

Effects of experimental canopy gaps on mangrove recruitment: lack of habitat partitioning may explain stand dominance

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Summary

1 Few species of Indo-pacific mangroves co-occur at spatial scales of canopy gaps despite environmental heterogeneity and a flora that has varied physiological and morphological traits, but experiments on why such communities are species poor are uncommon.

2 Lack of habitat partitioning, in concert with competitive exclusion, may explain low species richness at canopy gap scales. This study examined whether mangrove recruitment differs among species with respect to the effect of forest gap size, ground disturbance, position along an intertidal gradient and canopy membership.

3 The canopy of a tropical mangrove forest in northern Australia was experimentally manipulated to create two gap sizes (50 m² and 225 m²) in low and high intertidal forests with or without sediment disturbance. Propagules of six species, from three mangrove families, were sown into treatments and their predation, establishment, growth and survival measured for 5 years.

4 All species established, and five survived, in canopy gaps in both high and low intertidal positions. Interspecific difference in establishment, growth and survival of seedlings in two intertidal positions were not closely matched to canopy membership and hence this does not explain zonation.

5 No seedlings survived under the canopy and there was little evidence for shade-tolerant species. The interactions between canopy treatments and sediment disturbance that would have indicated gap partitioning were not detected. Seedling growth and survival was enhanced in large canopy gaps but there were no growth differences among species that matched canopy membership of plots.

6 Most species appear to be able to recruit in canopy gaps if there is no dispersal limitation. Rather, the range of species available to fill gaps is limited because predation of propagules advantages species that are from the adjacent canopy. Lack of partitioning of resources within gaps by species may result in the exclusion of competitors that are not canopy members, further reducing coexistence.

Key-words: co-existence, gap partitioning, regeneration niche, shade tolerance, zonation

Journal of Ecology (2004) **92**, 203–213

Introduction

Hundreds of species can coexist in a single hectare of lowland tropical forest, yet, in adjacent mangroves, few species co-occur. Studies of why so many species co-occur dominate community ecology whilst the reciprocal question is less frequently asked; why do so few species of mangroves co-occur? Recruitment in mangroves,

like other closed forest communities, is controlled by gaps in the canopy generated by disturbances (Smith 1992; Smith *et al.* 1994; Clarke & Kerrigan 2000; Sherman *et al.* 2000). Natural disturbances that form gaps in mangroves arise from windstorms, lightning, cyclones, pathogens and wood borers (Smith 1992; Feller & McKee 1999; Clarke & Kerrigan 2000), resulting in changed light, sediment and biological interactions such as predation by crabs (Smith 1987a,b; Osborne & Smith 1990; Smith 1992; Smith *et al.* 1994; Smith *et al.* 1994; Minchinton 2001; Clarke & Kerrigan 2002; Allen

et al. 2003; Krauss & Allen 2003). Many species of mangroves might therefore be expected to coexist in the Indo-Pacific region because there is also a moderately diverse flora with varied physiological and morphological traits (Tomlinson 1986; Duke 1992; Clarke *et al.* 2001; Ball 2002). However, at spatial scales of canopy gaps (10–100 m²) (see Smith 1992; Feller & Mckee 1999; Clarke & Kerrigan 2000) few species co-occur compared with the total pool of species available (Ball 1998; Clarke *et al.* 2001) and most stands are dominated by one or two species. In addition, the moderate salinity levels of sediments in high rainfall mangrove regions are within the range of salinity tolerances of many more species than naturally co-occur (Ball 1998, 2002; Clarke & Kerrigan 2000).

Low species richness in Indo-Pacific mangroves, at spatial scales of canopy gaps, may be explained by the lack of habitat partitioning, followed by competitive exclusion, but this has never been tested. The gap partitioning hypothesis explains species coexistence in forests by proposing that environmental gradients created by gap formation are too varied to be dominated by a single best competitor (Ricklefs 1977). Alternatively, the stochastic availability of gaps and recruitment limitation can reduce competitive exclusion (Brokaw & Busing 2000; Wright 2002). Studies of coexistence or its corollary, competitive exclusion, in both rain forests and mangroves have focused on natural 'experiments' because large spatial and temporal scales make it difficult to do field experiments. Tropical mangrove forests contrast with other tropical forests because there is no seed bank, the vertical structure is relatively simple and seeds are large (Tomlinson 1986; Clarke & Kerrigan 2000). These characteristics provide a model system for testing whether habitat partitioning affects species richness as we can manipulate canopy gap characteristics and the location of canopy gaps across environmental gradients such as the position along the intertidal shoreline. The lack of a dormant seed bank in mangroves also enables recruitment to be studied more easily than in other forest systems because the composition and density of the seed bank can easily be

manipulated in order to control for dispersal and recruitment limitation.

The aim of this study was to test the effects of creating gaps with different characteristics on the establishment, growth and survival (together termed recruitment) of six mangrove species in three families in northern Australia using a manipulative field experiment. The manipulations tested for differences in recruitment (i) among gap sizes and between gap and canopy, (ii) between disturbed and undisturbed sediments (to mimic tree fall pattern), (iii) between high shore and low shore environments, and (iv) among plots with different canopy members. If habitat partitioning is present, then there should be a statistical interaction between species and one or more of the experimental factors.

Methods

SPECIES AND STUDY SITES

Water-dispersed mangroves from a range of plant families, growth forms and habitats were selected. Seeds of six tropical species of mangroves (Table 1) were collected by picking mature fruit from trees or from recently dispersed propagules from the strandline. All diaspores were collected from mangrove stands at Lucinda and Cape Cleveland within 100 km of Townsville, Australia (19°17' S, 147°03' E) and were screened for predispersal insect damage (Robertson *et al.* 1990; Minchinton & Dalby-Ball 2001; Sousa *et al.* 2003). Nomenclature follows Tomlinson (1986) and Duke (1992). Henceforth the six species are referred to by genus name only except for the two species of *Bruguiera*.

Experiments were initiated in the mangrove forests at Bowling Green Bay on the north-east coast of Australia (19°17' S, 147°03' E) during the wet season of 1995–96. Fourteen species of mangroves are found at Bowling Green Bay, of which *B. exaristata*, *Ceriops* and *Rhizophora* were dominant at the experimental site (Table 2), which is adjacent to that used by Smith (1987a). *Rhizophora* formed a dominant stand (6–8 m

Table 1 Mangrove species used in experiments and their characteristics. Data from Clarke *et al.* (2001) or (*) from Clarke & Kerrigan (2002)

Species	Family	Growth form	Mean seed fresh mass, g (SE)	Root initiation (days)	Initial growth in sea water (sw)	Mean seed predation by crabs	Intertidal position
<i>Aegiceras corniculatum</i>	Myrsinaceae	Shrub	0.51 (0.01)	8	Optimal growth in 5% sw	100	Low shore creek lines
<i>Avicennia marina</i> var. <i>eucalyptifolia</i>	Avicenniaceae	Tree	5.16 (0.14)	4	No salinity effect	97.1	Low and high shore
<i>Bruguiera exaristata</i>	Rhizophoraceae	Tree	4.30 (0.15)	8	Optimal growth in 5% sw	77.3	High shore
<i>Bruguiera gymnorhiza</i>	Rhizophoraceae	Tree	24.96 (0.97)	14	Optimal growth in 0–50% sw	57.1	Mid and high shore
<i>Ceriops australis</i>	Rhizophoraceae	Small tree	1.60 (0.03)	8	No salinity effect	70.6	High shore
<i>Rhizophora stylosa</i>	Rhizophoraceae	Tree	35.37 (1.09)	14	Optimal growth in 50–100% sw	22.5	Low shore

Table 2 Canopy gap and matrix characteristics in mangrove stands used for experimental manipulations

Treatment	Intertidal position (replicates)	Area of gap (m ²)	Mean PAR, ($\mu\text{ mol s}^{-1}$) (SE)	Matrix species, height (m)	Matrix stem density (stems m ⁻²)	Soil conductivity ($\mu\text{S m}^{-1}$)
Large gap	Low shore (2)	225 (15 × 15)	1173 (199)	<i>R. stylosa</i> (8)	0.35	8.6 (1.2)
	High shore (2)	225 (15 × 15)	818 (186)	<i>C. australis</i> , <i>A. marina</i> (7)	1.65	15.9 (2.2)
Small gap	Low shore (2)	50 (5 × 10)	1440 (94)	<i>R. stylosa</i> , <i>A. marina</i> (7)	1.02	7.6 (0.4)
	High shore (2)	50 (5 × 10)	584 (218)	<i>C. australis</i> , <i>B. exaristata</i> (6)	1.05	18.4 (0.7)
Small gap plus shade	Low shore (2)	50 (5 × 10)	507 (221)	<i>R. stylosa</i> , <i>A. marina</i> (7)	0.75	7.4 (0.1)
	High shore (2)	50 (5 × 10)	95.5 (33)	<i>C. australis</i> , <i>B. exaristata</i> (6)	0.58	17.3 (0.8)
Canopy matrix	Low shore (2)	None	206 (42)	<i>R. stylosa</i> (8)	0.68	7.8 (0.2)
	High shore (2)	None	47 (14)	<i>C. australis</i> , <i>B. exaristata</i> (7)	1.05	17.9 (0.7)

tall) at the seaward edge of the mangroves, about 100 m wide, within which were occasional *Avicennia*. At the upper tidal level *Ceriops* and *B. exaristata* dominate patches of forest about 10–20 m wide, interspersed with mixed stands of *B. exaristata* with occasional *Avicennia* and *B. gymnorrhiza*. The experimental manipulation of canopy was imposed on stands of *Rhizophora* (lower intertidal, 50 tides per month) and of *Ceriops* and *B. exaristata* (upper intertidal, five tides per month) (Table 2). The most important propagule predators at the experimental location were the large herbivorous crabs *Sesarma messa*, *S. smithii* and *S. fourmanori* (Grapsidae) (Mitcheli 1993). The experiment commenced during the summer of 1996 after a relatively dry summer and below average rainfall fell during the first year of establishment, growth and survival; thereafter, above average rainfall conditions were experienced.

EXPERIMENTAL DESIGN

In each of two forest areas (low and high intertidal), four canopy treatments were applied with two replicate patches per treatment, creating 16 experimental plots (Table 2). Plots were separated by at least 10 m of intact canopy and were no closer than 10 m to the forest edge. The four canopy treatments were large gaps (*c.* 225 m²), small gaps (*c.* 50 m²), small gap with a shade cloth cover (50% light transmission) and adjacent forest sites with natural canopy cover (Table 2). These gap sizes were selected on the basis that Smith (1992) reported a median gap size of about 50 m² in an extensive survey in northern Australia whilst Clarke & Kerrigan (2000) found a mean gap size of 253 m² in their survey of an adjacent region. The shaded treatment was imposed to mimic the effects of shade provided by the canopy. To create gaps, all seedlings, stems and branches were removed by hand from the site but the stumps up to 50 cm high were left in place. Larger stems were salvaged for craft wood whilst the remaining material was

distributed throughout the forest to decompose. No stems re-sprouted, nor was there any clonal re-sprouting of stem bases or roots.

Two levels of ground disturbance, sediment dug over to a depth of 20 cm with a pitch fork or sediment undisturbed, were imposed in randomized patches (50 × 50 cm) within each of the 16 experimental plots to mimic the effects of uprooting of fallen trees after a severe storm. In each combination of treatments three replicate 50 × 50 cm patches were randomly selected for sowing of the six species. The sown areas were spaced evenly within a gap so that they were no closer than 50 cm from each other and were at least 1 m from the gap edges. In each sown area 10 propagules were enclosed in mesh cages (*c.* 1 cm²) to prevent dispersal and reduce predation by crabs. Survival of propagules of palatable species outside cages had been found to be low (Clarke & Kerrigan 2002). The enclosures were kept in place for approximately 1 month, after which they were removed.

Predation of propagules, establishment, survival and growth were measured at daily intervals for the first week, then weekly for several months and then at monthly intervals for the first year. After the first year, plants were measured annually for 5 years. A propagule was considered dead following the conventions used in previous studies (Smith 1987a,b; Smith *et al.* 1989; McKee 1995; McGuinness 1997a,b; Sousa & Mitchell 1999). Heights of seedlings were measured above the cotyledonary scar as differences in the hypocotyl lengths can confound the interpretation of early growth measures. Most seedlings had developed lateral branches after 3 years of growth and at this stage they were classified as saplings regardless of height.

DATA ANALYSES

The design was partially nested with two between-plot factors (intertidal position and canopy treatment) with two plots for each combination. The within-plot factors

were disturbance and species. Note that both factors were randomized within the plots and each species was sown in separate caged areas. Growth data (height) were analysed for a simplified, partially nested model where disturbance was removed as a factor because it was not significant ($P > 0.25$) and the canopy treatment was reduced to two levels (large and small gap) because few seedlings survived under either the simulated or natural canopy. *Aegiceras* was also removed from analyses for survival and growth because few propagules established. The response variables of numbers of seedlings were arcsine transformed. All analyses used a partially nested ANOVA with replication.

Survival data for older saplings were unable to be analysed for the complete designs due to the low numbers of individuals surviving in some treatment levels. Survival analyses were applied to these data. Survival analyses were performed on right censored data using a proportional hazard regression model with time to death as the variable (Cox & Oakes 1984). When an experiment 'ends' before all events are completed then data for non-events are right censored. Whilst comparison of survival functions are useful, the number of census points precluded detailed parametric analyses of survival functions. However, analyses of differences in survival among treatments (strata) can be undertaken where the underlying hazard functions are proportional (Cox & Oakes 1984). Initial plots of log cumulative hazard vs. time for different treatments (low vs. high shore, canopy vs. large gap vs. small gap) were generally parallel, indicating proportionality. The likelihood ratio test was used to evaluate whether the levels of covariates make a significant contribution to the global model. Chi-squared tests were used to test

for each level of covariates in expanded models after the hazard functions were examined for proportionality. The exponent of the regression coefficient (e^B) gives the relative risk of mortality for a seedling subjected to a hazard (canopy treatments or position on shore).

To assess any density effects of seedlings between each species, pairwise correlation of densities were made after 5 years of growth. In addition, correlation of density and height were made within and between each species after 5 years of survival and growth.

Results

SEEDLING ESTABLISHMENT AND PREDATION

Establishment of seedlings at the end of 2 months differed significantly among canopy treatments but not between intertidal level or sediment disturbance treatments (Table 3) (Figs 1 and 2). Species also differed in their establishment but their responses were consistent among treatments (*Avicennia* > *Ceriops* > *Rhizophora* > *Bruguiera exaristata* > *Bruguiera gymnorrhiza* > *Aegiceras*). There was also no correlation between propagule size and establishment success of each species ($r^2 = 0.14$).

All species established best in large gaps (Fig. 1a). There was, however, a species–plot interaction (Table 3) that indicated that plot characteristics might be influencing establishment. All species established well in plots that had canopy members of the same species, but species that were not canopy members also established (Fig. 2a,b). For example, the high shore species *Ceriops* established on the low shore where *Rhizophora* dominated and conversely *Rhizophora* established on

Table 3 ANOVA table for the partially nested design with two orthogonal between-plot factors (intertidal position and canopy treatments) and two within-plot factors (sediment disturbance and species). Response variables were numbers of seedlings establishing after 2 months, numbers of seedlings killed by predators, numbers of seedlings surviving 1 year and numbers of seedlings surviving 2 years. Significant effects in bold. All disturbance by species interactions not significant

	Establishment			Killed by predators			Survival year 1			Survival year 2		
	d.f.	<i>F</i>	<i>P</i>	d.f.	<i>F</i>	<i>P</i>	d.f.	<i>F</i>	<i>P</i>	d.f.	<i>F</i>	<i>P</i>
Between plots												
Intertidal position I	1	2.83	0.13	1	0.21	0.65	1	0.43	0.53	1	0.76	0.40
Canopy C	3	10.32	< 0.01	3	2.48	0.13	3	4.05	0.05	3	3.46	0.04
I × C	3	0.24	0.87	3	0.12	0.93	3	6.14	0.01	3	2.13	0.17
Plot P (IC)	8	1.36	0.21	8	7.82	< 0.001	8	0.87	0.54	8	2.21	0.02
Within plots												
Disturbance D	1	0.67	0.43	1	0.15	0.70	1	2.18	0.17	1	3.94	0.09
I × D	1	0.39	0.54	1	0.43	0.53	1	0.40	0.54	1	1.14	0.31
C × D	3	0.47	0.71	3	0.74	0.55	3	1.17	0.38	3	1.41	0.30
I × C × D	3	0.85	0.50	3	0.44	0.73	3	1.45	0.29	3	1.26	0.35
P (IC) × D	8	0.91	0.50	8	1.41	0.18	8	1.68	0.10	8	1.79	0.08
Species S	5	22.02	< 0.001	5	154.9	< 0.001	4	1.02	0.41	4	2.46	0.05
I × S	5	1.45	0.22	5	0.83	0.54	4	0.26	0.89	4	0.74	0.56
C × S	15	1.18	0.32	15	1.21	0.30	12	0.64	0.78	12	1.57	0.15
I × C × S	15	0.83	0.63	15	0.83	0.63	11	1.52	0.18	11	2.61	0.01
P (IC) × S	37	1.6	0.01	37	2.4	< 0.001	30	1.06	0.38	30	0.91	0.6
D–S interactions			> 0.5			> 0.3			> 0.1			> 0.2

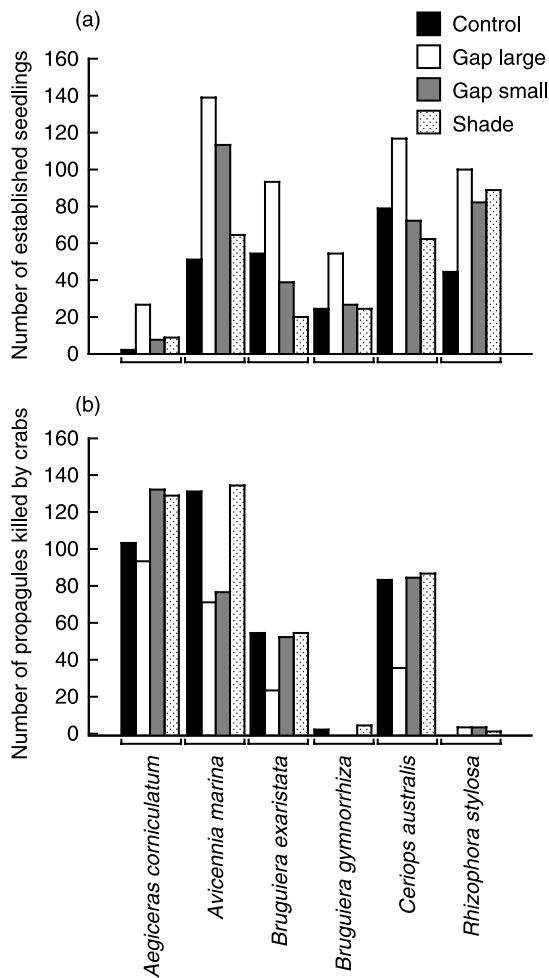


Fig. 1 Total numbers of seedlings (a) establishing and (b) killed by crab predators for each of four canopy treatments for each of six mangrove species. Large gaps were 225 m² and small gaps with and without shade were 50 m².

the high shore where it was absent. Overall, it appears that canopy membership did not preclude species from establishing in gaps.

Exclosures reduced mortality of propagules preyed upon by crabs, but there was significant mortality from crab predators during establishment in four species due to crabs burrowing under or climbing over the exclosures (Fig. 1b). Numbers of propagules killed by predators also varied among species and plots (Table 3) and more propagules appeared to be killed under canopies than in large gaps (Fig. 1b). Again, there were significant plot \times species effects (Table 3) but these did not match canopy membership patterns.

SEEDLING SURVIVAL AND GROWTH

Most mortality (> 75%) was in the first year and little mortality was recorded after the third year of growth. Seedling survival over the first year was poorly correlated with seed (propagule) mass, although the species with the smallest propagule (*Aegiceras*) had the lowest survival (0.1%) whilst the largest (*Rhizophora*) had the highest (23%).

Seedling survival at 1 and 2 years after establishment showed significant canopy treatment effects, including interaction with intertidal position, but no effects of sediment disturbance (Table 3, Fig. 3). In the first year there was no difference in survival among species for any factor (Table 3). In the second year, however, species differences became apparent and there was a significant species interaction with intertidal position and canopy. Overall, more seedlings survived in the large canopy gap (Fig. 3b). Few seedlings survived under the forest canopy but a few more seedlings of four species survived under the artificially shaded small gap (Fig. 3b). The low shore environment initially enhanced survival of three species (*Rhizophora*, *Bruguiera gymnorhiza* and *B. exaristata*), whilst *Avicennia* and *Ceriops* showed no significant effect of position on shore (Figs 3a and 4). Most species survived in plots that had canopy members, but equally, species that were not canopy members also survived (Fig. 4a,b). For example, both *Bruguiera* species survived on the low shore large canopy gaps where *Rhizophora* was dominant. Overall, it appears that canopy membership did not preclude species from establishing in gaps if they were sown (i.e. no dispersal limitation).

After 3 years, the artificial canopy shades became ineffective due to wind damage and were removed. A few seedlings of each species had survived under the artificial canopies compared with the absence of seedlings under natural canopies (Fig. 3b). However, of these seedlings, only those of *Rhizophora* survived and continued to grow well after the artificial canopy was removed (Fig. 5b).

Analyses of seedling height was performed at each of the major developmental stages of growth: at 2 months, when cotyledonary maternal reserves (autotrophic growth) would be exhausted; at 7 months, when any effects of propagule predators are decreased; and after 3, 4 and 5 years (Table 4). These analyses showed a consistent effect of species differences that appeared within 2 months of growth (Table 4, Fig. 5), with *Avicennia* becoming the tallest species in gaps. Early growth was similar among all species except for *Ceriops*, which along with a few plants of *Aegiceras*, was slow to grow. Species interactions with disturbance and canopy effects were not significant, indicating that all species responded in the same way to the manipulations (Table 4). Growth was enhanced in the large canopy gaps for all species (Fig. 5b). Species interactions with position on shore were often significant and revealed changing height relationships through time (Table 4, Fig. 5). *Avicennia* was initially of similar height to the other species but grew taller high on the shore. Both *Ceriops* and *Rhizophora* were initially taller low on the shore but after 5 years grew taller high on the shore (Fig. 5a). Only the two *Bruguiera* species showed consistent patterns through time where low shore plants were marginally taller than high shore ones.

Plot effects accounted for increasing amounts of variance through time, and by 5 years there was a significant

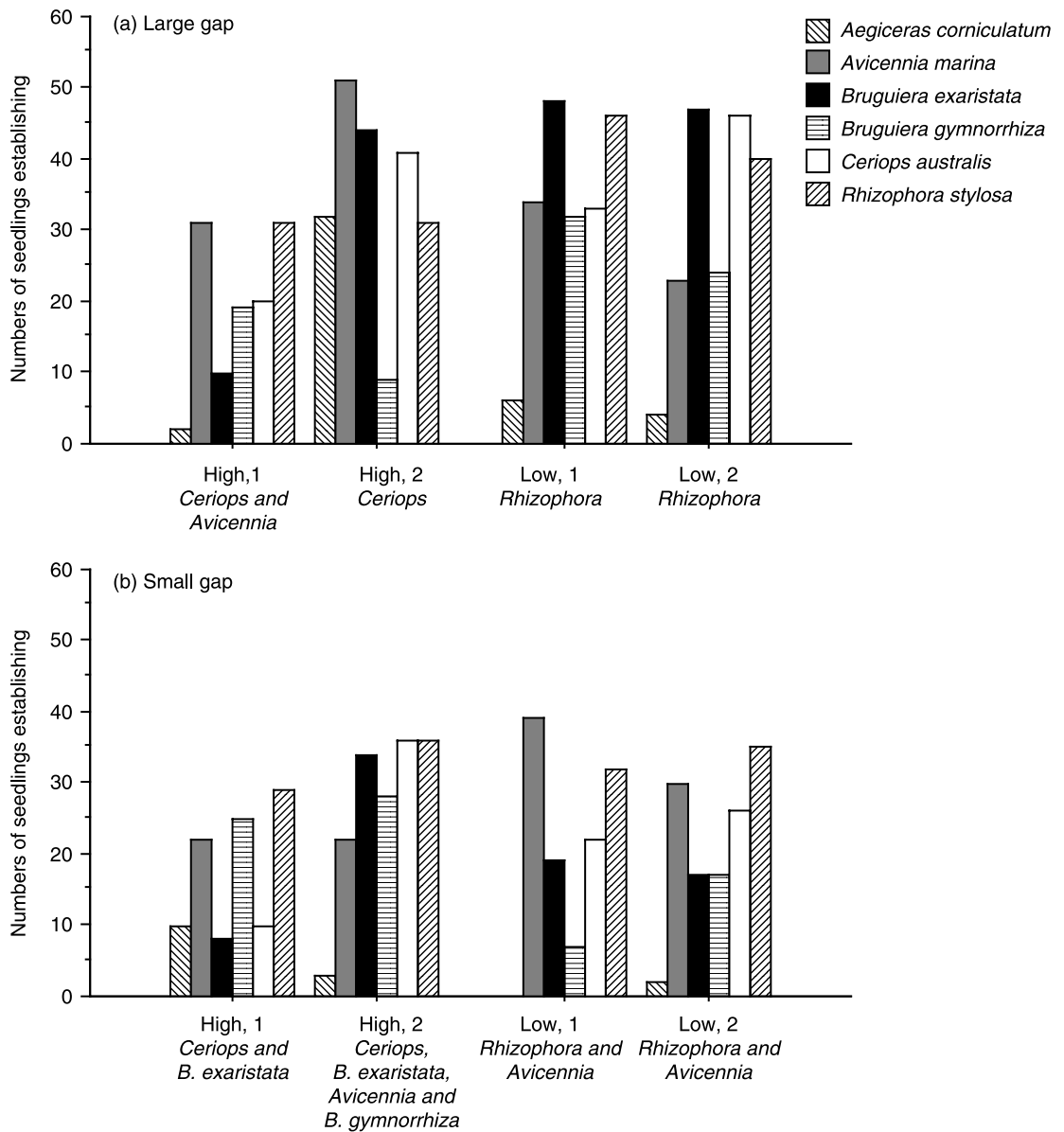


Fig. 2 Total numbers of seedlings establishing after 2 months in each plot for (a) large gaps and (b) small gaps for each of six mangrove species. Canopy membership of plots shown below plot label in each of high and low tidal positions.

plot by species interaction (Table 4). These effects were, however, unrelated to canopy membership as there was mass mortality of all species in one plot (large gap, high shore, plot 2). To assess whether density was a confounding factor among plots, correlation of densities within and between species were made and no significant effect was found. Nor was there a correlation of plot sapling density and any negative effect on the height of species ($r^2 < 0.10$).

SURVIVAL ANALYSES

Survival analyses were performed on each species for up to 5 years after initial establishment. For the purposes of these analyses only the effects of canopy gap and position on shore on the relative hazard of mortality was modelled. The likelihood ratio test, used to evaluate the contribution of covariates to the global

model, was significant in all species tested and all species had significant regression coefficients indicating decreased risk of mortality in canopy gaps (Table 5). *Avicennia* had the most reduced hazard in gaps, followed by *B. exaristata*, and then all other species had similar hazard functions in gaps. Position on shore hazard functions were more varied, with no significant hazard effect in two species (*Avicennia* and *B. gymnorrhiza*), but three species (*B. exaristata*, *Rhizophora* and *Ceriops*) had decreased survival high on the shore (Table 5).

Discussion

HABITAT PARTITIONING AND INTERTIDAL ELEVATION

One of the most pronounced patterns in mangrove stands is the shore-aligned distribution (zonation) of

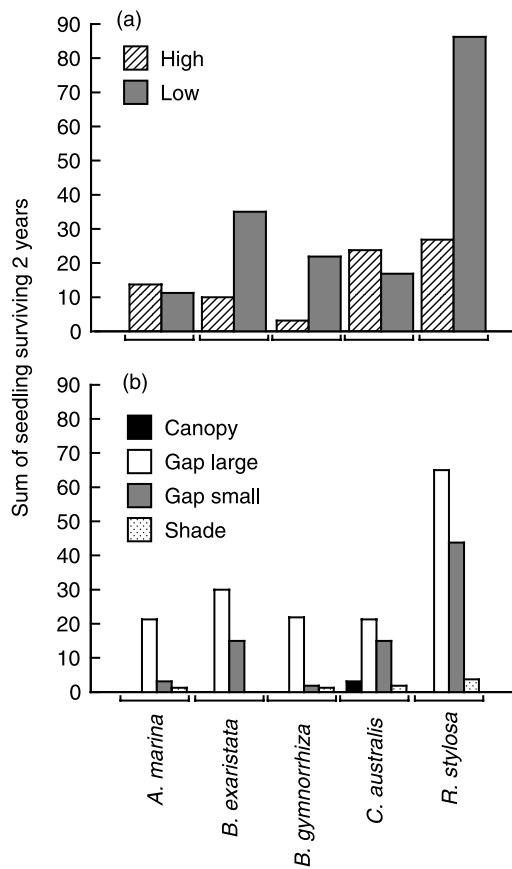


Fig. 3 Total numbers of seedlings surviving after 2 years in (a) high and low shore intertidal positions and (b) in each of four canopy treatments for each of six mangrove species.

species associated with tidally maintained environmental gradients. The simplest explanation of this pattern is that there are interspecific differences in stress tolerance in space and time that are modified by biotic interactions such as predation and competition (habitat partitioning mediated by physiological tolerance) (Smith 1992; Ball 1998, 2002). If this is the case,

then seedling establishment and growth should mirror canopy composition at different topographic positions.

In the present study there was no difference in the ability of species to establish in high and low shore environments. Some difference in growth and survival was found among species across the two intertidal positions (interactions of species and habitat). However, attributing this difference to the physical conditions of the tidal position was difficult because of the effects of seed predators that impose establishment patterns (Clarke & Kerrigan 2002). Differential predation pressure (*sensu* Louda 1989) does not, however, appear to be a mechanism for structuring mangrove communities because canopy membership and intensity of predation by crabs at different tidal levels were unrelated.

To what extent did differences in establishment, growth and survival among species in our experiment explain 'zonation' at our site? Firstly, three of the six species (*Aegiceras*, *Avicennia*, *Rhizophora*) used in the experiment had establishment patterns consistent with zonation patterns and this remained consistent in seedling survival. In addition, seedlings of *Ceriops* had better initial survival in the high intertidal plots where it was a canopy member, although after 5 years *Ceriops* and *B. exaristata* had lower survival in the high shore. Only two species (*Avicennia* and *Ceriops*) grew taller where canopy conspecifics were present. The results of growth were more perplexing for *Rhizophora*, which although it survived best in the low intertidal, had shorter saplings there than on the high shore, where it was absent from the canopy (Fig. 5).

I conclude that interspecific differences in establishment, growth and survival of seedlings in different intertidal positions were not closely matched to canopy membership and hence this does not fully explain 'zonation'. All species were capable of establishing in both intertidal positions and five species grew to sapling stages in both high and low intertidal positions, thus zonation does not appear to be explained by

Table 4 ANOVA table for the partially nested design with two orthogonal between-plot factors (intertidal position and canopy treatments) and one within-plot factor (species). Note that the canopy effects were reduced to two levels because few seedlings survived under the canopy or shade treatments. Response variables were height at 2 and 7 months, and 3, 4 and 5 years. Significant effects in bold

	2 months			7 months			Year 3			Year 4			Year 5		
	d.f.	F-ratio	P	d.f.	F-ratio	P	d.f.	F-ratio	P	d.f.	F-ratio	P	d.f.	F-ratio	P
Between plots															
Intertidal position I	1	1.39	0.30	1	8.32	0.04	1	2.79	0.19	1	0.23	0.89	1	1.03	0.37
Canopy C	1	0.92	0.39	1	0.70	0.44	1	15.7	0.02	1	2.45	0.05	1	1.42	0.29
I × C	1	1.32	0.31	1	9.24	0.03	1	0.16	0.92	1	0.25	0.64	1	0.62	0.77
Plot P (IC)	4	1.68	0.15	4	0.60	0.6	4	46.46	0.005	4	14.4	< 0.001	4	4.41	0.001
Within plots															
Species S	4	1.19	0.36	4	13.1	0.002	4	6.25	0.05	4	8.59	0.03	4	4.36	0.08
I × S	4	3.81	0.03	4	6.33	0.005	4	3.41	0.13	4	1.16	0.44	4	0.55	0.71
C × S	4	1.48	0.26	4	4.87	0.01	4	1.14	0.43	4	0.54	0.62	4	0.24	0.86
I × C × S	3	1.38	0.29	3	4.01	0.03	0	—	—	0	—	—	0	—	—
P (IC) × S	12	0.6	0.81	12	0.15	0.99	3	1.85	0.11	3	1.84	0.12	3	3.61	0.01

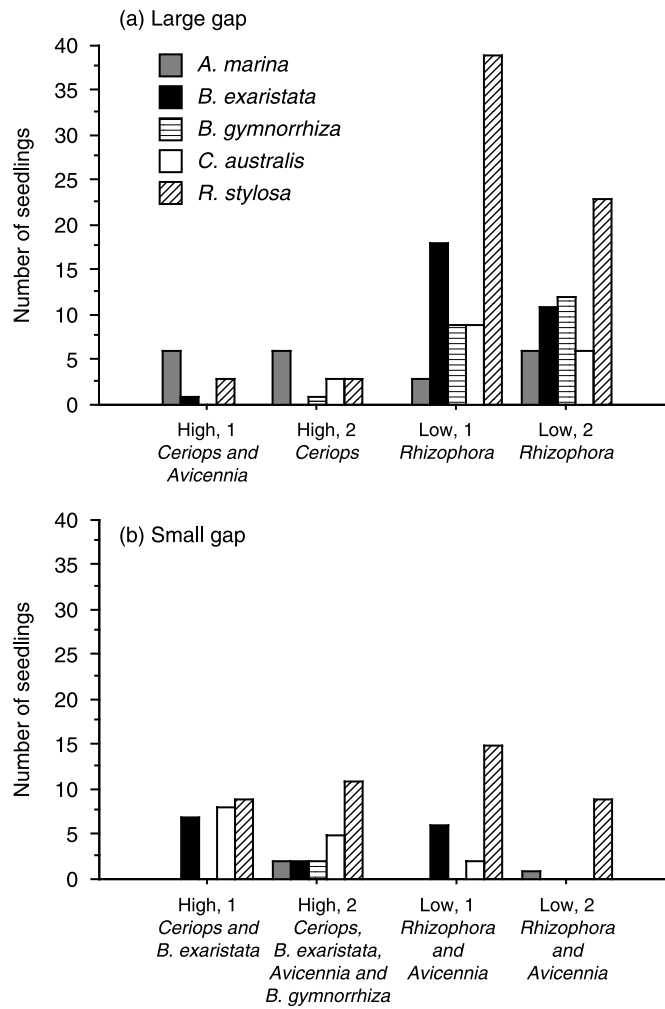


Fig. 4 Total numbers of seedlings surviving after 2 years in each plot for (a) large gaps and (b) small gaps for each of five mangrove species. Canopy membership of plots shown below plot label in each of high and low tidal positions.

Table 5 Proportional hazard models for seedling survival over 5 years

Species	Treatment	Beta coefficient	P (Ward)	Interpretation
<i>Avicennia marina</i> var. <i>eucalyptifolia</i>	Position on shore	1.03	> 0.5, NS	No significant survival hazard
	Canopy gap	0.65	< 0.01	Survival hazard decreases 35% with large gaps
<i>Bruguiera exaristata</i>	Position on shore	1.9	< 0.001	Survival hazard increases 90% with high shore position
	Canopy gap	0.72	< 0.01	Survival hazard decreases 28% with large gaps
<i>Bruguiera gymnorrhiza</i>	Position on shore	0.92	> 0.4, NS	No significant survival hazard
	Canopy gap	0.83	< 0.05	Survival hazard decreases 17% with large gaps
<i>Ceriops australis</i>	Position on shore	1.22	< 0.05	Survival hazard increases 22% with high shore position
	Canopy gap	0.73	< 0.01	Survival hazard decreases 17% with large gaps
<i>Rhizophora stylosa</i>	Position on shore	1.92	< 0.001	Survival hazard increases 92% with high shore position
	Canopy gap	0.72	< 0.01	Survival hazard decreases 18% with large gaps

interspecific differences in establishment by the sapling stage. This highlights the issue of how disjunct distributions of species are maintained given the opportunities for establishment.

GAP PARTITIONING

Gap partitioning occurs when species show different distribution, abundance and performance along environmental

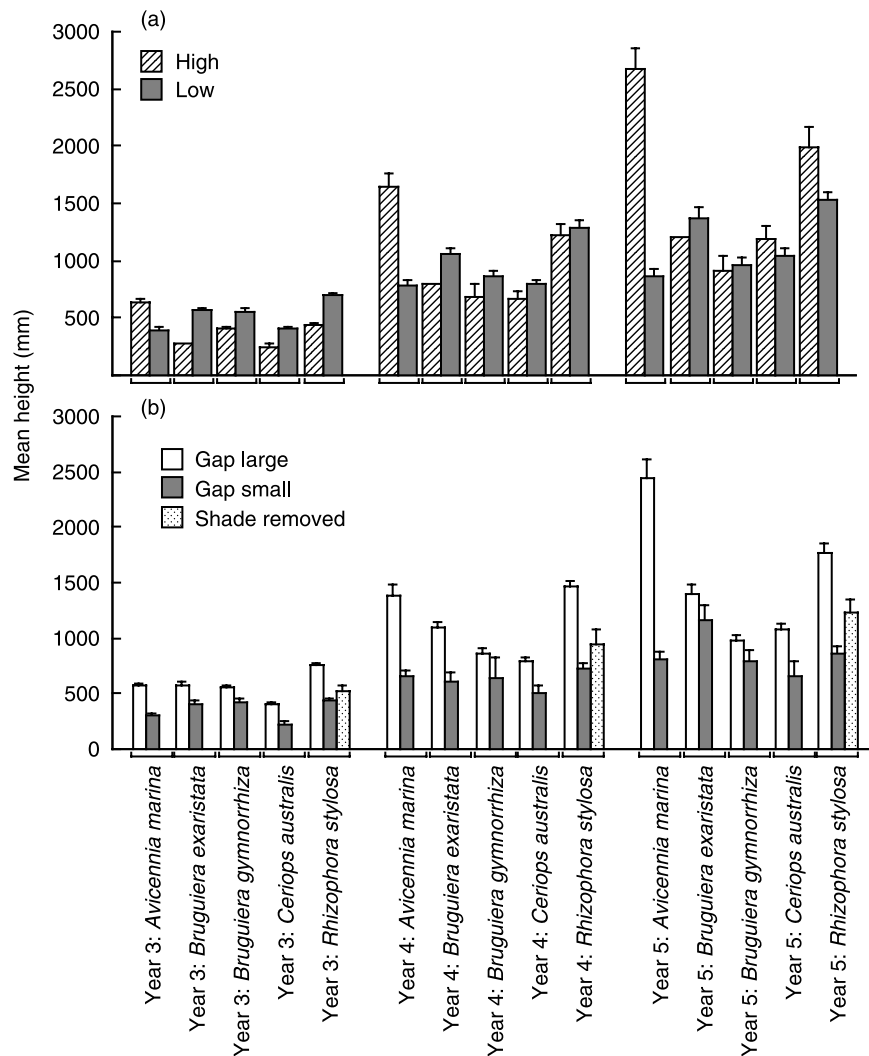


Fig. 5 Mean height (SE) of six mangrove species in years 3, 4 and 5 after establishment; (a) high and low shore intertidal positions and (b) in each of three canopy treatments.

gradients within gaps or among gaps of different size (e.g. Brokaw & Busing 2000; Pearson *et al.* 2003). I found few effects of treatments (canopy \times species or canopy \times tidal position–species interactions) to indicate strong differences in species response to the creation of canopy gaps. Similarly, there were no sediment disturbance effects (disturbance–species interactions) to indicate that the species showed differences in survival or growth within gaps. The lack of strong interactions of species and treatments was surprising given the variety of species used and the different rates of shoot initiation observed in field and laboratory studies (Clarke *et al.* 2001; Ball 2002).

Initial patterns of establishment were not as strongly related to the effects of crab predators on establishment as in a previous study (Clarke & Kerrigan 2002). Interspecific differences in predator preference were, however, similar to previous studies (Smith 1987a,b; Smith *et al.* 1989; Osborne & Smith 1990; McGuinness 1997a,b; Clarke & Kerrigan 2002; Krauss & Allen 2003). The lack of strong species differences with gap size or disturbance does not support a model for separation of establishment niches among gaps driven by predation.

Five species survived and attained greater heights in large canopy gaps than in smaller gaps, and no species survived under the canopy. These results are consistent with other survival and growth studies of mangrove that have shown no evidence for shade-tolerant species or specialized gap colonists (Sukardjo 1987; Clarke & Kerrigan 2000; Sherman *et al.* 2000; Ball 2002). Only one species (*Rhizophora stylosa*) survived under an artificial shade, and then grew when it was removed. This result is consistent with the large propagule mass of *Rhizophora*, which would allow it to survive longer in the understorey than other species. This could be interpreted as shade tolerance, but it simply reflects maternal investment in the viviparous propagule (Ball 2002). The relative height difference between small and large gap treatments of two species (*Rhizophora* and *Avicennia*) suggests that they are better competitors in large gaps. This effect is consistent with field observations of increased dominance of these species in some gaps (Clarke & Kerrigan 2000), although growth studies in the field using congeners of *Bruguiera*, *Ceriops* and *Rhizophora* have shown that the relative responses of all

species to canopy effects were similar (Ball 2002). I conclude that a wide range of species can colonize large canopy gaps if dispersed into them and that there was no gap partitioning among the species used in this experiment.

HOW IS STAND DOMINANCE MAINTAINED?

Five mangrove species were able to establish, grow and survive for 5 years in large canopy gaps under a range of tidal positions when predation by crabs was reduced. Similar, but much reduced, numbers of seedling also established in a related experiment where predators had free access to propagules (Clarke & Kerrigan 2002). Hence, most species appear to be able to recruit into canopy gaps if there is no dispersal limitation. How then is stand dominance maintained and why do so few species co-occur? First, the range of species available to fill gaps is limited because predation of dispersed propagules advantages species that are local canopy members (Clarke & Kerrigan 2002). In contrast to studies of tropical tree diversity, recruitment limitation in mangroves does not appear to facilitate coexistence. This arises because local propagules are less likely to be preyed upon by crabs than those dispersed from distant sources, thus reducing the pool of species for establishment (Clarke & Kerrigan 2002). Secondly, there appears to be no partitioning of resources within gaps. At this stage coexistence may be further limited by exclusion of competitors in which canopy conspecifics become dominant because their seedlings are more numerous or grow faster. To test for exclusion of competitors, saplings will need to be followed in a range of mixtures and tidal positions.

Acknowledgements

The staff at the Australian Institute of Marine Science (AIMS) provided support throughout the project. In particular, I am grateful to Barry Clough, Dan Alongi, Lindsay Trott, Paul Dixon and Alistair Robertson, for sponsorship at AIMS and logistical support. I am indebted to Raelee Kerrigan, Paul Dixon and Otto Dalhaus for setting up the experiment and assisting with data collection. Kellie Mantle, John Steer, Greg Calvert, Christine Westphal, Karyn Andersen, Chris Cooper and Angus Galletly assisted in collecting field data. Joe Wright and the referees and editors provided constructive comments and improved the manuscript. The Queensland Department of Primary Industries and the National and Marine Parks Services granted permission for seed collection and the cutting of gaps. The project was funded by an Australian Research Council grant A19530936.

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Received 2 June 2003

revision accepted 4 October 2003

Handling Editor: Paul Adam