Journal of Tropical Ecology (1997) 13:293–302. With 3 figures

Seed predation in a tropical mangrove forest: a test of the dominance-predation model in northern Australia

KEITH A. McGUINNESS

School of Biological Sciences, Northern Territory University, Darwin NT 0909, Australia

ABSTRACT. Studies of predation on propagules of the mangroves *Avicennia marina*, *Bruguiera exaristata*, *Ceriops tagal* and *Rhizophora stylosa* were made in a forest in northern Australia to test the generality of the dominance–predation model. This model states that an inverse relationship exists between the dominance of a species in the canopy of mangrove forests and the rate of predation on the propagules of that species. Significant differences in predation were found among the four species, and among patches of forest dominated by the different species. Predators attacked more than 50% of the propagules of all species except *R. stylosa*, so are likely to significantly affect forest structure. The intensity of predation did not, however, vary as the dominance–predation model predicted. Instead, predation on the propagules of a species appeared to depend on the availability of propagules of other, more highly preferred, species.

KEY WORDS: *Avicennia*, *Bruguiera*, *Ceriops*, crabs, intertidal mangroves, *Rhizophora*, seed predation, tree dominance

INTRODUCTION

Smith (1987a) wrote 'Current hypotheses do not adequately account for the observed tree species distribution patterns across the intertidal region in mangrove forests.' In a series of experiments he demonstrated that predation by grapsid crabs on mangrove propagules was often severe, and was potentially a major determinant of forest structure and the zonation of species (Smith 1987a,b). He found, for instance, that predation on *Avicennia marina* (Forskål) Vierh. propagules eliminated this species from mid-shore regions, although it could survive and grow if predators were excluded. Later studies have confirmed that predation on propagules can severely limit survival (McGuinness 1996, McKee 1995, Osborne & Smith 1990, Smith *et al.* 1989).

Smith (1987a) also found a negative correlation between the rate of predation on the propagules of a species and the dominance of that species in the canopy, with 'significantly higher losses of propagules in forests where conspecifics were rare or absent than in forests where conspecifics were dominant'. Smith *et al.* (1989) further tested this 'dominance-predation' model, confirming it for some species at some sites. They proposed that this pattern might result from the differential distribution of seed predators and suggested that some differences among sites in the relationship between predation and dominance might arise from regional variations in the composition of the seed predator guild.

If this 'dominance-predation' model proved to be generally applicable to tropical mangroves, even if only for a subset of species, it would represent an important step towards an understanding of the factors structuring these forests. It would also contribute to the general understanding of the effect of seed predators on plant communities. Such predators often have a major effect on the survival of plant propagules (Janzen 1971) and the structure of plant communities (Connell 1971, Janzen 1970), although the dynamics of these interactions are not completely understood (Burkey 1994, Connell *et al.* 1984, Notman *et al.* 1996, Schupp 1988).

Despite its potential significance, however, Smith (1987a) and Smith *et al.* (1989) provide the only tests of the model. The latter study did encompass four regions (North and Central America, Malaysia and Australia), each with one or two sites. All the work reported from Australia, which has extensive mangrove forests covering much of the north of the continent, has, however, been done at sites in a small part of Queensland: it is not clear if these results are typical of tropical Australia.

This study addressed the questions: (1) Is the relationship between seed predation and tree species dominance in a northern Australian mangrove forest consistent with the model of Smith (1987a)? (2) What factors might influence seed predation at a site? Addressing these questions should allow a better evaluation of the generality of the dominance-predation model, and of the role of seed predation in structuring tropical mangrove forests.

MATERIALS AND METHODS

Study sites and species

Experiments were done in mangrove forests at Ludmilla Creek (12°25′S, 130°51′E), 4 km north of Darwin, Northern Territory, Australia (see McGuinness 1992, 1994, 1996 for additional site descriptions). The mangrove communities near Darwin are among the most diverse and extensive in Australia, with nearly 40 species recorded (Wightman 1989). Approximately 16 species are found at Ludmilla Creek, with five commonly dominant in the canopy: *Avicennia marina*, *Bruguiera exaristata* Ding Huo, *Ceriops tagal* var *australis* C. White, *Lumnitzera racemosa* Willd. and *Rhizophora stylosa* Griffith (nomenclature follows Tomlinson 1986). *C. tagal* dominates mid-shore regions at Ludmilla Creek, often in association with *B. exaristata*. *L. racemosa* fringes the landward margin of the forest, while *R. stylosa* lines creek-banks. Scattered *A. marina* occur across the intertidal, but at Ludmilla Creek this species is most abundant near creek-banks in association with *R. stylosa*. The major seed predators appear to be grapsid crabs (see Smith 1987a, Smith *et al.* 1989), in particular the red mangrove crab *Sesarma (Neosarmatium) meinerti* de Man (McGuinness 1996).

Experiments were done with four of the species most abundant in this forest: *A. marina*, *B. exaristata*, *C. tagal* and *R. stylosa*. These species produce different numbers and sizes of propagules: *A. marina* trees give rise to approximately 300 propagules weighing 3.4 g, *B. exaristata* give 51 weighing 3.0 g, *C. tagal* give 170 weighing 1.4 g, and *R. stylosa* give 100 weighing 30.3 g (F. Perrett *pers. comm.*, Smith 1987a).

Experimental design

Experiments were done during the wet season from December 1993 to January 1994 and followed the methods of Smith (1987a) closely. Predation was measured by following the fate of propagules tethered on 1 m lengths of monofilament line tied to large (6 cm) galvanised iron roofing nails pushed into the sediment. Controls, pieces of line with nothing attached, were not used because the results of Smith (1987a) indicated that they were not required.

Experimental plots were approximately 60 m^2, a size selected by Smith (1987a) to ensure that tethered propagules did not significantly increase the natural density in the area, and that adjacent propagules did not become entangled. Plots were haphazardly selected where each of the species was dominant and was moderately abundant (sub-dominant). Dominance was estimated by measuring the total basal area (TBA), and basal area of conspecifics (CBA), in each plot, using the method of Cintron & Novelli (1984), then calculated as: DOM = CBA/TBA (see Smith 1987a). A species was considered dominant if DOM $\geq$ 0.70, and sub-dominant if DOM $\geq$ 0.30 but DOM < 0.70.

Twenty propagules were tethered per plot, a density within the range observed for three of the four species (Table 1). Propagules of each of the

Table 1. Description of the experimental areas at Ludmilla Creek, northern Australia, in terms of tree species dominance, propagule and crab hole density. Am = *Avicennia marina*, Be = *Bruguiera exaristata*, Ct = *Ceriops tagal*, Rs = *Rhizophora stylosa*, Am Sub = *A. marina* sub-dominant, Be-Ct Sub = *B. exaristata* and *C. tagal* sub-dominant, Rs Sub = *R. stylosa* sub-dominant (n = 5 for dominance; n = 15 for propagule density and crab holes).

	Forest type						
	Am	Be	Ct	Rs	Am Sub	Be-Ct Sub	Rs Sub
Dominance of species (Conspecific Basal Area/Total Basal Area)							
Am	0.99	0.03	0.00	0.05	0.54	0.00	0.63
Be	0.00	0.97	0.06	0.05	0.23	0.61	0.02
Ct	0.00	0.00	0.93	0.00	0.15	0.34	0.00
Rs	0.01	0.00	0.00	0.87	0.08	0.07	0.33
Density of propagules (m^{-2})							
Am	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Be	0.0	2.1	0.1	0.1	1.6	0.1	0.6
Ct	0.0	0.3	17.8	0.1	1.5	0.1	0.5
Rs	0.1	0.1	0.0	0.5	0.0	0.1	0.4
Density of crab holes (m^{-2})							
< 2 cm diam.	19.5	15.4	17.1	9.1	27.4	15.6	20.5
2–5 cm diam.	1.4	3.3	6.0	5.8	6.7	5.7	7.6
> 5 cm diam.	0.0	0.1	0.2	0.1	0.1	0.1	0.0

focal species were tethered in the forest where it was dominant, where it was sub-dominant, and in the forest where each of the other species was dominant (five types of forest for each species; Table 1). Thus, each species was tested in patches where conspecific adults were very abundant (five plots), moderately abundant (five plots), and rare (15 plots). This design was used because of the limited areal extent of some types of forest, and the limited numbers of some types of propagules. *A. marina* were tethered on 28 January 1994, and *B. exaristata*, *R. stylosa* and *C. tagal* propagules were tethered on the 3 December, 17 December, and 25 December 1993, respectively. There was sufficient time between the different species to ensure that interference among them was unlikely (predation asymptoted in 10–12 d; see Results).

Plots were checked every few days for two weeks, then one week later (Figure 1). Propagules were recorded as viable (capable of growth), nonviable (incapable of growth) or missing (the line and nail were missing). Only a few propagules could not be traced (mean = 0.6%). Following Smith (1987a), propagules were considered nonviable if they met any of three criteria: (1) at least half of the mass had been consumed, (2) the propagule had been taken down a crab burrow, or (3) the plumule and cotyledonary buds had been removed along with the proximal portion of the propagule.

Naturally occurring propagules were counted in three replicate 1-m^2 quadrats in each plot from 23–29 December 1993. At the same time, the numbers of small (< 2 cm diameter), medium (2–5 cm) and large (> 5 cm) crab burrows in each quadrat were also recorded.

Statistical analyses

Mean amounts of predation were compared at 20–22 d using a two-factor analysis of variance (ANOVA; Winer 1981): predation had reached an asymptote by this time (Figure 1). Forest type (*A. marina*, *B. exaristata*, *C. tagal*, *R. stylosa* or mixed: fixed) and species of propagule (*A. marina*, *B. exaristata*, *C. tagal* or *R. stylosa*: fixed) were the factors. Tukey's test ($\alpha = 0.05$) was used to compare means after the ANOVA (Winer 1981).

RESULTS

Averaged over all species and treatments, the percentage of propagules eaten by predators in 20–22 d was 63.3 ± 3.4%. Significant differences in predation existed among species of propagule ($F_{3,80} = 97.60$; $P < 0.001$; Figure 2) and forest types ($F_{4,80} = 4.15$; $P < 0.01$; Figure 2). Predation was greatest on *A. marina* (100.0%), least on *R. stylosa* (19.2), and intermediate and similar on *C. tagal* and *B. exaristata* (71.0 and 63.0, respectively; Tukey's test). Tukey's test could not separate the mean amounts of predation in the different forest types, but predation was greatest in the *R. stylosa* dominated forest (70.3%) and least in the *B. exaristata* dominated forest (52.5; Figure 2). A non-significant interaction ANOVA ($F_{12,80} = 0.84$; $P > 0.60$) indicated

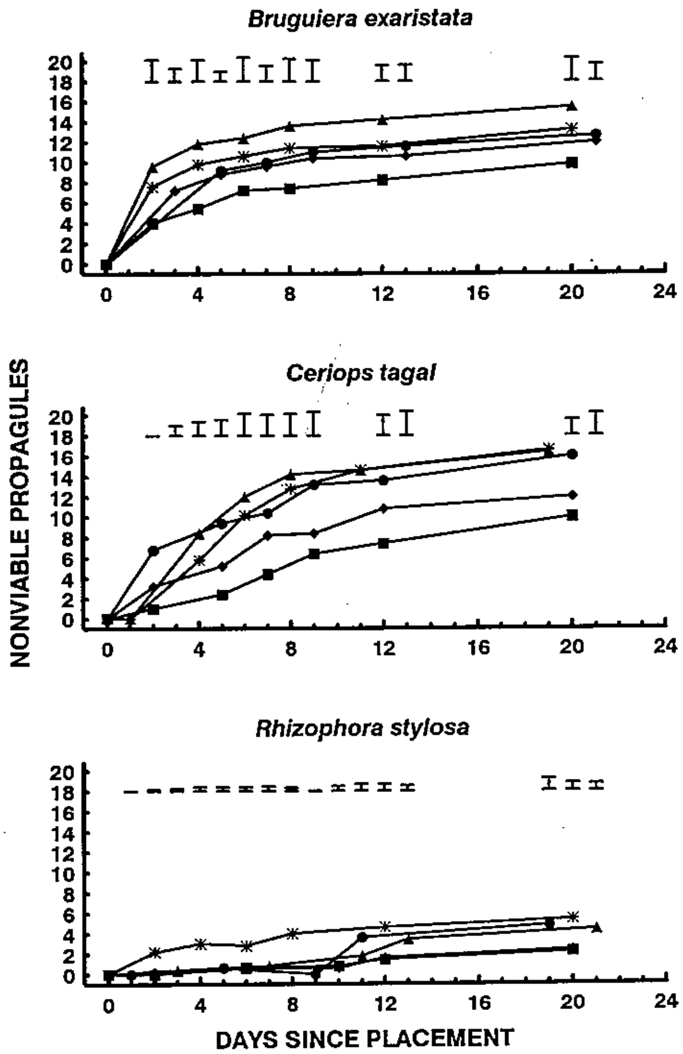

Figure 1. Cumulative predation on mangrove propagules at Ludmilla Creek, northern Australia. Bars give 1–SE at each time, averaged over the five types of forests. Key to forests: ● = *Avicennia marina*; ■ = *Bruguiera exaristata*; ◆ = *Ceriops tagal*; ▲ = *Rhizophora stylosa*; ✱ = mixed (species sub-dominant). Predation on *A. marina* propagules is not plotted because after 7 d only 2.2% were still viable.

that the rank-order of predation in the different types of forest was consistent (Figure 2).

There were no significant relationships between conspecific dominance and predation (Table 2; Figure 3). Predation on *R. stylosa* propagules was, however, positively correlated with the dominance of *A. marina* and negatively correlated with the dominance of *B. exaristata* (Table 2). Predation on *B. exaristata* and *C. tagal* propagules was negatively correlated with the density of naturally occurring *B. exaristata* propagules (Table 2). Predation on *R. stylosa* propagules was also negatively correlated with the abundance of large crab burrows, but large

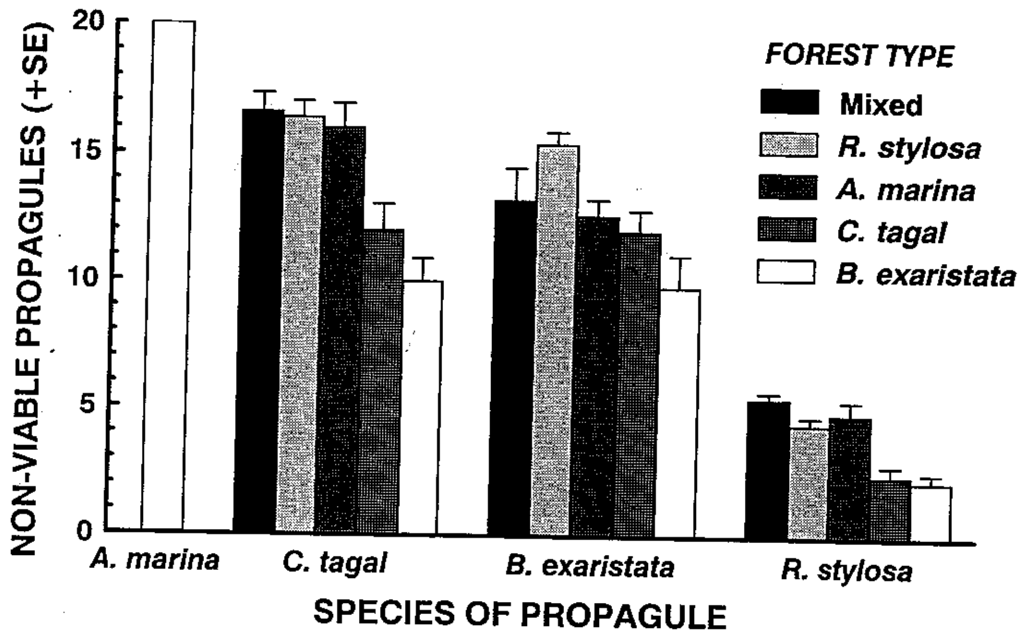

Figure 2. Predation on mangrove propagules in five types of forest at Ludmilla Creek, northern Australia after 20–22 d. Only one bar is plotted for *Avicennia marina* because all propagules were non-viable in all forests by 20 d (SE = 0).

Table 2. Correlations between predation on mangrove propagules at Ludmilla Creek, northern Australia, and the variables characterising the plots at 20–22 d (n = 25). No results are given for predation on *Avicennia marina* because all propagules were nonviable at 20–22 d. * $P \leq 0.05$.

	Predation on		
	B. exaristata	*C. tagal*	*R. stylosa*
Dominance of			
Avicennia marina	0.02	0.22	0.49*
Bruguiera exaristata	−0.22	−0.28	−0.42*
Ceriops tagal	−0.09	−0.17	−0.32
Rhizophora stylosa	0.33	0.24	0.22
Background propagule density			
A. marina	0.00	0.00	0.00
B. exaristata	−0.43*	−0.51*	−0.35
C. tagal	−0.20	−0.20	−0.29
R. stylosa	0.07	−0.07	0.15
Crab burrows			
Small	−0.05	0.24	0.14
Medium	−0.16	−0.09	−0.05
Large	0.08	−0.12	−0.58*

Figure 3. Relation
and conspecific dom
▲ = *Rhizophora stylo*

burrows were
were uncomm

Smith (1987a)
dominance in
cluded that 're
thesis' and the
but not in Flo
relationship b
and the abund
own (Table 2)
dominance-pr
Ludmilla Cre
were consume
100% had bee
Smith *et al.*
places and n
regions. It is l
1989), but th
obtained. Firs
monitor pred
though they

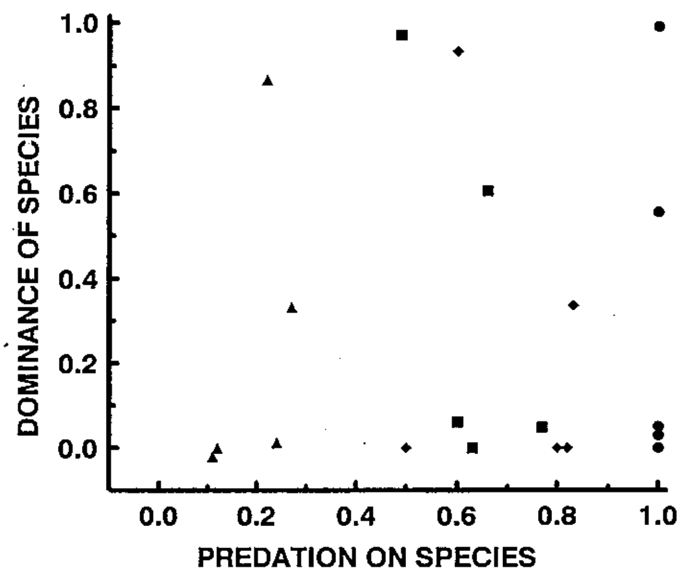

Figure 3. Relationship at Ludmilla Creek, northern Australia, between predation on mangrove propagules and conspecific dominance. Key to species: ● = *Avicennia marina*; ■ = *Bruguiera exaristata*; ◆ = *Ceriops tagal*; ▲ = *Rhizophora stylosa*. Each point represents an experimental plot.

burrows were found in only five of the 25 *R. stylosa* plots and even here they were uncommon (a total of eight were counted).

DISCUSSION

Smith (1987a) found a negative correlation between predation and canopy dominance in 'four of the five species studied', while Smith *et al.* (1989) concluded that 'results for *Avicennia* clearly support the dominance-predation hypothesis' and the 'model appears to hold for *Rhizophora* in Malaysia and Australia, but not in Florida or Panama'. In the present study, in contrast, there was no relationship between the amount of predation on the propagules of a species and the abundance of conspecifics in the canopy, either for each species on its own (Table 2) or for all species combined (Figure 3). On these results, the dominance-predation model does not apply to any of the species studied at Ludmilla Creek. *A. marina* is a possible exception: propagules of this species were consumed so rapidly that meaningful conclusions cannot be drawn (78–100% had been attacked after only 1–2 d).

Smith *et al.* (1989) suggested that one reason the model might apply in some places and not others was that seed predator guild might differ between regions. It is likely that such differences do exist (see McKee 1995, Smith *et al.* 1989), but they do not appear to be the sole reason for the various results obtained. First, the sites used by Smith (1987a) and Smith *et al.* (1989) to monitor predation on *B. gymnorrhiza* (L.) Lamk. gave conflicting results even though they were separated by only a few kilometres and should, therefore, have had similar predator guilds. Second, the seed predators active at Ludmilla Creek appear to be similar those at the sites in north Queensland studied by Smith (1987a) and Smith *et al.* (1989).

The amounts of seed predation found here were, however, comparable to those reported by Smith (1987a) and Smith *et al.* (1989) for Indo-west Pacific forests. Further, the ranking of predation rates was exactly as found by Smith (1987a): *A. marina* was taken fastest, *R. stylosa* slowest, and *C. tagal* and *B. exaristata* at intermediate rates. Smith (1987a) showed that this ranking correlated closely with several characteristics of the propagules, including their size and chemical composition (protein, tannin, sugar and fibre). Steinke *et al.* (1993) also found that the rate at which *S. meinerti*, the dominant seed predator at Ludmilla Creek (McGuinness 1996), consumed mangrove leaves was negatively correlated with the concentration of tannins. These points clearly indicate that predators exhibit general preferences for propagules of particular species, based, at least in part, on chemical and structural features.

In addition to the consistent ranking of predation on species, was the ranking of predation in the different types of forest: predation was consistently high in the *R. stylosa* and mixed plots; moderate in the *A. marina* plots; and low in the *B. exaristata* and *C. tagal* plots. This pattern may result from an interaction between the preference of predators for particular species and the differing background availability of propagules in the plots. Predation on *C. tagal* propagules, for example, was least in *B. exaristata* and *C. tagal* plots, and greatest in *R. stylosa*, *A. marina*, and mixed plots. In the latter two types of plots, *C. tagal* propagules are likely to be the more attractive food: *R. stylosa* are not preferred and *A. marina* are consumed very rapidly (86.2% within 2 d). In addition, predation on *B. exaristata* and *C. tagal* propagules was negatively correlated with the background density of *B. exaristata* propagules (Table 2), suggesting that, when the background density of *B. exaristata* was high, predators may have become satiated before consuming the tethered propagules. Such satiation has been observed in other communities (Burkey 1994).

Variations in the rate of predation did not appear to be related to the abundance of seed predators, in contrast to the conclusions of Osborne & Smith (1990) and the results of McGuinness (1996). Osborne & Smith (1990) found greater rates of predation higher on the shore and under the mangrove canopy, results which they attributed to the greater activity and abundance of crabs in these habitats (see also Smith *et al.* 1989). McGuinness (1996) found strong correlations between the rate of removal of tethered *C. tagal* propagules and the numbers of *S. meinerti* burrows. The lack of such relationships here may, however, simply reflect the fact that crab abundances were similar in these patches of forest (Table 1).

Overall, these results are not consistent with either the mangrove-specific hypothesis of Smith (1987a) and Smith *et al.* (1989), or with more general seed predator models which hypothesise a relationship between predation and distance from conspecifics (Connell 1971, Howe 1989, Janzen 1970). Smith and co-workers (Osborne & Smith 1990; Smith 1987a,b; Smith *et al.* 1989, 1991) have, however, demonstrated the important effects that predators have on the survival of propagules in tropical mangrove forests, particularly in the Indo-West Pacific. These results led Robertson (1991) to conclude that 'interactions involving plants and animals in tropical mangrove forests have important controlling influences on several population, community and ecosystem-level processes'. The results of the present study reinforce this view: the activities of seed predators are likely to exert a strong influence on the survival of mangrove propagules and, thus, on the structure of the forest. Some of these effects may be predicted from predator preferences and propagule availability, but are likely to be complicated by spatial and temporal variability in the abundance of both predators and propagules (and see Burkey 1994, Notman *et al.* 1996, Smith *et al.* 1989).

ACKNOWLEDGMENTS

This work was supported by grants from the Australian Research Council and the Northern Territory University. F. Perrett and A. O'Grady, with assistance from J. McMahon, established and monitored the field trials with their usual expertise. The manuscript benefited greatly from comments by K. Christian, P. Clarke, J. Warren, P. Wurm and three referees.

LITERATURE CITED

BURKEY, T. V. 1994. Tropical tree species diversity – a test of the Janzen-Connell model. *Oecologia* 97:533–540.

CINTRON, G. & NOVELLI, Y. S. 1984. Methods for studying mangrove structure. Pp. 91–113 in Snedaker, S. C. & Snedaker, J. G. (eds). *The mangrove ecosystem: research methods*. UNESCO, Paris. 251 pp.

CONNELL, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Pp. 298–312 in Den Boer, P. J. & Gradwell, G. (eds). *Dynamics of populations*. Wageningen, PUDOC.

CONNELL, J. H., TRACEY, J. G. & WEBB, L. J. 1984. Compensatory recruitment, growth, and mortality as factors maintaining rain forest tree diversity. *Ecological Monographs* 54:141–164.

HOWE, H. F. 1989. Scatter- and clump-dispersal and seedling demography: hypothesis and implication. *Oecologia* 79:417–426.

JANZEN, D. H. 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist* 104:501–529.

JANZEN, D. H. 1971. Seed predation by animals. *Annual Review of Ecology and Systematics* 2:465–491.

MCGUINNESS, K. A. 1992. Disturbance and the mangrove forests of Darwin Harbour. Pp. 55–62 in Moffatt, I. & Webb, A. (eds). *Conservation and development issues in North Australia*. Australian National University Press, Canberra. 277 pp.

MCGUINNESS, K. A. 1994. The climbing behaviour of *Cerithidea anticipata* (Mollusca: Gastropoda): the role of physical versus biological factors. *Australian Journal of Ecology* 19:283–289.

MCGUINNESS, K. A. 1996. Dispersal, establishment and survival of *Ceriops tagal* propagules in a north Australian mangrove forest. *Oecologia* (in press).

MCKEE, K. L. 1995. Seedling recruitment patterns in a Belizean mangrove forest: effects of establishment ability and physico-chemical factors. *Oecologia* 101:448–460.

NOTMAN, E., GORCHOV, D. L. & CORNEJO, F. 1996. Effect of distance, aggregation, and habitat on levels of seed predation for two mammal-dispersed neotropical rain forest tree species. *Oecologia* 106:221–227.

OSBORNE, K. & SMITH III, T. J. 1990. Differential predation on mangrove propagules in open and closed canopy forest habitats. *Vegetatio* 89:1–6.

ROBERTSON, A. I. 1991. Plant-animal interactions and the structure and function of mangrove forest ecosystems. *Australian Journal of Ecology* 16:433–443.

SCHUPP, E. W. 1988. Seed and early seedling predation in the forest understory and in treefall gaps. *Oikos* 51:71–78.

SMITH III, T. J. 1987a. Seed predation in relation to tree dominance and distribution in mangrove forests. *Ecology* 68:266–273.

SMITH III, T. J. 1987b. Effects of seed predators and light level on the distribution of *Avicennia marina* (Forsk.) Vierh. in tropical, tidal forests. *Estuarine Coastal and Shelf Science* 25:43–51.

SMITH III, T. J., K. BOTO, G., FRUSHER, S. D. & GIDDINS, R. L. 1991. Keystone species and mangrove forest dynamics: the influence of burrowing by crabs on soil nutrient status and forest productivity. *Estuarine Coastal and Shelf Science* 33:419–432.

SMITH III, T. J., CHAN, H. T., MCIVOR, C. C. & ROBBLEE, M. B. 1989. Comparisons of seed predation in tropical, tidal forests from three continents. *Ecology* 70:146–151.

STEINKE, T. D., RAJH, A. & HOLLAND, A. J. 1993. The feeding behaviour of the red mangrove crabs *Sesarma meinerti* de man, 1887 (Crustacea: Decapoda: Grapsidae) and its effect on the degradation of mangrove leaf litter. *South African Journal of Science* 13:151–160.

TOMLINSON, P. B. 1986. *The botany of mangroves*. Cambridge University Press, London. 413 pp.

WIGHTMAN, G. M. 1989. *Mangroves of the Northern Territory*. Conservation Commission of the Northern Territory, Darwin. 130 pp.

WINER, B. J. 1981. *Statistical principles in experimental design*, 2nd edition. McGraw-Hill, New York, New York. 907 pp.

Accepted 30 August 1996