Australian Journal of Ecology (1993) **18**, 307–315

The intertidal distribution of the grey mangrove (*Avicennia marina*) in southeastern Australia: The effects of physical conditions, interspecific competition, and predation on propagule establishment and survival

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Abstract The upper and lower limits of the distribution of mature *Avicennia marina* lie between mean high water and mean sea level in open estuaries in southeastern Australia. Newly established seedlings are highly variable in abundance, but are rarely found in the saltmarsh or on mudflats. Their distribution is unlikely to be limited by dispersal because propagules disperse into the saltmarsh and to intertidal mudflats, but their establishment may be limited by physicochemical conditions, interspecific competition and predation.

The model that physicochemical conditions control the intertidal limits of establishment of seedlings was accepted for propagules stranding in the saltmarsh but rejected for those stranding on mudflats. No seedlings established on saltmarsh sediments but similar numbers of seedlings established within light gaps in adult mangrove stands and on intertidal mudflats. The model that interspecific interaction with freeliving macroalgae (*Hormosira banksii*) reduces the establishment of seedlings on mudflats covered with macroalgae or in stands with a ground cover of macroalgae was accepted. Under controlled conditions five times as many propagules established on cleared ground compared with ground covered with macroalgae. Predators also reduce seedling establishment, but the model that they preferentially act on propagules stranding on the mudflat was rejected. The low number of seedlings found on mudflats without macroalgae appears to relate to wave and current effects on establishment and the effects of waterlogging or fouling on survival.

INTRODUCTION

Important contributions to our understanding of the intertidal distribution of mangrove and saltmarsh species were made in southeastern Australia by Clarke and Hannon (1967, 1969, 1970, 1971). They highlighted the potential for interactions among the various biotic and abiotic factors in determining the distribution and abundance of intertidal vascular plant species. In their final paper they presented a list of tentative dispersal and physiological models to explain the limits in distribution of mangroves across the intertidal zone in southeastern Australia. However hypotheses that arise from these models have remained untested despite the emergence of demographic and experimental field methods in plant ecology.

Accepted for publication July 1992.

The grey mangrove *Avicennia marina* var. *australasica* (Walp.) Moldenke (Duke 1991), henceforth referred to as *Avicennia*, is found in most open estuaries in mainland southeastern Australia. It is distributed between about mean sea level and the mean high water neap level, although its precise elevation limits have not been described adequately. Stands of *Avicennia* are often intermixed with the river mangrove *Aegiceras corniculatum* (L.) Blanco in New South Wales, and at higher elevations both mangrove species intermingle with saltmarsh vascular plants (Adam 1990). Along the lower tidal limit of *Avicennia*, in marine-dominated estuaries, the freeliving form of the macroalgae *Hormosira banksii* (Turner) Decaisne can be found as a ground cover that extends onto open mudflats (King 1981) beyond which *Zostera* seagrass beds are common.

Intertidal 'boundaries' between *Avicennia* and saltmarsh in Botany Bay have been examined through time from aerial photographs and by sediment analysis. These studies show a gradual landward invasion of saltmarsh by mangroves (Mitchell & Adam 1989a,b). Mitchell and Adam (1989a) also suggest that saltmarsh species were the initial colonists of intertidal areas and subsequently the lower intertidal was invaded by mangroves. Radiocarbon dating of an *Avicennia* stump from Botany Bay indicates that *Avicennia* was present in the bay 6000 years ago (Roy & Crawford 1979). If *Avicennia* has been present in the bay for millennia then why has it not invaded and replaced the saltmarsh completely? We address this and the related question of what limits the lower distribution of *Avicennia*.

Quantitative observations were made of the intertidal distribution of *Avicennia* in relation to seagrass, macroalgae and saltmarsh, together with the establishment patterns of *Avicennia* seedlings. Following these observations, models were tested to assess the effects of: (i) physicochemical conditions; (ii) interspecific interaction; and (iii) predation, on limiting seedling establishment and subsequent survival.

MODELS AND HYPOTHESES

Seedlings of *Avicennia* are usually restricted to the same intertidal limits as those of their parents. This might be explained by poor dispersal or unfavourable physical conditions inhibiting seedling establishment outside the parental range. This model predicts that propagules placed outside these limits would fail to establish if interspecific competition and predation are controlled.

Interspecific interactions and predators might also inhibit the establishment of seedlings if physicochemical conditions are not limiting. Seedling densities are often low in the presence of dense macroalgae (*Hormosira banksii*). A plausible explanation for this is that *H. banksii* prevents the establishment of propagules. This model predicts that propagules would establish if algae were removed from the sediment surface and other confounding factors were controlled. In the absence of macroalgae the sparsity of seedlings on open mudflats might also reflect the action of predators preventing the establishment of seedlings. Thus under controlled conditions more seedlings should establish on mudflats when predators are excluded.

METHODS

Distribution of plants and frequency of tidal inundation

The distribution of plant species across the intertidal zone was measured in two bays in southeastern Australia (Botany Bay, Towra Point, 33°48′S, 151°12′E and Jervis Bay, Cararma Inlet, 34°50′S, 150°42′E), using two line transects in creeks entering each bay. Along each transect the presence of plant species and the elevation above tidal datum (to within 1 cm) were recorded at 1 m intervals. Heights were measured relative to Australian height datum and converted to height against mean sea level. These transects were later used to interpret rectified aerial photography at a scale of 1:4000 to provide a broader interpretation of vegetation patterns.

Distribution and abundance of *Avicennia* seedlings

The density of newly established seedlings was measured in four undisturbed intertidal zones during January 1988. These zones were: seaward of the lower edge, in the middle and at the upper edge of the mangrove zone, and in the saltmarsh landward of the mangrove zone. Seedlings were counted in 10 random quadrats (0.5×0.5 m) in two patches adjacent to each of the two line transects mentioned above. Thus differences in abundance could be analysed in a four-factor nested ANOVA, where 'zones' were a fixed factor with four levels, bays were random with two levels, transects were nested in bays with two levels, and patches were nested in transects with two levels.

Space and time variation in propagule establishment

The small-scale spatial variability in the number of propagules establishing was initially determined in a pilot experiment. At Towra Point, two locations with undisturbed canopies were selected and within each two patches were randomly defined. In each patch four replicate cages (0.5×0.5 m) made from polythene mesh (5×5 mm) were placed randomly and in each cage ten propagules with their

pericarps still attached were placed on the sediment surface at low tide. This density was used in this and subsequent field experiments as it approximates the average natural density of new seedlings in the field. The number of propagules taking root was counted at regular intervals until the numbers stabilized. Differences in establishment among locations and patches within locations were analysed in a nested ANOVA.

The effect of elevation on establishment and survival

Propagules were placed at two elevations outside their normal range (saltmarsh and mud-flat) and two elevations within their normal range (upper and lower mangrove). Potential confounding factors of predators were controlled for by exclusion while interspecific interactions were controlled for by restricting the propagules to areas clear of other plants and with an open canopy. At each elevation four cages, each containing 10 propagules, were established in two transects at Towra Point (Woolooware Bay and Weeny Bay). The number of seedlings that had taken root and were standing were observed after 25 days and 36 days, after which the cages were removed and the survival and height of uncaged seedlings were followed for 42 months. These data were analysed in a two-factor ANOVA with elevation as a fixed factor and location as a random factor for each observation. Soil variables of penetrability, conductivity and moisture content were measured initially for surface samples taken adjacent to replicate cages. These data were analysed in a two-factor ANOVA as for seedling establishment.

The effect of macroalgae on establishment

The treatments were: macroalgae *in situ*, removal of macroalgae, addition of macroalgae, and bare ground. These were applied below the adult distribution of *Avicennia* and within the lower distribution of stands in light gaps. The experiment was spatially replicated in two patches at two locations (Towra Point in 1986 and Jervis Bay in 1989). In each patch four replicate cages each containing 10 propagules were fixed in each of the four treatments. Data were analysed in a four-factor mixed model ANOVA where algal treatments were fixed with two levels, elevation was fixed with two levels, locations were random with two levels, and patches were nested in locations.

The effect of predators on establishment and survival

Treatments applied were: exclusion of large crabs, fish and other vertebrates, exclusion of small crabs, large gastropods, large crabs, fish and other vertebrates, an exclusion control and a control open to all potential predators. Parts of the experimental structure were originally designed and constructed to investigate the effects of predation on intertidal gastropods (Kaly, 1988). However the models and predictions tested in the experiment reported here are entirely different. The partial exclusion treatment consisted of fences ($2 \times 2 \times 1.5$ m) marked out with 5 mm nylon fishing mesh on four sides. These areas exclude large crabs and fish but not the macro-invertebrates. Inside these fences a smaller five-sided cage (0.5×0.5 m) made from plastic mesh (0.5×0.5 cm) excluded small crabs but not small gastropods. To prevent propagules from dispersing, all propagules were tethered to nylon fishing line. Treatments were applied in two patches at two elevations (the upper mangrove level and the level between mangroves and seagrass). In each treatment 10 propagules were tethered in each of four replicates. The experiment was repeated over 2 years at Towra Point. In the first year the establishment of seedlings was assessed after 21 days and the survival of seedlings was monitored at regular intervals for 12 months; in the second year only the establishment success after 21 days was measured. The data were analysed in a three-factor mixed model ANOVA. Treatments were fixed with four levels, elevations were fixed with two levels, years were random with two levels, and patches were nested in elevations.

RESULTS

Distribution of plants and tidal inundation

Over all transects *Avicennia* was observed between mean sea level (m.s.l.) and 0.42 m above m.s.l., which corresponds closely with mean high water level. Seedlings and small trees were also observed at higher elevations but were not sampled in the transects. Several herbaceous saltmarsh species (*Samolus repens, Sarcocornia quinqueflora, Sporo-*

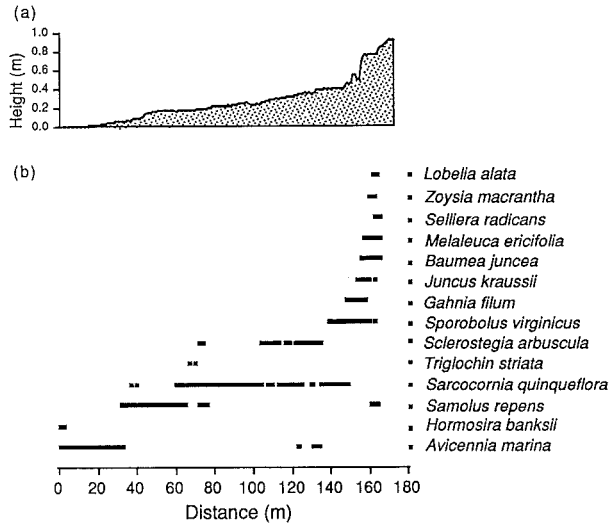

Fig. 1. Example of transect distributions for Jervis Bay. (a) Height above mean sea level (m.s.l.); (b) distributions of macrophytes.

bolus virginicus and *Triglochin striata*) and one shrub (*Sclerostegia arbuscula*), overlap with the distribution of *Avicennia* (Fig. 1). However most saltmarsh plants are restricted to elevations above mean high water. The macroalga *Hormosira banksii* was recorded in several transects and generally it was found to extend from about mean low water neap (40 cm below m.s.l.) to about 0.20 m above m.s.l.

Distribution and abundance of *Avicennia* seedlings

No seedlings were found in quadrats located in the saltmarsh zone, although the occasional seedling was noted outside the quadrats at three of the four transects. In all transects the highest numbers of seedlings were found at the upper mangrove level while the least numbers were found at the mudflat level (Fig. 2). Overall the density of newly established seedlings was 0–156 m^{-2} with an average of 24 m^{-2}. The density of seedlings varied among the transects studied (Table 1). However, the elevation component alone contributes the next highest variance component (16.7%), which reflects the large differences among elevations (Fig. 2).

Space and time variation in propagule establishment

There was little small-scale spatial variation in propagule establishment in undisturbed stands as shown by the lack of significant differences in the number of propagules establishing in patches within locations or between the two locations with canopies (Table 2). Caged propagules lose their

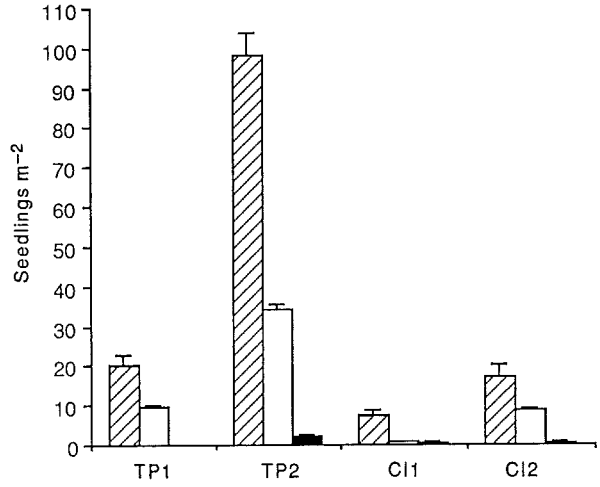

Fig. 2. The density of newly established seedlings at three elevations, upper mangrove (*ca* 40 cm above m.s.l. ▨), mid mangrove (*ca* 20 cm above m.s.l. □), and mudflat (*ca* m.s.l. ■). TP Towra Point transects, CI Cararma Inlet transects. Standard errors are shown.

Table 1. Four-factor nested ANOVA comparing the density of newly established seedlings

Source of variation		d.f.	MS	MS denominator	F	% sum of variance
Elevation	(A)	2	1570.4	(A×B)	2.31^{NS}	16.7
Estuary	(B)	1	1722.7	(C(B))	3.57^{NS}	15.4
	(A×B)	2	678.8	(A×C(B))	1.41^{NS}	7.6
Transect	(C(B))	2	482.7	(D(C(B)))	16.53***	11.4
	(A×C(B))	4	484.2	(A×D(C(B)))	94.94***	36.1
Patch	(D(C(B)))	4	29.2	(R)	3.84**	1.1
	(A×(D(C(B)))	8	5.1	(R)	0.67^{NS}	0.4
Residual	(R)S	216	7.6			11.4

**$P<0.025$, ***$P<0.010$, NS not significant.

pericarp within the first few days. Following this the hypocotyl extends and at the same time a ring of radial roots emerges. After the roots have anchored the seedling the hypocotyl straightens and raises the cotyledons off the sediment. This process can occur within 14 days but most propagules took 3–5 weeks for plants to establish (Fig. 3). However after four weeks of confinement an average 62% of propagules had rooted successfully on undisturbed sediments with a semi-closed canopy.

The effect of elevation on establishment and survival

Propagules caged in the saltmarsh failed to establish because of desiccation within the first 48 h. For the other elevations there was no consistent spatial trend in the establishment of seedlings during the first 25 days of the experiment (Table 3, Fig. 4). After 36 days, however, some significant site differences were detected, with more propagules establishing at Woolooware Bay (69.3%) than at Weeny Bay (45.3%; Fig. 4). Significant differences in sediment penetrability were detected among elevations and sites. In all locations the mudflat elevation was softer, while within the mangrove elevations the Woolooware Bay site was softer than the Weeny Bay site.

No significant differences in seedling survival were detected during the first 2 years of observations, but thereafter seedlings at the mudflat elevation had greater mortality (Fig. 5a). An interesting trend in seedling growth was also detected, with seedlings on the mudflats growing taller before dying than those surviving at the upper levels (Fig. 5b).

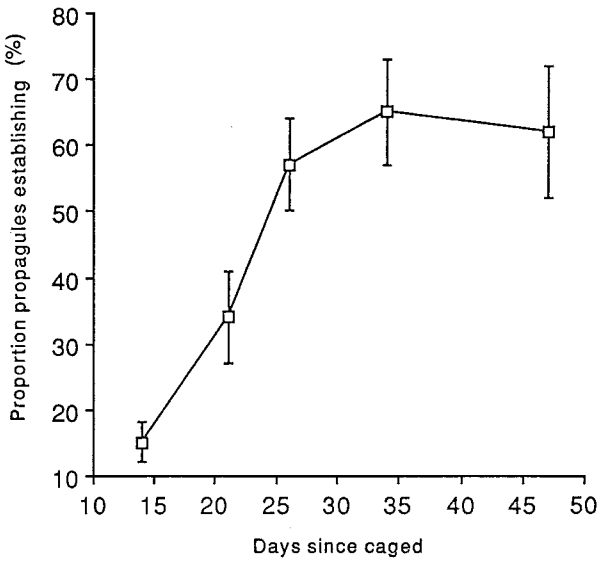

Fig. 3. The proportion of caged propagules establishing over a 48 day period within the mangrove stand. All spatial factors pooled. Standard errors are shown.

The effect of macroalgae on establishment

The mean number of propagules establishing in areas clear of *Hormosira* was 3.1 while only 0.6 established in the treatments with *Hormosira*. There were no significant differences in the number of propagules establishing among locations or among plots in locations. These factors were therefore pooled with the residual and the main effects tested over the pooled residual. Significant differences were detected for the algal treatment but not for the elevation treatment (Table 4).

The effect of predators on establishment and survival

The number of propagules establishing or surviving in patches and among years was not significantly different and these effects were pooled with the residual for statistical analysis. After 3 weeks twice as many seedlings established in the cages that excluded small potential predators, than in all other experimental treatments (Table 5; Fig. 6). However no significant differences in the proportion of seedlings surviving were detected among treatments after 12 months (Table 6).

Table 2. Two-factor nested ANOVA comparing establishment success at five different times

Source of variation	d.f.	14 days MS	14 days *F*	21 days MS	21 days *F*	26 days MS	26 days *F*	34 days MS	34 days *F*	47 days MS	47 days *F*
Location (A)	1	0.56	0.10	1.00	0.42	0.25	0.69	0.00	—	0.06	0.04
Patch (B(A))	2	5.31	1.81	10.25	4.32	3.62	0.62	8.10	1.45	13.80	2.00
Residual	12	2.93		2.37		5.79		5.62		6.89	

All *F*-ratios not significant.

Table 3. Two-factor ANOVA comparing numbers of seedlings establishing at three elevations over two locations

		25 days			36 days		
Source of variation	d.f.	MS	*F*	*P*	MS	*F*	*P*
Elevation (A)	2	10.0	0.6	NS	0.2	<0.1	NS
Location (B)	1	7.5	3.5	NS	43.2	24.6	NS
(A×B)	2	16.2	8.6	***	16.1	9.7	***
Residual	24	1.9			1.7		

***$P<0.01$, NS not significant.

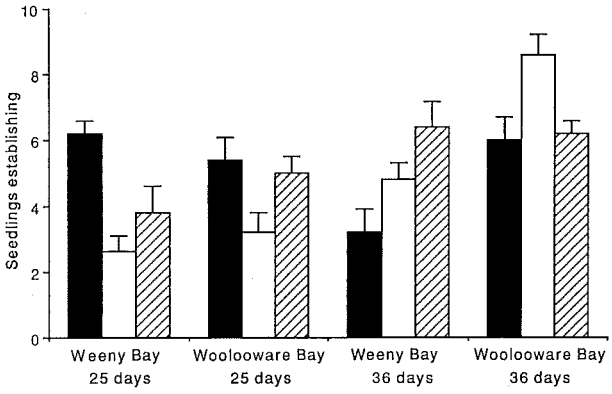

Fig. 4. The number of caged propagules establishing at three elevations within a mangrove stand across two sites and two times. Standard errors are shown. (■) Mudflats; (□) Low mangroves; (▨) Upper mangroves.

Table 4. Two-factor ANOVA comparing numbers of seedlings establishing with macroalgae (*Hormosira banksii*) treatments across two elevations

Source of variation	d.f.	MS	*F*	*P*
Treatment (A)	1	107.64	72.52	***
Elevation (B)	1	3.52	2.37	NS
(A×B)	1	3.52	2.37	NS
Residual	60	1.48		

Location and patch factors have been pooled. ***$P<0.01$, NS not significant.

DISCUSSION

Intertidal distribution

Mature stands of *Avicennia marina* are distributed between about mean sea level and mean high water neap tidal level in the two locations investigated. However the extent to which this distribution holds true in rivers and lagoons with tidal attenuation requires further study. The upper limits of the distribution of *Avicennia* overlap with the dis-

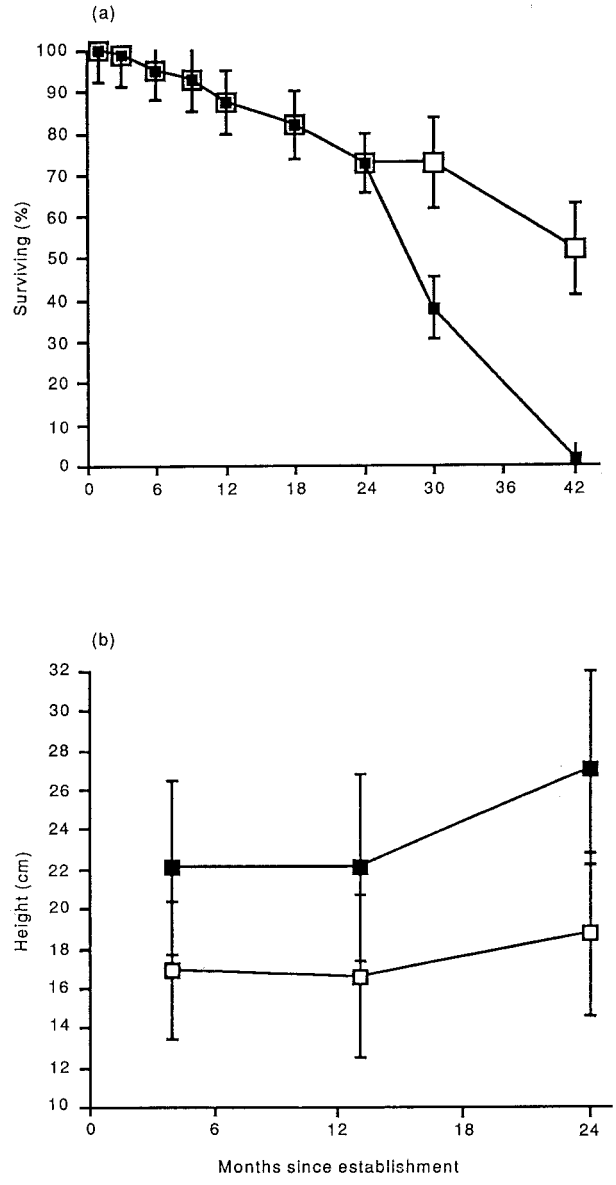

Fig. 5. (a). The proportion of established seedlings surviving in mangroves (□), and on mudflats (■). (b) The height of seedlings in mangroves (□), and on mudflats (■). Standard errors are shown.

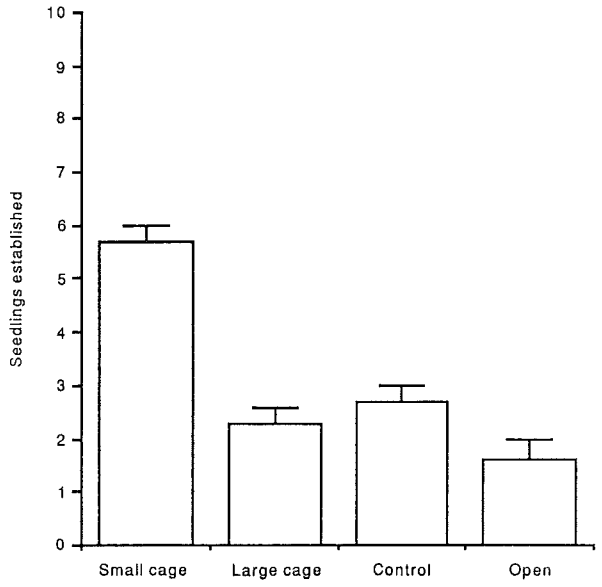

Fig. 6. The number of seedlings establishing over four treatments manipulating the exclusion of potential predators. Space and time factors pooled. Standard errors are shown.

Table 5. Two-factor ANOVA comparing numbers of seedlings establishing in relation to four predation treatments across two elevations

Source of variation	d.f.	MS	*F*
Treatment (A)	3	51.27	28.97***
Elevation (B)	1	1.00	0.56^{NS}
(A × B)	3	2.54	1.44^{NS}
Error	56	1.77	

Patch and year effects have been pooled.*** $P<0.01$, NS not significant.

Table 6. Two-factor ANOVA comparing the proportion of seedlings surviving after 12 months in relation to four predation treatments across two elevations

Source of variation	d.f.	MS	*F*	*P*
Treatment (A)	3	886.5	1.05	NS
Elevation (B)	1	232.1	0.27	NS
(A × B)	3	2321.5	2.74	NS
Error	23	847.7		

Patch and year effects have been pooled. NS not significant.

tribution of saltmarsh plants whereas the lower limits overlap with the macroalga *Hormosira banksii* and, occasionally, with the seagrass *Zostera capricorni*. These observations are similar to those of Clarke and Hannon (1967), who also found a continuum of species distribution from a mangrove-dominated zone through to a saltmarsh-dominated zone.

Seedlings are found above and below the elevation limits of adults, but in general they are found close to the adult population and at low densities. Within undisturbed stands of *Avicennia* there is considerable variability in the density of newly established seedlings. This patchy distribution does not appear to be related to heterogeneity of sediments, as establishment was uniformly successful under controlled conditions. Instead we propose that it is simply a function of variable fecundity and patchy dispersal. Trees vary in their yearly reproductive status (Clarke & Myerscough 1991a) and the majority of propagules are dispersed unevenly (P. J. Clarke unpubl. data). Seedling survival within the mangrove stand was uniform. This differs from that reported for *A. marina* in northern Australia where more seedlings survived at higher elevations than at lower elevations within mangrove stands (Smith 1987a).

Upper intertidal limits

The lack of newly established seedlings in the saltmarsh and the low number of older seedlings in the saltmarsh may reflect poor propagule supply and dispersal, or alternatively, it could reflect limits to establishment and survival of seedlings. Dispersal of propagules was one factor listed by Clarke and Hannon (1970) as limiting the landward distribution of *Avicennia* while Rabinowitz (1978), and Jimenez and Sauter (1991), suggest dispersal characteristics of propagules can influence zonation within central American mangrove forests.

Propagules of *Avicennia* are dispersed annually in late summer on the central coast of NSW although supply is variable from year to year (Clarke & Myerscough 1991a). Propagules remain buoyant in full seawater for several tidal cycles and many strand close to parent trees (Clarke & Myerscough 1991b). It is therefore possible for propagules to reach the saltmarsh zone and strand there during spring tides, although their densities may be lower. Observations of low densities of older seedlings in the saltmarsh show that this has occurred in past years. It seems that propagules, albeit in low densities, do disperse into the saltmarsh. Thus, events during establishment and survival are more likely to influence the upper intertidal limits of stands than dispersal.

Apart from dispersal, Clarke and Hannon (1970) also listed waterlogging and salinity as variables that influence the intertidal limits of mangroves. Knowledge of the physiology of *Avicennia* has increased greatly in the past 20 years from glasshouse experiments (e.g. Downton 1982; Clough 1984; Curran *et al.* 1986; Ball 1988). Unfortunately, physiological models for determining the distribution limits of mangroves have rarely been field-tested for critical life history stages. Reciprocal transplants of mangrove propagules within mangrove zones to test for differential survival have been attempted for *Avicennia bicolor* Standley and *Rhizophora racemosa* Meyer in Costa Rica (Jimenez & Sauter 1991). It was suggested that the latter species did not establish and survive in the former's range because of the drier and more saline conditions. Unfortunately these results were equivocal because the potentially confounding factors of predation and competition were not controlled for. A similar reciprocal transplant experiment has been undertaken with *A. marina* in northern Australia that suggested that zonation was not simply a reflection of some fundamental physiological niche (Smith 1987a).

Unfavourable physicochemical conditions (e.g. salinity, soil moisture, sediment type) that covary with intertidal elevation may inhibit seedling establishment (Clarke & Hannon 1971). This model predicts that propagules placed outside adult limits would fail to establish or survive under controlled conditions. Our experiments lead us to accept this hypothesis in the case of the upper limit but reject it in the case of the lower limit, as no seedlings established on saltmarsh sediment but similar numbers established among mangrove and mudflat levels. Clarke and Hannon (1971) list low water availability, higher temperature, higher light intensity and lower humidity as factors that prevent establishment in the saltmarsh. The precise cause of establishment failure is not known but all propagules placed on saltmarsh sediment became desiccated within a few days indicating moisture stress. Propagules stranding on saltmarsh plants are likely to suffer the same fate although this was not tested experimentally.

Occasionally, recently established seedlings are observed in the saltmarsh. This possibly reflects spatial variability in the moisture conditions of the saltmarsh. The presence of older seedlings may also reflect temporal variability in moisture conditions, for example, establishment in a year that had heavy rain during dispersal of propagules. Longer-term temporal shifts in the moisture conditions of the saltmarsh might explain the widespread colonization of saltmarsh by *Avicennia* in southeastern Australia over the past 50 years (McTainsh *et al.* 1986; Mitchell & Adam 1989b; P. J. Clarke, pers. obs. 1988).

Lower intertidal limits

Low seedling densities were observed in patches with a dense cover of the macroalga *Hormosira banksii*. A plausible explanation for this observation is that *Hormosira* prevents the establishment of propagules. This model predicts that propagules would establish if the algae were removed from the sediment surface and if other confounding factors were controlled for. This hypothesis was tested and the model retained, thus establishment of *Avicennia* seedlings may be restricted by interspecific competition if *Hormosira* is present. The precise mode of action that prevents the seedling from anchoring requires further study, but initial observations indicate that the hypocotyl and the roots extend normally and are restricted from anchoring by tidal action because of the extra distance (*ca* 1 cm) they have to grow to find sediment.

Many intertidal mudflats in the region of study and outside New South Wales are not covered by macroalgae. Nevertheless, seedlings are rarely found on mudflats, and if they are present, they do not survive. Sediment conditions such as waterlogging do not account for this pattern as propagules can readily establish at this level if caged (see results of first and second experiments). Similarly, predators are unlikely to be a factor as there was no difference in predation among elevations. Although factors affecting seedling establishment were controlled, factors affecting seedling survival were not; hence poor survival on the mudflat could not easily be attributed to a single factor. We propose that low numbers of seedlings found on mudflats are due to the mechanical effects of tides and currents on establishment. We also suggest that those propagules that do establish fail to survive because of either waterlogging or prolific algal and barnacle growth.

Predation

The results of the post-dispersal predation experiment deserve further discussion in view of the role

of predators in the distribution and abundance of trees in tropical mangrove communities (Robertson 1991). In our study macroconsumers such as fish, large crabs and mammals, appear to have little effect on seedling establishment as there were no significant differences between the large exclosure and the controls. However, the effect of a small exclosure was to increase propagule establishment by about 61 per cent. Thus small macroinvertebrates, such as crabs and gastropods, appear to interfere with the establishment phase. Propagules were partially consumed rather than completely destroyed, nevertheless a small amount of damage appears sufficient to inhibit establishment. There were no direct observations of propagules being consumed by predators, but their chew marks suggest they were attacked by small crabs, possibly *Helograpsus haswellianus* (Whitelegge), *Paragrapsus levis* (Dana) and *Sesarma erythrodactyla* (Hess). This contrasts with propagule predators found in tropical Australian mangrove forests where grapsid crabs consumed 96 per cent of *Avicennia* propagules over a 3 week period (Smith 1987b). Differences in the amount of predation of *Avicennia* propagules were also found across the intertidal zone (Smith 1987b) and between canopy gaps and the understorey in tropical Australian mangroves (Osborne & Smith 1990). Our study found no differential effects of predation by invertebrates across the intertidal zone. Predation of seedlings of *Avicennia* by agile wallabies (*Macropus agilis* Gould) has also been reported in northern Australia (Smith 1987a). The absence of macropods from the study area precluded any test to see if they influenced establishment and survival.

ACKNOWLEDGEMENTS

We thank John Clarke and Luke Grant for their assistance in the field. Ushi Kaly kindly donated the experimental exclosures for the predator experiments. The New South Wales National Parks and Wildlife Service allowed access to the Towra Point Nature Reserve.

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