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Dispersal, establishment and survival of *Ceriops tagal* propagules in a north Australian mangrove forest

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Abstract Studies of the ecology of mangroves show that a wide variety of factors, including salinity, desiccation, disturbance, competition and predation, may affect the distribution and abundance of species. Field studies were done to examine the relative importance of several of these factors in the establishment and early survival of *Ceriops tagal*, a species common in mid- to high-shore regions of mangrove forests in northern Australia. The fate of marked and tethered propagules was followed to estimate the range of dispersal and the intensity of predation. Propagules were artificially planted under different thicknesses of shade cloth (none, 30%, 80%) and in different habitats (clearing, forest, clearing-forest fringe) to examine the effects of light and soil conditions on survival and growth. Results suggested that dispersal was very limited: only 9% of marked propagules were ever found more than 3 m from the parent tree. Losses to predators were great, with 83% of tethered propagules being damaged or consumed within 3 months. On average, 56% of planted propagules survived for at least 6 weeks and 76% of these initiated growth. Survival in clearings was lower than in other habitats, with 29% fewer surviving six weeks and 48% fewer surviving 15 months. The growth of seedlings was correlated with soil temperature, but the effects of treatments were complex. Overall, results indicated that poor dispersal and establishment were the main factors likely to limit the colonisation and population growth of this species.

Key words Seedling recruitment · Dispersal · Predation · Physico-chemical · Mangrove population ecology

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Introduction

A major aim of plant ecology is to understand the factors determining the distribution and abundance of species (Harper 1977). Before establishment, processes such as dispersal and predation influence initial patterns of distribution and abundance (Harper 1977; Smith 1987a, b; McKee 1995). After establishment, stress, competition and other factors may restrict species to a portion of the original range (Harper 1977; Bertness 1991; McKee 1995). Studies of the ecology of mangroves demonstrate that all these factors may influence the abundance and distribution of species (e.g. Clarke and Hannon 1970; Smith 1987a, b; Roth 1992; Clarke 1993; Clarke and Allaway 1993; Clarke and Myerscough 1993; Ellison and Farnsworth 1993; Ball and Pidsley 1995; McKee 1995) but few studies have examined the relative importance of different factors for individual species (but see Smith 1987a, b; Osborne and Smith 1990; Clarke 1993; Clarke and Allaway 1993; Clarke and Myerscough 1993; McKee 1995). Such studies are required, however, to better understand how abiotic and biotic factors interact to structure mangrove communities. This type of information is important, given the increasing threats to the viability of mangrove communities (Hatcher et al. 1989), and will increase our general understanding of plant dynamics.

Although mangrove propagules may travel great distances (Tomlinson 1986; Hutchings and Saenger 1987), the normal dispersal abilities of species are not well-known (Clarke 1993). Some workers (e.g. Rabinowitz 1978b; Ball and Pidsley 1988; McKee 1995) examined features of propagules, such as longevity and floating time, that determine the limits to, but do not reveal the normal range of, dispersal. Clarke (1993) found that few *Avicennia marina* propagules dispersed over 10 km and most stranded within 500 m. There is also little information on the rate at which stranded propagules become established. Clarke and Myerscough (1993) found that about 20% of *A. marina* propagules established successfully while McKee (1995) reported that about 40% of *Rhizophora mangle* and *Avicennia germinans* propagules failed to root. These studies used tethered propagules, however, and may have overestimated natural establishment.

Established propagules must cope with the prevailing biotic and abiotic factors. Rabinowitz (1978a) observed considerable variability in the survival and growth of propagules planted at different heights on the shore. She also observed that propagules did not always grow best where conspecific adults were most abundant (and see Smith 1987a). Several factors are known to contribute to this variability. Predators can greatly affect the survival of propagules and seedlings (Smith 1987b; Osborne and Smith 1990; Robertson 1991; Clarke and Myerscough 1993; McKee 1995; McGuinness 1996). Smith (1987a) found increased survival and growth in light gaps although other studies have not (Grant et al. 1993). Clarke and Allaway (1993) found effects of position up-river, nutrients, predators and sediment disturbance (see also Clarke and Myerscough 1993), and McKee (1995) documented the role of several biotic and abiotic factors. Several studies concluded that interspecific competition plays a major role in determining which species eventually dominate a site (Clarke and Hannon 1970; Lugo and Snedaker 1974; Ball 1980).

Here I examine the role of several factors on the establishment and early survival of *Ceriops tagal*, a species common in mid- to high-shore regions of forests in northern Australia (Semeniuk 1983, 1985; Hutchings and Saenger 1987). The aim was to gain an understanding of the principal processes influencing the colonisation of sites by this species. The specific objectives were to determine (1) the pattern of dispersal and success of establishment of propagules, (2) the rate of predation on propagules, and (3) the effect of physical factors, particularly light and soil conditions, on early survival and growth.

Materials and methods

Species and study sites

C. tagal var. *australis* is a small shrub or tree growing from 2 to 6 m in mid- to high-shore regions of north Australia, where it often forms dense thickets (Tomlinson 1986; Wightman 1989). It flowers from October to January, seedlings appear from December to March, and the hypocotyl grows to 4–10 cm before falling from the tree (Tomlinson 1986; Hutchings and Saenger 1987; Ball and Pidsley 1988; Wightman 1989). *C. tagal* dominates the mid-tidal regions of the mangrove forest at Ludmilla Creek, near Darwin, Australia (see McGuinness 1994), although individuals and stands of other species – particularly *Bruguiera exaristata*, *A. marina* and *Aegialitis annulata* – are also common (Semeniuk 1983, 1985; McGuinness 1994). This forest was damaged by cyclone Tracy in December 1974 and, although much vegetation has re-established since then (Stocker 1976; McGuinness 1992), patches remain that have not been recolonised or have been cleared by subsequent disturbance. These patches may lack adult vegetation but are undergoing recolonisation (McGuinness 1992; personal observation).

Three such clearings, referred to as sites 1, 2 and 3 (these correspond to clearings 3, 4 and 5 of McGuinness 1994), were studied in the work presented here. All clearings were elongate, but the clearing at site 2 was about twice the size of that at site 3, which was about twice the size of that at site 1. There was still considerable debris from the cyclone (tree trunks and large branches) present at sites 1 and 3, but less remained at site 2. Sites 1 and 3 were about 6.5 m above extreme spring low water and inundated on approximately 150 days per year. Site 2 was 0.5 m higher on the shore and inundated on approximately 75 days per year.

Dispersal

Fifty propagules were marked with bands of paint while they were still attached on three trees in the clearing and three trees in the nearby forest at sites 1 and 2 in November 1991 (a total of 600 propagules). At this time, the propagules were grown but not ready to fall. Over the following 6 months, the number of propagules still on the tree, lying on their side on the substratum, or embedded vertically in the substratum were recorded (sampling dates in Table 1). These counts were made in three "zones" around the tree: ≤ 1 m, > 1 and ≤ 3 m, and > 3–8 m. The number of propagules remaining on the trees after 24 and 51 days were compared among habitats (clearing versus forest; fixed factor) and sites (1 versus 2; fixed factor) using two-factor analyses of variance (ANOVAs); counts on the three trees in each habitat by site combination were the replicates. Variances were homogeneous (Cochran's test) so data were not transformed.

Predation

The methods of Smith (1987b) were used to estimate the rate of predation on *C. tagal* propagules near the same trees monitored for dispersal (see above). Propagules were tethered with mono-filament line to heavy, galvanised roofing nails which were pushed into the substratum. Twenty propagules were tethered near each tree from 31 January to 3 February 1992. On 14 occasions over the following 3 months, the propagules were examined and recorded as intact (undamaged), damaged (chewed by predators) or taken (missing completely). Even when the propagule was missing, it was usually possible to relocate the nail and tether (the recovery rate was always at least 85%). On 28 February 1992, the number of burrows of the crab *Sesarma meinerti* within 3 m of each tree were counted to estimate the abundance of one potential predator (Macnae 1966; Micheli et al. 1991). The survival curves for intact propagules were compared between the habitats (clearing versus forest) and sites (1 versus 2) using the Cox-Mantel test (Cox 1959, 1972; Mantel 1966). The percentage of propagules remaining intact at the end of the study was also compared among habitats (fixed factor) and sites (fixed factor) using a two-factor ANOVA. In the latter analysis, the sets of 20 propagules tethered near each tree were regarded as replicates. Variances were homogeneous (Cochran's test) so data were not transformed.

Physical factors

The effects of some physical factors on the survival and growth of seedlings of *C. tagal* were examined by planting propagules in three experimental treatments in the clearing, forest fringe and forest. These treatments were (1) shaded with 80% shade cloth, (2) shaded with 30% shade cloth, and (3) unshaded (control). The shade cloth used was a green, woven nylon mesh which has minimal effects on the spectral characteristics of photosynthetically active radiation (PAR; D. Eamus, personal communication). The 30% shades were intended to mimic natural levels of PAR under the forest fringe, with the 80% shades intended to simulate conditions under a full canopy. Subsequent measurements (see below) indicated that PAR under the full canopy and in the forest fringe did not differ greatly and was similar to conditions under the 30% shades. The shade cloth was supported by wire attached to fencing posts projecting 60 cm from the substratum. The experimental plots were 3×2 m with the long axis aligned east-west but propagules were planted in a 1×1 m square in the centre of the plot. All treatments in the forest fringe and forest were set up in small light gaps. The treatments were replicated three times each at sites 1 and 3.

Fifty propagules were planted in each plot from 15 to 22 January 1992. At the start of the experiment, ten propagules were haphazardly selected from those planted in each plot and tagged for studies of growth. At intervals over the following 15 months, the survival and growth of these propagules were monitored (see Fig. 4 for sampling times). Growth was monitored by counting the number of leaves present, and by measuring shoot length from the top of the hypocotyl to the top of the plant. Any tagged seedlings which died were replaced by haphazardly selecting and tagging individuals from those remaining in the plot.

The environmental conditions in each of the plots, and under the canopy nearby, were monitored in spring tides on 9–10 September 1992 and in neap tides on 28–29 October 1992. Six variables were recorded: air temperature, relative humidity, PAR, soil temperature, soil moisture content and soil salinity. Air temperature and relative humidity were measured using a Viasala HMP35A temperature and humidity probe. Soil temperature was measured with a Fluke 51KJ thermometer during neap tides and a HI8314 combination temperature-pH meter during spring tides. PAR was measured with a LiCor quantum sensor. Surface soil moisture and salinity were estimated by collecting a sample of sediment from the centre of each plot. In the laboratory, the samples were split. One-half was weighed, dried in a microwave oven, then reweighed to estimate moisture content. The salinity of the remaining half was estimated by extracting the salt from dried sediment into a known volume of water (Rhoades 1982). This method measures the salts present in the soil and can be used in situations, as in this study, where the soil dries completely and conventional methods cannot be used.

Environmental data were analysed using four-factor ANOVAs with the following factors: Tide (spring, neap; fixed); Habitat (clearing, forest-fringe, forest; fixed); Shade (0, 30, 80; fixed); and Site (1 versus 3; fixed). Survival data were analysed using four-factor repeated-measures ANOVAs with the following factors: Habitat (clearing, forest fringe, forest; fixed); Shade (0, 30, 80; fixed); Site (1 versus 3; fixed) and Time (eight times; fixed). In testing the significance of the repeated-measures factor Time and its interactions, the Greenhouse-Geisser method was used to correct for heterogeneity problems (Winer 1971). Growth data were analysed using similar procedures but the factor Site was omitted because of the poor survival of seedlings at site 1 (see Results); furthermore, only the last six sampling times were analysed because there was no growth before this. The growth data were square-root-transformed to stabilise variances. Correlations and multiple regressions among survival, growth and environmental variables were also calculated.

Results

Dispersal

Approximately 30% of the propagules had fallen by 24 days after marking, and by 70 days, 99% had fallen (Table 1). There was no difference among habitats or sites in the number of propagules remaining on the parent tree after 24 or 51 days (ANOVA, all $P > 0.05$). The number of marked propagules that could be found decreased rapidly, particularly after the main seed fall (Fig. 1). Approximately 40% of the fallen propagules were found at 24 and 51 days, but less than 10% after 4 months.

Averaged over all sampling times, 91% of fallen propagules found were within 3 m of the parent and 76% within 1 m. On only two occasions were less than 75% of the propagules found within 1 m of the parent: immediately after the main seed fall, and at the last time point, when very few propagules were found. Very few of the marked propagules became established. The greatest number found embedded in the sediment was 26, after 51 days, representing only 6% of those which had fallen up to then. At the end of the study, only 4 seedlings could be found which were growing (0.7% of the 600 marked); 3 of these were within 1 m of the parent.

Predation

By the end of the study, only 33% of the propagules remained and only half of these were undamaged (Fig. 1). Predation was consistently greater at site 2 (Cox-Mantel test, $P < 0.05$; ANOVA, $F = 5.92$, $df = 1,8$; $P < 0.05$) but there was no difference between habitats (Cox-Mantel test, $P > 0.05$; ANOVA, $F = 0.03$, $df = 1,8$; $P > 0.05$) and no interaction (ANOVA, $F = 0.24$, $df = 1,8$; $P > 0.05$). There was a strong negative correlation between the percentage of intact propagules and the number of crab burrows ($P < 0.05$ for samples from 14 to 89 days; Fig. 2). The number of burrows was greater at site 2 (ANOVA, $F = 9.97$, $df = 1,8$; $P < 0.05$; Fig. 2).

Table 1 Numbers of marked *C. tagal* propagules found in the dispersal study at different distances from the parent tree (data aggregated for all trees, habitats and sites)

Date	Days	Found	On tree	≤ 1 m	>1 to ≤ 3 m	>3–8 m
12 Nov 1991	0	600	600	0	0	0
6 Dec 1991	24	483	424	52	2	5
2 Jan 1992	51	312	130	91	80	11
21 Jan 1992	70	129	7	107	10	5
17 Feb 1992	97	95	0	80	9	6
25 Mar 1992	134	44	0	36	5	3
14 Apr 1992	154	33	0	25	5	3
5 May 1992	175	16	0	12	2	2
28 May 1992	198	6	0	4	1	1

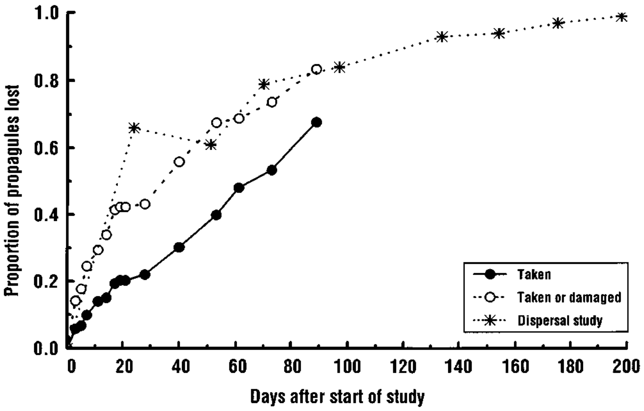

Fig. 1 Rate of loss of propagules in the dispersal and predation studies. Results for the predation study are the proportion of propagules taken by predators (*Taken*) and taken or damaged (*Taken or damaged*)

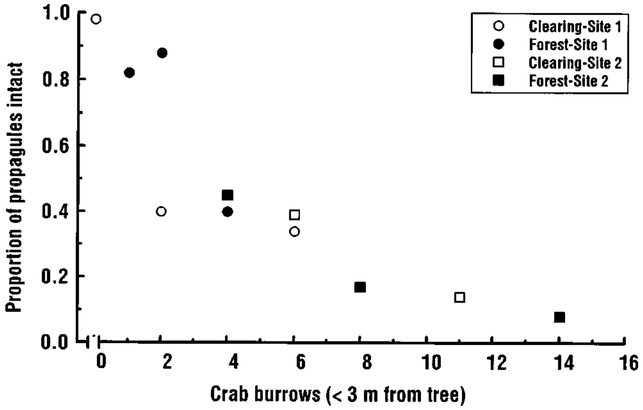

Fig. 2 Relationship between proportion of intact propagules and number of crab burrows. Data are plotted separately for the clearing and forest at the two sites

Physical factors

Environmental conditions

Air temperature decreased with increasing shade but highest temperatures were recorded in the forest fringe (Table 2; Fig. 3). Relative humidity also increased with shading, and from the clearing into the forest (Fig. 3). PAR was very low under the 80% shades and did not differ greatly among habitats (Fig. 3). PAR under the 30% shades was similar to the unshaded plots in the forest fringe and forest. Results for soil conditions were as expected: the shades caused a reduction in soil temperature and salinity and an increase in moisture content (Table 2; Fig. 3).

Most of the environmental variables were significantly correlated in the neap observations but fewer were correlated at spring tide (Table 3). Light was correlated with air temperature in neap tides and with relative humidity during spring tides. Light and

Table 2 Results of analyses of the environmental conditions in the control (0%), 30% and 80% plots in the study of physical factors. The table lists the sources of variation which were significant ($P < 0.05$) for each variable (see text for design). Data for light were log-transformed; variances for soil temperature were still heterogeneous after transformation

Variable	Significant sources of variation
Light	Tide, Habitat, Shade, Shade × Site
Air temperature	Tide, Habitat, Shade, Site, Habitat × Site
Relative humidity	Tide, Shade, Site, Habitat × Site
Soil temperature	Tide, Habitat, Shade, Tide × Habitat, Tide × Shade, Habitat × Shade
Soil salinity	Tide, Habitat, Shade, Site, Tide × Site
Soil moisture	Tide, Habitat, Shade

Fig. 3 Variation in aerial and soil environmental conditions in the shade experiment. The three columns in each group represent, from left to right, the clearing (*open bars*), forest fringe (*hatched bars*) and forest (*solid bars*). The *lines extending above the columns* give 1 SE

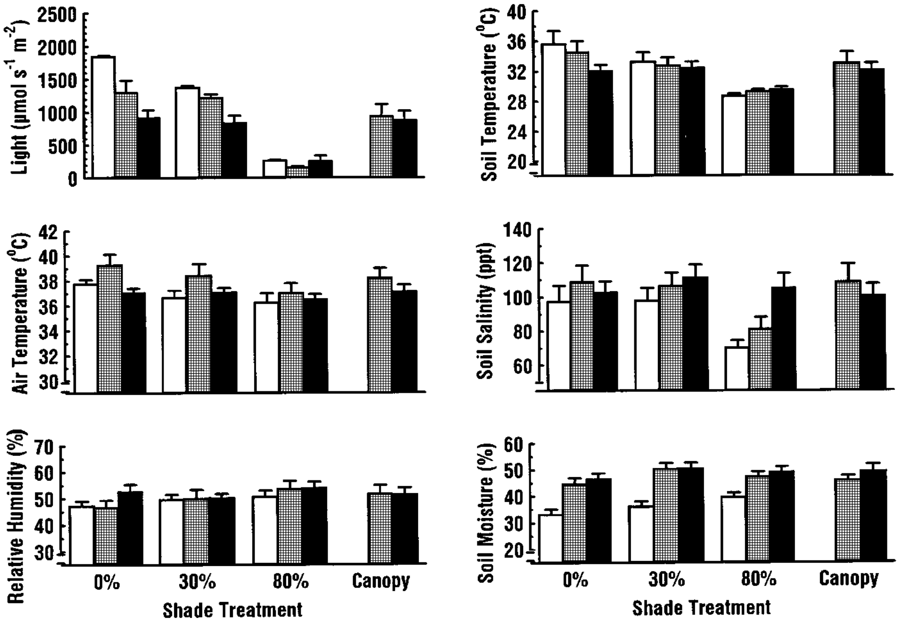

Table 3 Correlation coefficients for the environmental variables in the study of physical factors. Correlations marked with an *asterisk* were significant ($P < 0.05$). Entries above the diagonal are for samples taken during spring tide, those below the diagonal are for neap tide (*RH* relative humidity)

	Air temperature	Soil temperature	RH	Light	Moisture	Salinity
Air temperature		0.362*	−0.831*	0.350	0.005	0.185
Soil temperature	0.432*		−0.252	0.423*	−0.069	0.208
RH	−0.895*	−0.405*		−0.440*	0.145	−0.038
Light	0.397*	0.892*	−0.340		−0.279	0.133
Moisture	−0.050	−0.498*	0.137	−0.372*		0.445*
Salinity	0.155	0.114	−0.161	0.213	0.573*	

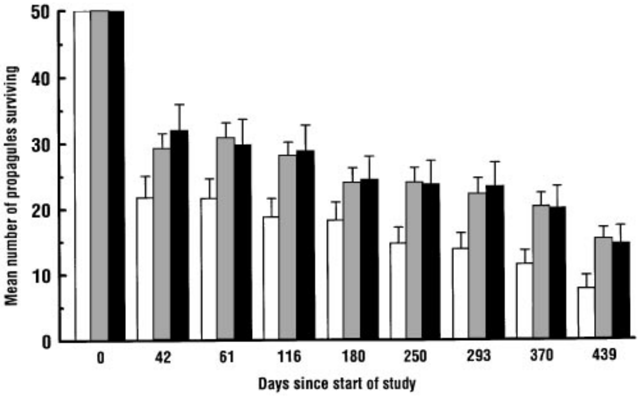

Fig. 4 The mean number of seedlings remaining in the three habitats in the shade experiment: *open bars* are the clearing; *hatched bars* are the forest fringe; and *solid bars* are the forest. The *error bars* show 1 SE

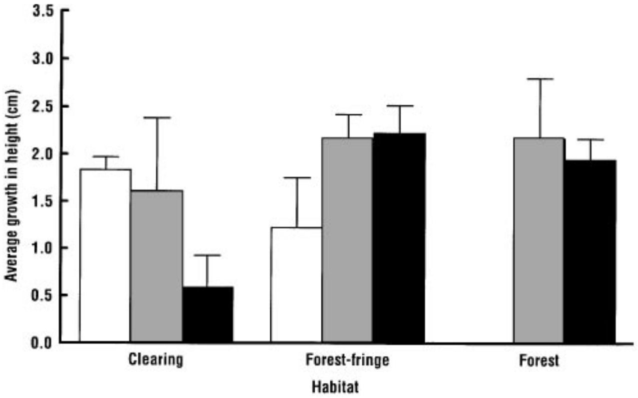

Fig. 5 The effects of habitat and shade treatment on the average growth of *C. tagal* propagules (116–439 days): the *open bars* are for the no-shade treatment; the *hatched bars* are the 30% shade treatment; and the *solid bars* are the 80% shade treatment. The *error bars* show 1 SE

salinity were not correlated at either time, light and soil moisture were correlated only during the neap tide, but light and soil temperature were correlated at both times.

Survival and initiation of growth

A difference in survival among habitats was apparent at the first sampling time, after 41 days, and persisted to the end of the experiment; approximately 20% fewer propagules survived in the clearing than in the other habitats (ANOVA, $F = 21.39$, $df = 1{,}34$, $P < 0.05$; Fig. 4). There were also consistently fewer surviving at site 1 than at site 3 (ANOVA, $F = 5.10$, $df = 2{,}34$, $P < 0.05$; Fig. 4). There was some evidence of an interaction between shade and time (ANOVA, $F = 3.68$, corrected $df = 6.0{,}102.5$, $P < 0.05$), but heterogeneity problems mean that this test may be unreliable. Tukey's test indicated that survival under the 80% shades was higher than in the other treatments at the second sampling time, but the treatments did not differ at other times. Results for the number of propagules starting to grow were very similar (all correlations between the number of propagules surviving at a time, and growing at that time, were greater than 0.80; mean $R = 0.92$).

The number of propagules surviving to the end of the study correlated with spring and neap soil moisture, and with neap soil salinity ($P < 0.05$). The number of propagules initiating growth by the end of the study was correlated only with neap soil salinity ($P < 0.05$). Multiple-regression analysis showed that site and neap-tide salinity contributed significantly to predicting numbers of seedlings remaining at the last sampling time ($R^2 = 0.45$).

Growth

The increase in height of the seedlings was affected by both shade treatment and habitat (ANOVA, $F = 3.69$, $df = 4{,}15$, $P < 0.05$). The pattern of response was, however, complex (Fig. 5), and multiple-comparison tests could not separate means. In the clearing, growth decreased with increasing shade. In the forest fringe and forest, in contrast, growth increased with increasing shade, with no growth at all in the unshaded plots in the forest. There was also an interaction between shade treatment, habitat and time (ANOVA, $F = 2.69$, corrected $df = 11.3{,}42.2$, $P < 0.05$), but this simply resulted from the differences among treatments emerging as the propagules grew. Multiple-regression analysis showed that shade treatment, neap-tide soil temperature and number of seedlings remaining at the previous time all contributed significantly to predicting growth in height at the last sampling time ($R^2 = 0.43$).

Discussion

Dispersal, predation and establishment

Averaged over all sampling times, 76% of the marked *C. tagal* propagules were found within the inner (1 m) search zone around the parent, an area of just 3 m^2. In contrast, only 15% of the propagules were found in the next search zone, although this covered an area of some 25 m^2. Thus, the dispersal of *C. tagal* propagules from these sites appears to be very limited. Clarke (1993) also found dispersal of *A. marina* propagules to be relatively limited, recovering most from the strandline 10–500 m from the point of release but, since he used different methods, his results are not directly comparable with mine. Yamashiro (1961) concluded that most *Kandelia candel* travelled more than 50 m but he ignored predators and assumed that any propagules not found within the study plot were dispersed. *C. tagal* is, however, most abundant high on the shore and the limited tidal inundation may well result in this species having a more restricted dispersal than other species.

Predators removed or damaged many propagules, as found by other workers (Smith 1987b; Smith et al. 1989; Osborne and Smith 1990; Clarke and Myerscough 1993; McKee 1995; McGuinness 1996). In fact, it is possible that predators were responsible for the removal of all the propagules lost in the study of dispersal (the “taken or damaged” plot in Fig. 1 largely overlaps the plot for propagules lost in the dispersal study). The importance of this pre-dispersal and pre-establishment predation probably varies among localities and species. For instance, Smith (1987b), Smith et al. (1989) and McGuinness (1996) all report large differences in predation on the propagules of different species. Smith (1987b) attributed these to differences in the chemical composition of the propagules.

Smith et al. (1989) also found differences in predation among sites and geographic regions. Differences among sites probably result from small-scale variations in the abundance of predators, as was the case here, whereas differences among regions may represent changes in the predator guild (Smith et al. 1989). Osborne and Smith (1990) found differences among habitats, with predation usually lower in clearings. Such a pattern was not observed here but this may be because propagules were tethered under adult *C. tagal* (where they would tend to fall) and *S. meinerti* burrows were common amongst the tree roots (personal observation). Thus, although *S. meinerti* are usually less common in clearings at Ludmilla (McGuinness 1992, 1994) and predation should be lower in such areas, that was not seen here.

Only about 1% of the seedlings in the dispersal study became established and were growing at the end of the observation period. In contrast, a high proportion (~75%) of the artificially planted propagules in the shade experiment became established and started to grow, though in particular areas, such as the clearing, the subsequent survival of these propagules was low. McKee (1995) reported that approximately 40% of the mortality of *A. germinans* and *R. mangle* propagules resulted from difficulty stranding. Clarke and Myerscough (1993) report establishment rates of about 15–85%, depending on tidal height and other factors (e.g. predation and competition; see also Clarke and Allaway 1993). These studies followed tethered or caged propagules, and the establishment of unconstrained and unprotected propagules may well be lower.

Survival and growth

The survival of planted propagules was correlated with soil moisture and salinity, and was lower in the clearing than in small light gaps in the forest fringe and forest. This suggests that the indirect effects of light on soil conditions were more important than its direct effects on the plants themselves. Consistent with this was the lack of differences in survival among shade treatments in the clearing and forest fringe, despite large differences in PAR. These environmental conditions may not have been the only factors varying between the forest and clearing. Predation is not likely to account for the difference in survival because predatory crabs are less common in clearings (Osborne and Smith 1990; McGuinness 1992, 1994). As noted earlier, debris was present in some of the clearings and, moved by the wind and tide, may have damaged seedlings, an effect which has been reported elsewhere (Tamai and Iampa 1988).

The subsequent growth of these propagules was affected by shade treatment and habitat: growth was positively correlated with shade and seedling density, and negatively correlated with soil temperature. This suggests that growth was affected by both the direct availability of light and its effects on soil conditions, being limited by low light levels in the forest but also limited in clearings because of adverse soil conditions. The positive correlation with seedling density may just be evidence of small-scale patchiness in environmental characteristics; some plots had more favourable conditions, so higher survival and growth. Previous field studies of the direct effects of light on the survival and growth of mangrove seedlings have found either limited (Smith 1987a) or no (Clarke and Allaway 1993; Grant et al. 1993) effects. Workers have, however, found that light may interact with other factors to have pronounced effects. Clarke and Allaway (1993) found enhanced seedling survival on disturbed sediments under canopy gaps and suggested that resources were limiting. McKee and Feller (1994) found greater growth after the addition of nutrients, and reduction in light; again resources were apparently limiting but physical stress was also important.

Conclusions

Clarke and Hannon (1970) first discussed the multiplicity of factors affecting mangroves from the stage of propagule to adult. Recent studies tend to operate within the context of the regeneration niche, where seedlings require "a specific combination of conditions for recruitment to the adult population" (McKee 1995). This focus, however, may tend to understate the importance of those factors acting prior to, or during, establishment (and see Clarke and Allaway 1993; Clarke 1995; McKee 1995). The present work indicates that this phase is critical in the life history of *C. tagal* and this may be true for many species. Survivorship curves drawn by Clarke (1995) for *A. marina* show greatest mortality early in the life history, prior to recruitment to the sapling stage, and studies have shown that predators alone can greatly limit early recruitment of several species (Smith 1987b; Smith et al. 1989; Osborne and Smith 1990). McKee (1995) concluded that mortality of *R. mangle* and *A. germinans* "was highest during the establishment phase and major causes were failure to strand before viability was lost, consumption by predators and desiccation".

As for *C. tagal* here, factors acting after establishment also affect survival and growth. McKee (1995) suggested that the subsequent survival and growth of seedlings were affected by stress and the availability of resources; Clarke and Allaway (1993) emphasised the importance of the latter factor for *A. marina*. These factors appear, however, to be merely modifying patterns already largely determined by earlier processes (and see McKee 1995).

Overall, these results suggest that the rate at which mangroves colonise, or recolonise, a habitat is likely to be most affected by those processes acting during the first few months to, at most, the first few years of the life of individuals. The pre-occupation in studies of zonation with the roles of competition and physicochemical factors has, perhaps, led to an overemphasis of the importance of factors acting later in the life history. It is, however, important that efforts to manage the effects of human impacts on mangroves give due attention to the role of factors acting during the establishment phase. Furthermore, it is possible that more studies of these factors will provide a better understanding of the still unresolved question of mangrove zonation.

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