistent infestations consume much of the interior of the propagule (Fig. 1b), producing large quantities of rust-colored frass that is emitted in conspicuous plumes from entrance holes (Fig. 1c).

To date, Onuf et al. (1977) is the most detailed published study of the interaction between *Coccotrypes* and *Rhizophora*. Their study measured rates of insect herbivory on *Rhizophora* trees growing on the fringe of small nearshore islands on the Atlantic coast of Florida, USA. A high proportion of developing propagules became infested with *Coccotrypes*, and when such propagules were experimentally planted, they had much lower rates of establishment and survival than uninfested ones. We have confirmed the latter result with similar experimental plantings (Sousa et al. 2003). Onuf et al. (1977) did not, however, examine the consequence of propagule predation by *Coccotrypes* on forest structure or dynamics; ours is the first study to do so.

Currently, it is not known whether *Coccotrypes* is native to the New World or an introduced species. It has been found in Florida, Mexico, Belize, Panama, Ecuador, and the Galapagos Islands, but Wood (1982, 1986, personal communication) believes it was transported by humans to the region from its presumed native range in Indonesia-SW Asia. Atkinson and Peck (1994) argue, however, that *Coccotrypes*' wide geographic distribution could simply reflect natural dispersal, facilitated by the circumtropical distribution of the genus *Rhizophora*. We are presently conducting molecular genetic studies to help evaluate the species' status in this regard. This determination is central to any inferences one might make concerning evolutionary aspects of this host-plant interaction and the history of its impact on mangrove forest structure.

Experimental assay of the effect of forest floor environment on mortality due to beetle attack

We conducted a mensurative experiment (sensu Hurlbert 1984) to quantify variation in a seedling's risk of mortality due to beetle attack as a function of its position relative to a light gap. As described in detail below, we planted uninfested *Rhizophora* propagules along transects starting inside a canopy gap and extending into the surrounding understory, and assessed their fates after 19 weeks.

In the first week of September 1996, three light gaps within low intertidal, mixed species stands of *Rhizophora* and *Laguncularia* were selected as experimental sites (Table 1). All three had formed within 2 years of the start of the experiment, and were undergoing natural regeneration; most of the vegetation was less than 2 m tall. Propagules were planted along three replicate transects radiating outward from each gap. An effort was made to spread the directions of the transects as uniformly as possible around the circumference of the gap with the restrictions that they avoid river channels, other

Fig. 1 **A** Female *Coccotrypes rhizophorae* (scale bar =1 mm). **B** Cross-sections of *Rhizophora* hypocotyls showing extensive excavations by beetles and clusters of developing larvae (scale bar =1 cm). **C** *Rhizophora* seedling with plume of frass emitted from beetle entrance hole

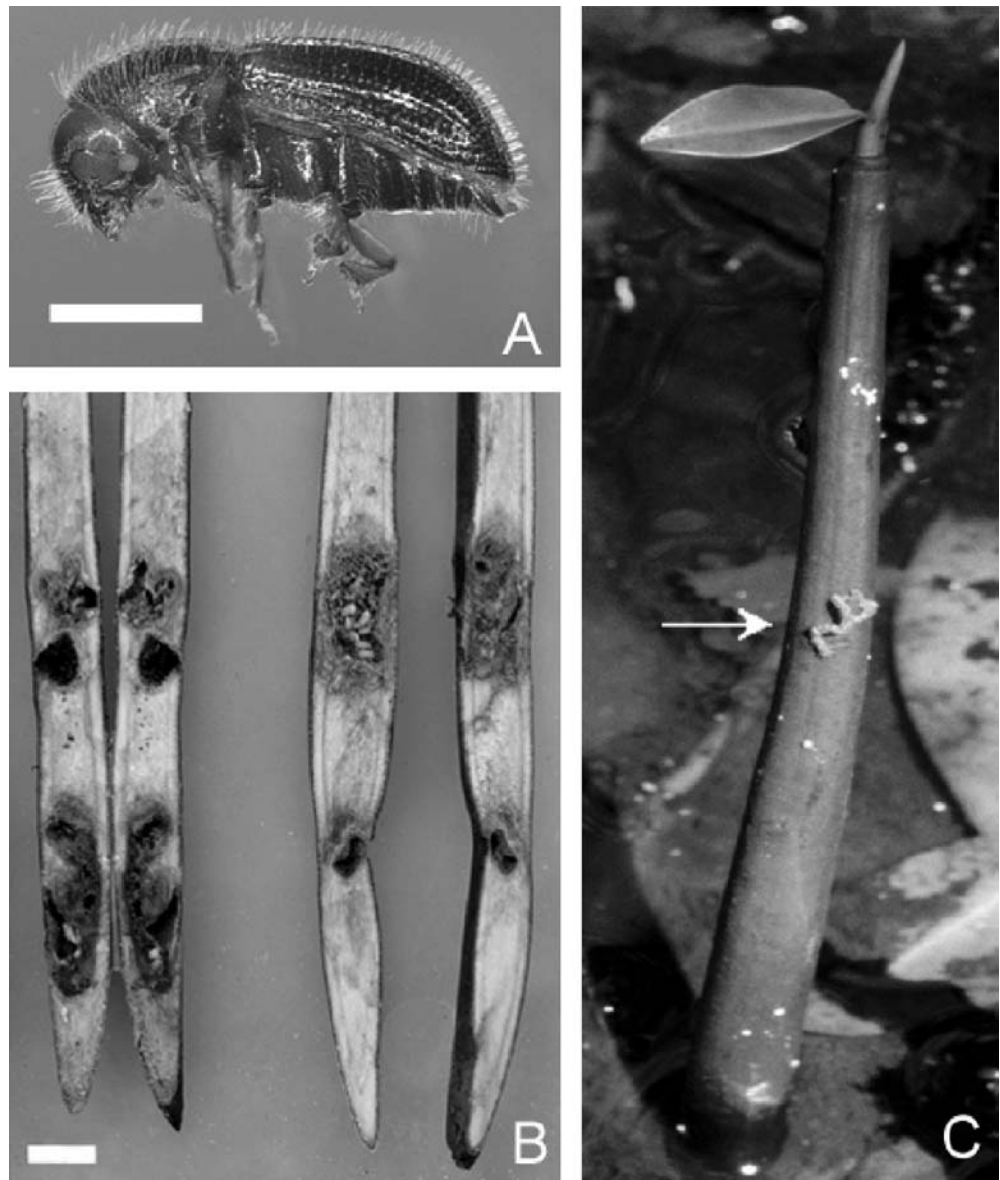


Table 1 Characteristics of light gaps used for the experimental assessment of the risk of mortality due to beetles as a function of position relative to a gap. Gap area was estimated geometrically from measurements of eight, center-to-edge radii taken at 45°

Gap	Estimated area (m ²)	Local species composition of canopy trees (%)	
		<i>Rhizophora</i>	<i>Laguncularia</i>
BM-9401	545	21.0	79.0
PL-9502	363	34.5	65.5
PE-9501	364	48.3	51.7

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

stand types, and other gaps that would alter the unidirectional gap-to-understory environmental gradient. Six groups of propagules were planted along each transect, at 5 m intervals, starting at 5 m inside the edge of the gap and progressing 20 m into the understory (hereafter expressed as distance from gap edge: -5 m, 0 m, 5 m, 10 m, 15 m, 20 m). Each group contained seven propagules that were planted in a 50 cm diameter circle at equally spaced intervals; the radicle end of each propagule was inserted 5 cm directly into

the soil. All groups had the same distribution of propagule lengths ranging from 15.0–25.0 cm, with a mean length of 20.7 cm. The propagules were visually screened for external signs of active beetle infestations (see Study species: beetles) immediately prior to planting on 6 September 1996. They were harvested on 16 January 1997 for analysis.

Death by beetle attack was ascertained by dissecting dead propagules or seedlings and inspecting them for the presence of an

active infestation, or evidence of past beetle activity, including tunneling and frass. For each position along a transect, we calculated the proportion of planted propagules that had been killed by beetles. A small number of propagules were excluded from these calculations because their status with regard to beetle attack was uncertain. These included propagules that had been killed by crabs (Sousa and Mitchell 1999), probably *Ucides cordatus* (Ocypodidae); the hypocotyl was either cut off a couple centimeters above the soil or was severely lacerated. Although the remaining tissue showed no signs of beetle activity, we could not be certain that the missing parts of the hypocotyl had not been attacked by beetles prior to being consumed by crabs. Similarly, we could not rule out beetle infestations in the few propagules that simply disappeared, probably having been carried off by crabs. We also excluded from the calculations a few propagules that died intact or with only minor crab damage, but showed no evidence of beetle attack. Because the planted propagules were not continuously monitored, we had no way of knowing how long such propagules had been exposed to beetles before they died. They may have died shortly after being planted, and hence were only briefly available to dispersing beetles. Accurate estimates of the relative risk of beetle attack required that all seedlings were equally available to beetles throughout the study.

The effects of position relative to the gap edge and of different light gaps on proportion of propagules killed by beetles were analyzed with a two-way, mixed model ANOVA. Distance from gap edge was treated as a fixed factor, and gap as a random factor in the analysis. Within-cell variances of the proportions were homogeneous (Cochran's test: $C=0.1405$, $df=2$, 18 , $P>0.05$), so no transformation was performed. A posteriori comparisons among gaps were made with Tukey's HSD procedure. We tested for a linear trend in beetle-caused mortality as a function of distance using the method described in Winer et al. (1991, p 470).

Studies of forest structure

The experiment described above was conducted over relatively small spatial and temporal scales. To evaluate whether the patterns of beetle-induced mortality it revealed contribute to the dynamics of natural forest stands, we analyzed data from a number of long-term observational studies of the structure and regeneration of forest stands, asking whether these patterns were consistent with our experimental findings.

Size-structure of *Rhizophora* in undisturbed stands

To document spatial and temporal variation in the species composition and size-structure of trees at different positions along the tidal gradient, we established five permanent 50×50 m plots, in which all stems ≥ 1 cm dbh were individually tagged, measured, and mapped. We intentionally located the plots in mature, closed-canopy stands that showed no signs of recent disturbance by lightning or other processes. Two of these plots were located in low intertidal stands composed of a fairly even mixture of *Rhizophora* and *Laguncularia* trees. Here, we present information on the size-distribution of *Rhizophora* trees in one of these plots (plot A), which has remained undisturbed by lightning since it was first established, and for which we have the longest record (7 years). The second low intertidal plot was hit by a lightning strike about 2 years after it was established. Plot A was initially censused in July 1993, then again in June 1997 and June 2000.

When first established, plot A was gridded into 25 10×10 m cells to facilitate tagging and mapping. To measure the abundance, growth, and survival of seedlings and saplings < 1 cm dbh, we installed 15 permanent 1 m² quadrats in the plot in July 1997. These quadrats were positioned in a stratified random manner across the plot at the centers of three randomly selected 10×10 m cells in each of the five 10-m-wide rows of the grid. All plants < 1 cm dbh within the quadrats were individually marked with numbered plastic bird bands and their heights measured. Dispersing, unrooted propagules

were also counted in each quadrat. These quadrats have been recensused approximately every 6 months through July 2002.

Density and size-structure of *Rhizophora* inside versus outside of light gaps

We have sampled several light gaps over a number of years to document the course of natural gap regeneration, and to compare the density and size-structure of juvenile mangrove inside gaps as compared to surrounding areas with an intact adult canopy. In this paper, we present such data for juvenile *Rhizophora* associated with two lightning gaps that formed in stands where *Rhizophora* was a major component of the adult canopy. Gap PL-1 was formed in 1984 (E. Adams, personal communication), and first sampled in March 1985 by M. Geber, who has generously given us her data. We resampled the gap in July 1988 and July 1991. Gap PL-1 was 302.2 m² when first formed in a stand in which 43.2% of the canopy trees were *Rhizophora*, 48.7% *Laguncularia*, and 8.1% *Avicennia*. Gap BM-10 was formed in 1990. We first sampled it in July 1991, and again in July 1998. Gap BM-10 was 373.4 m² when first formed, and the composition of adult trees in the stand at the time of the disturbance was 40.9% *Rhizophora* and 59.1% *Laguncularia*.

On each date, 20 randomly positioned 1 m² quadrats were sampled inside and 20 outside of each gap, with the exception of Gap PL-1 in 1988, when 15 quadrats were sampled in each microhabitat. "Inside" quadrats were located at random grid points within the perimeter of the canopy gap, while "outside" quadrats were located at random positions along three or four 30 m transect lines equally spaced around the perimeter of the gap, and 5–15 m from the gap edge. Understory areas close to neighboring gaps were avoided. Living juvenile mangroves growing in each quadrat were identified to species and their heights measured. In M. Geber's 1985 sampling of Gap PL-1, she counted, but did not measure the heights of seedlings with only 1 or 2 pairs of leaves, while measuring all larger individuals. For the purposes of graphical display and statistical comparison we have assigned these smaller individuals the mean heights of plants with these same numbers of leaves measured in subsequent samplings of that gap.

For each gap, we used two-way, fixed factor ANOVAs to examine the effects of position (inside vs outside gap) and sampling date on the mean density and height of juvenile *Rhizophora*. The quadrat counts were transformed as $\log(\text{count} + 1)$ and heights as $\log(\text{height})$ to homogenize variances prior to analysis (Cochran's test, $P>0.05$). A posteriori pair-wise comparisons of cell means were made with Tukey HSD tests.

Results

Experimental assay of the effect of forest floor environment on mortality due to beetle attack

Both the specific gap and the position at which propagules were planted in relation to its edge strongly affected rates of seedling mortality caused by beetles (Gap: $F_{2,36}=8.53$, $P=0.0009$; Distance: $F_{5,10}=10.52$, $P=0.001$). There was no evidence of an interaction between these factors ($F_{10,36}=0.44$, $P=0.9146$). Propagules planted at Gap PE-9501 suffered significantly higher mortality than those planted at Gaps BM-9401 or PL-9502, which did not differ from each other (Fig. 2A). This variation in the rate of beetle attack among sites is probably attributable to the fact that *Rhizophora* comprised a considerably higher proportion of the canopy trees in the stand surrounding Gap PE-9501 than in the stands surrounding

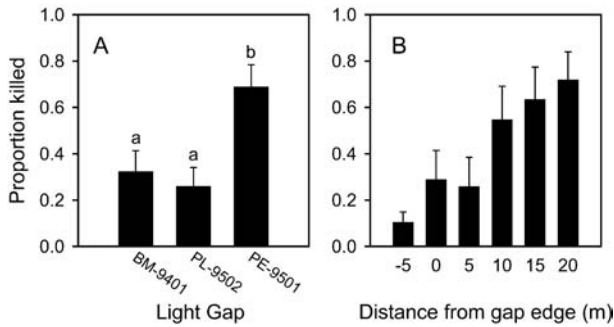


Fig. 2A, B Mean proportions (+ 1 SE) of *Rhizophora* seedlings killed by *Coccotrypes* at different positions relative to the edges of experimental light gaps. **A** Variation in mortality among the three experimental gaps (distances pooled). Letters above bars summarize results of a Tukey HSD test; means marked with different letters are significantly different at $P < 0.05$. **B** Variation in mortality with distance from gap edge (gaps pooled)

the other two gaps (Table 1). A higher density of adult *Rhizophora* means a greater supply of resources (propagules and aerial roots) and thus a larger local population of beetles, resulting in higher rates of attack on the experimental propagules.

The rate of mortality due to beetles increased with distance from the gap (Fig. 2B). The linear component of this trend accounted for 98.1% of the variation among distances and was highly significant ($F_{1,36} = 8.64$, $P < 0.01$). None of the quadratic trend components was significant.

Size-structure of *Rhizophora* in undisturbed, closed canopy stands

The size-distribution of *Rhizophora* trees in permanent plot A is typical of low intertidal closed-canopy forest stands at Punta Galeta. There are few saplings < 5 cm dbh, and their numbers within the plot have declined over the 7 years of monitoring (Fig. 3). We documented very similar patterns in the other low intertidal permanent plot prior to its having been hit by a lightning strike, and at lower tidal levels along each of three forest transects that we established as a means of quantifying changes in forest structure along the tidal gradient (W. Sousa and B. Mitchell, unpublished data). These patterns will be reported in a separate paper on forest structure.

The rarity of *Rhizophora* saplings in the forest was not for lack of recruitment. The average combined density of seedlings and propagules in plot A ranged from 0.47 to 4.47/m² in the 11 semiannual seedling censuses conducted between July 1997 and July 2002. Extrapolating to the entire 2,500 m² plot, the number of juvenile stages < 1 cm dbh on the forest floor at any census ranged from 1,175 to 11,175 (median = 2,175, mean = 3,331.1). Undoubtedly, these calculations underestimate the actual number of recruits since some probably established and died in the 6 months between our sampling dates.

Instead, the low numbers of *Rhizophora* saplings in the understory is caused by high mortality, which prevents

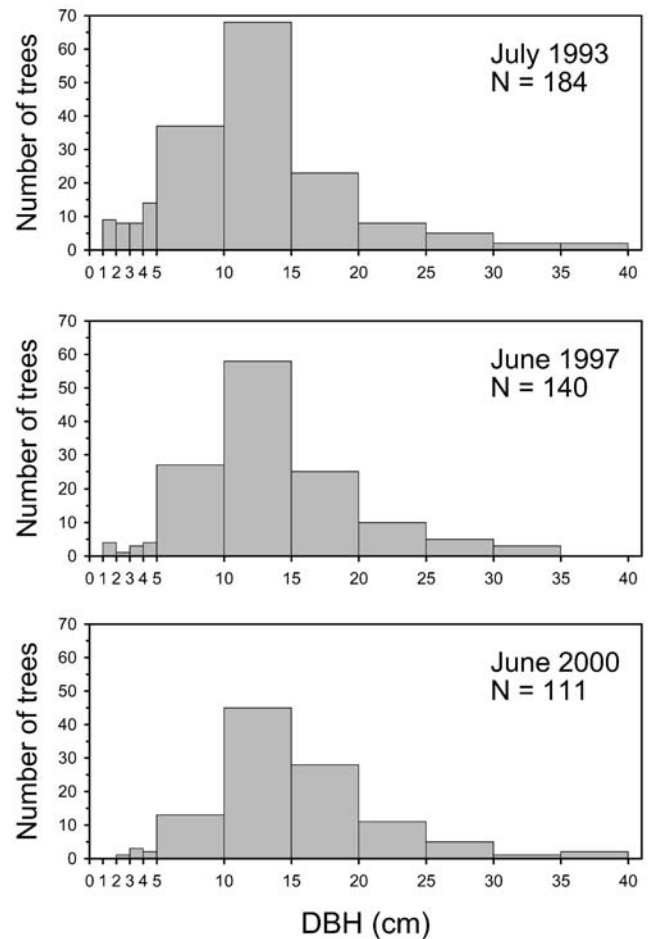


Fig. 3 Size structure of *Rhizophora* trees (≥ 1 cm dbh) in three censuses of 50x50 m plot A located in a low intertidal, closed canopy stand

seedlings from growing into the sapling size-class. Very few of the tagged seedlings survived more than 1 year, and most were dead by the first census (at 6 months) after they were initially marked. Many of the dying seedlings were infested with beetles. Few of the marked seedlings have grown to be more than 30 cm tall, and none has grown to 50 cm tall. Our main point is that despite regular recruitment of seedlings, the number of saplings stages has remained low, and in fact seems to be declining. This situation has apparently persisted for some time in the plot, given the absence of any plants between 50 cm and 2 m tall, roughly the height of a 1 cm dbh sapling. Our repeated measurements of marked seedlings (25–45 cm tall) indicate a growth rate in the shaded understory of only 1 cm or even less a year, so it would take many years for a plant to grow through this size interval without a disturbance to the canopy.

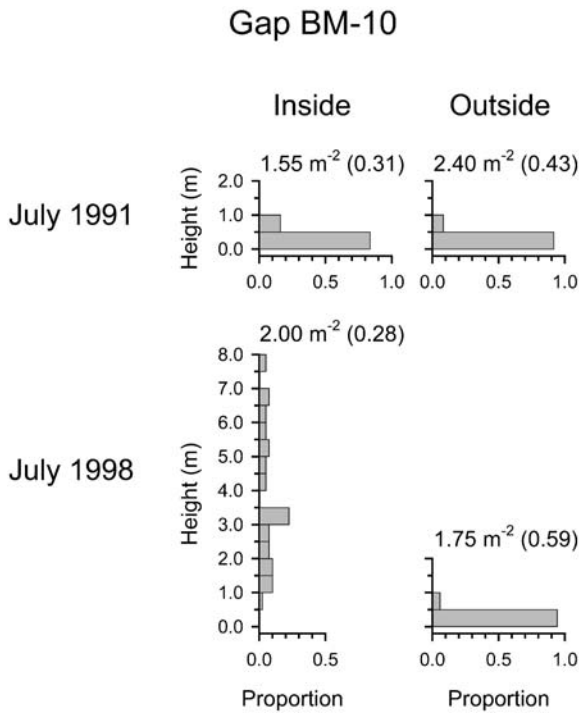


Fig. 4 Size structure and mean density (SE) of juvenile *Rhizophora* trees inside and outside of light gap BM-10 located in a low intertidal, *Rhizophora/Laguncularia* stand. The gap was created by a lightning strike in 1990, first sampled in July 1991, then again in July 1998

Density and size-structure of *Rhizophora* inside versus outside of light gaps

Our long-term sampling of light gaps indicates that although the density of *Rhizophora* seedlings that establish annually in the forest understory is equal to or greater than that inside gaps, only those that establish within gaps survive to grow into saplings. For gap BM-10 (Fig. 4), juvenile *Rhizophora* were relatively more abundant in the understory than inside the gap in 1991, but the opposite pattern obtained in 1998, producing a significant interaction effect between position and year ($F_{1,76}=4.26$, $P=0.042$). However, in neither year was there a significant difference in the absolute densities in the two microhabitats (Tukey tests, $P>0.1$). For gap PL-1 (Fig. 5), there was no difference in the density of juvenile *Rhizophora* inside versus outside the gap at any of the three censuses ($F_{1,104}=0.153$, $P=0.696$), and there was no interaction between position and year ($F_{2,104}=0.498$, $P=0.609$), but the overall density of juvenile *Rhizophora* was lower in 1991, than in the two earlier censuses ($F_{2,104}=3.710$, $P=0.028$).

In contrast to the weak influence of gaps on seedling density, a large disparity in size developed between juveniles that established in gap versus understory environments. This difference in size grew larger with time as reflected by significant year \times position interactions for both gap BM-10 ($F_{1,150}=2.293$, $P<0.001$) and

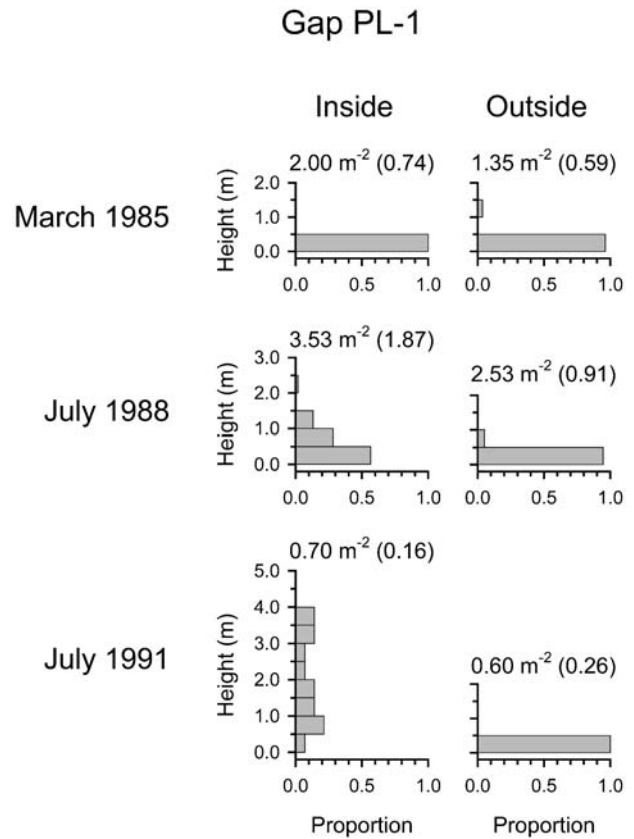


Fig. 5 Size structure and mean density (SE) of juvenile *Rhizophora* trees inside and outside of light gap PL-1 located in a mid intertidal, *Rhizophora/Laguncularia* stand. The gap was created by a lightning strike in 1984, first sampled in March 1985, then again in July 1988 and July 1991

gap PL-1 ($F_{2,178}=26.625$, $P<0.001$). For gap BM-10 (Fig. 4), the mean height of juvenile *Rhizophora* inside the gap was greater than that of plants in the understory in both 1991 (mean height \pm SE: inside = 35.9 ± 2.4 cm, outside = 26.9 ± 1.7 cm, Tukey test, $P<0.05$) and 1998 (inside = 375.0 ± 30.7 cm, outside = 29.8 ± 1.8 cm, Tukey test, $P<0.05$). The mean height of plants growing in the gap increased more than 10-fold over the 7 years between samplings (Tukey test, $P<0.05$), but there was no significant change in the mean height of plants in the understory (Tukey test, $P>0.05$). At both sampling dates, the population of understory plants comprised largely young-of-the-year recruits, indicating a high turnover rate. Therefore, the disparity in size that developed between gap and understory plants reflected both better survival and growth inside the gap.

Very similar height relationships were observed in gap PL-1 (Fig. 5). There was no difference in the mean heights of juvenile *Rhizophora* inside versus outside of the gap in 1985 (mean height \pm SE: inside = 31.4 ± 0.9 cm, outside = 31.9 ± 4.3 cm, Tukey test, $P>0.05$), but inside plants were larger than outside plants in 1988 (inside = 60.7 ± 4.9 cm, outside = 31.7 ± 1.8 cm, Tukey test, $P<0.05$), and this disparity was even greater in 1991

(inside = 182.2 ± 30.3 cm, outside = 33.1 ± 2.6 cm, Tukey test, $P < 0.05$). At each sampling date, *Rhizophora* growing inside the gap were significantly taller than they had been in the previous sample (Tukey tests, $P < 0.05$). In contrast, the mean height of juveniles in the understory did not change over time (Tukey tests, $P > 0.05$). At each sampling date, as in gap BM-10, the juvenile *Rhizophora* measured in the understory were largely young-of-the-year recruits.

Discussion

In discussions of the relative roles of propagule predation and microsite limitation in determining the numbers of adult plants, the suitability of a microsite for recruitment is often assumed to be independent of the risk of predation for propagules that disperse to it. Our results clearly demonstrate an interaction between the quality of microsites for recruitment and growth and the risk of *Rhizophora* propagules and seedlings being attacked and killed by *Coccotrypes*. While *Rhizophora* seedlings establish across the forest floor each year, beetle-caused mortality prevents their recruitment to the sapling size-class except within lightning-created gaps and the areas immediately surrounding them, which provide a spatial refuge from beetle attack. This pattern of herbivory accounts for observed spatial variation in stand structure: within the forest, sapling stages of *Rhizophora* are largely restricted to areas of recent canopy disturbance.

Such microsites also provide the resources necessary for juveniles to grow into the adult canopy. One might conclude, therefore, that *Rhizophora* density is limited by these recruitment microsites rather than by the number of propagules consumed by herbivores. However, the beetles are effectively eliminating a key regeneration strategy of *Rhizophora*, a long-lived canopy dominant: the filling of gaps by the growth of saplings that have been released from suppression by the adult canopy. This reduces the competitive impact of *Rhizophora* and may enhance the opportunity for shade intolerant *Laguncularia* juveniles to survive and grow into the canopy when a gap is formed, leading to co-dominance of low intertidal forests by these species.

Anderson (1989, p 310) argued that “even if predators prevented altogether the location of safe sites by seeds, they would still have a negligible impact on population size (i.e. they would reduce potential population size by only a small fraction) unless they interfered with the establishment of a seed bank capable of exploiting future changes in safe site abundance.” In effect, this is precisely what *Coccotrypes* predation does, but to a seedling bank rather than seed bank. An understory shade tolerant seedling bank acts much like a soil seed bank in providing a mechanism of “storing” future recruits (Warner and Chesson 1985; Chesson 1986). Just as seed predators can control plant recruitment by depleting the soil seed bank, so too can herbivores that prevent the establishment of shade tolerant juveniles beneath the adult canopy. Incorporating the influence of herbivores on the contribution of

advance regeneration to forest dynamics, as demonstrated in this study, will significantly enhance the generality of theories concerning the impact of seed and seedling predators on plant populations.

At present, we do not know why seedling mortality due to beetles is lower in light gaps than in the shaded understory. If mated female beetles disperse diurnally, they may actively avoid the potentially stressful high light and temperature conditions inside gaps. Alternatively, seedlings growing in the gap environment may develop morphological or chemical characteristics that deter beetles from burrowing into their stems. In our experiments, the difference in rates of attack in the two microenvironments developed within a few days after the seedlings were planted, probably more rapidly than could be accounted for by morphological changes in plant tissues. However, some form of light-activated, toxic secondary metabolite, or phototoxin, could be involved (L. Bjostad, personal communication). Such compounds are rapidly excited by absorption of light, accumulate relatively quickly under high light conditions, and can effectively defend against insect herbivores (Berenbaum 1987; Downum 1992). To our knowledge, phototoxins have not been looked for in *Rhizophora*, but have been found in more than 40 families of plants (Downum and Wen 1995; K. Downum, personal communication). An observation that argues against the involvement of phototoxins is that beetle populations continued to thrive in infested seedlings that were grown under high light conditions beneath a 2 m high, translucent fiberglass awning at the Galeta laboratory (Sousa et al. 2003). However, these beetles had already penetrated the epidermis of the propagules' hypocotyls by the time they were collected from shady understory sites prior to planting. The epidermis contains an abundance of chlorophyll, is photosynthetically active (Smith and Snedaker 2000), and is the likely location of any phototoxic compounds.

Information on the responses of dispersing scolytid beetles to environmental conditions is sparse and inconsistent, providing little insight to the patterns we have observed. Jordal and Kirkendall (1998) found that the scolytids that inhabit burrows within the petioles of neotropical *Cecropia* trees were less likely to colonize trees growing in sun-exposed sites. On the other hand, canopy openness did not affect the rate at which seeds of the rain forest tree, *Chlorocardium*, were infested by a scolytid beetle (Hammond et al. 1999). Optimal temperatures for flight are also poorly known, but the flight of some species appears to be deterred by high temperatures (e.g. Thompson and Moser 1986). A definitive answer to this question awaits additional study of the natural history and behavior of *Coccotrypes*.

Interactions between herbivory and light environment (or canopy cover) are common. In some cases, rates of herbivory are higher in the light, in others, under a canopy. The classic demonstration of such an interaction is Huffaker and Kennett's (1959) study of the biological control of the introduced Klamath weed, *Hypericum*

perforatum, in northern California by the leaf-feeding beetle, *Chrysolina quadrigemina*. Shortly after the beetle was introduced, *Hypericum* was largely eliminated from large sunny meadows where adult beetles prefer to lay their eggs, but persisted in smaller, tree-shaded refugia avoided by beetles. Other studies of insect herbivory on herbaceous species have documented the same (Louda et al. 1987; Louda and Rodman 1996) or opposite (Maiorana 1981; Schemske 1984; Louda et al. 1987) pattern. In a Belizean mangrove forest, very similar in tree species composition to our sites, Ellison and Farnsworth (1993) found that insect herbivores consumed more than twice the leaf area of *Rhizophora* seedlings growing in the shaded understory as compared to seedlings growing in small, experimental gaps. This is the same pattern we documented for attacks on *Rhizophora* seedlings by stem-boring *Coccotrypes*. Hulme (1996, 1997) found that the pattern of seed predation with respect to canopy cover varied with the kind of herbivore: rodents removed more seeds from under shrubs than from open areas, whereas ants did the opposite. A survey of studies that compared rates of propagule predation inside versus outside light gaps in tropical and temperate forests (Sousa and Mitchell 1999) shows that while the rates often differ, there is no consistent pattern in the relative risk of attack between these microhabitats. In some studies it is higher in gaps, and in others, in the understory, probably reflecting the species-specific habitat preferences and foraging behaviors of the seed predators in each study system.

Since *Coccotrypes* is causing the highest mortality of *Rhizophora* propagules and seedlings in areas of the forest where this tree species is most abundant, the beetle cannot be responsible for maintaining the present distribution of their host species along the tidal gradient. Only if beetles were causing mortality that was inversely related to the abundance of adult *Rhizophora* could they be playing a role in maintaining this distribution (e.g. Louda 1982, 1983, 1989b; Louda et al. 1987). Rather, in our study forests, herbivory by *Coccotrypes* may be acting to disrupt current distribution patterns. The occurrence of lightning gaps that afford safe sites from beetle predation for recruitment of *Rhizophora* is critical to persistence of this species as a canopy dominant in low intertidal forests on the Caribbean coast of Panama.

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