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Propagule predators in Kenyan mangroves and their possible effect on regeneration

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Abstract. Grapsid crabs can play a considerable role in the predation of mangrove propagules and possibly are a threat to the regeneration of mangroves, whether natural or artificial. Experiments consisting of artificial plantation of mangrove juveniles were set up in Gazi Bay (Kenya). Grapsid crabs, particularly *Neosarmatium meinerti* in the most landward fringe and *N. smithii* and *Sesarma guttatum* in the middle fringe of the mangrove forest, were found to be a regeneration-limiting factor. Almost 100% (n = 40) of the landward plantations were cleared. There was a slight initial preference for *Rhizophora* propagules lying horizontally on the mangrove floor, which simulates the position of a stranding propagule. In Mida Creek (Kenya) the snail *Terebralia palustris* was observed predating mangrove propagules. This study shows that crabs may affect the regeneration potential of mangroves, and snails might also be a factor in predation. A need to actively search for ways to protect re-afforestation plots from predators of mangrove tree juveniles is necessary.

Extra keywords: mangrove, regeneration, predation, crabs, *Terebralia palustris*, Kenya

Introduction

Mangroves are a unique ecosystem with highly adapted plant species (facultative halophytes) thriving in the intertidal zone. In Kenya, mangrove tree species form more or less well defined zones (Walter and Steiner 1936; Macnae 1968; Chapman 1976; Ruwa and Polk 1986; Gallin *et al.* 1989; Gang and Agatsiva 1992; Ruwa 1990, 1993; Van Speybroeck 1992).

Several mangrove species have juveniles which further develop after fertilization when still on the parent tree, a phenomenon known as viviparity. When the propagule drops from the parent tree at low water, it can plant itself into the mud; this is termed the planting strategy (Van Speybroeck 1992). A second possibility is that the propagule falls in the water at high tide and then floats to another site where it settles and develops; this is termed the stranding strategy (Van Speybroeck 1992). Regeneration and colonization of a naked habitat is logically only possible by means of the stranding strategy. The planting strategy dominates in an undisturbed mangrove forest in Gazi Bay (Kenya), whereas the stranding strategy is dominant in an exploited and open forest (Van Speybroeck 1992).

Predation on mangrove juveniles can involve decapods (Smith 1987*a*, 1987*b*; Smith *et al.* 1989; Osborne and Smith 1990; Anon. 1991; McKee 1995; Dahdouh-Guebas *et al.* 1997; McGuinness 1997), snails (Smith *et al.* 1989; McKee 1995), insects (Robertson *et al.* 1990; Anon. 1991; Ellison and Farnsworth 1993), monkeys (Chan *et al.* 1984) and fish (Macnae 1969). Amongst these, predation by crabs or snails has been observed most frequently. This might be a threat, particularly to artificial regeneration plots in some mangrove areas, even though crabs are known to contribute to the dispersal of juveniles elsewhere (Thornton 1996).

It is important that the mangrove forest be maintained and that a sustainable management of this vegetation is pursued if there is a need for exploitation. The aim of this study is to assess crab pressure on mangrove propagule establishment in the light of restoration and regeneration of mangal ecosystems in Kenya. Preliminary data on gastropod pressure are also presented.

Materials and methods

Site description

The research was performed along the Kenyan coast in Gazi Bay (04°25′S,39°50′E), about 50 km south of Mombasa, and Mida Creek (03°20′S,40°00′E), about 100 km north of Mombasa (Fig. 1). Gazi Bay is a wide, open creek fed by two seasonal rivers. In contrast, Mida Creek has a very small opening to the ocean and is not fed by any overland fresh water. The field experiments were conducted from July to September 1993.

Predation by crabs

Two transects were studied: one in an undisturbed mangrove area (250 m length), and one in a disturbed area (100 m). The disturbed area showed

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extensive gaps in the mangrove forest due to logging of the trees. Along each transect, 15 evenly dispersed quadrats of 5 × 5 m were outlined, the vegetation was described using the Braun-Blaquet relevé method, and in each plot 40 tagged mangrove juveniles were haphazardly planted. The proportion of the species reflected the actual proportions in the forest area and involved the species *Avicennia marina* (Forsk.) Vierh., *Bruguiera gymnorrhiza* (L.) Lam., *Ceriops tagal* (Perr.) C.B. Robinson, *Rhizophora mucronata* Lam., *Sonneratia alba* Sm. and *Xylocarpus granatum* Koen.; nomenclature according to Tomlinson (1986). Also, within each species 50% of the propagules planted represented the planting strategy (Van Speybroeck 1992), i.e vertical planting, and 50% were laid on the forest floor and tied with a nylon wire to a stick, simulating the stranding strategy.

The plantations in the disturbed and undisturbed area were regularly checked for 48 and 47 days respectively (usually at one-day intervals) and the juveniles were classified 'predated' according to one of the three possible ways proposed by Smith (1987*a*, 1987*b*): *(i)* the epicotyl was eaten, *(ii)* at least 50% of the hypocotyl was cut through, or *(iii)* the propagule was pulled into the burrow of a predator. Monitoring also involved visual observations of the crab fauna around the plantations at low tide.

Analyses of the data took into account the different zones of vegetation (order from landward to seaward side): for the undisturbed forest, *Avicennia* zone (plots 1 and 2; $n = 2$ plots), mixed zone (plots 3 and 4; $n = 2$), *Ceriops/Rhizophora* zone (plots 5 to 11; $n = 7$) and *Avicennia/Rhizophora/Sonneratia* zone (plots 12 to 15; $n = 4$); for the disturbed forest, *Avicennia* zone (plots 1 to 3; $n = 3$), *Ceriops/Rhizophora* zone (plots 4 to 9; $n = 6$), clear-cut zone (plots 10 to 12; $n = 3$) and *Avicennia/Rhizophora/Sonneratia* zone (plots 13 to 15; $n = 3$). Two-way analysis of variance (ANOVA unbalanced design) was used to compare propagule predation between the disturbed and undisturbed forest. Student's *t*-test was used to compare propagule loss by predation and by being washed away, propagule predation for horizontally and vertically placed juveniles, and propagule predation among species in each of the zones. Between-zone differences were investigated by one-way ANOVA.

The dominance–predation hypothesis (Smith 1987*a*, 1987*b*) was tested for each mangrove species present in the undisturbed mangrove area; this hypothesis states that predation of propagules of a certain species is higher in areas where adult conspecifics are rare or absent than in those where adult conspecifics are dominant. To verify this, the point-biserial correlation coefficient r_p test (Kent and Coker 1992) was performed on the data obtained after 13, 32 and 47 days of monitoring; this test is particularly appropriate in situations where one variable is in presence/absence or binary form (here 'dominance of adult trees') while the other variable is continuous (here 'predation intensity').

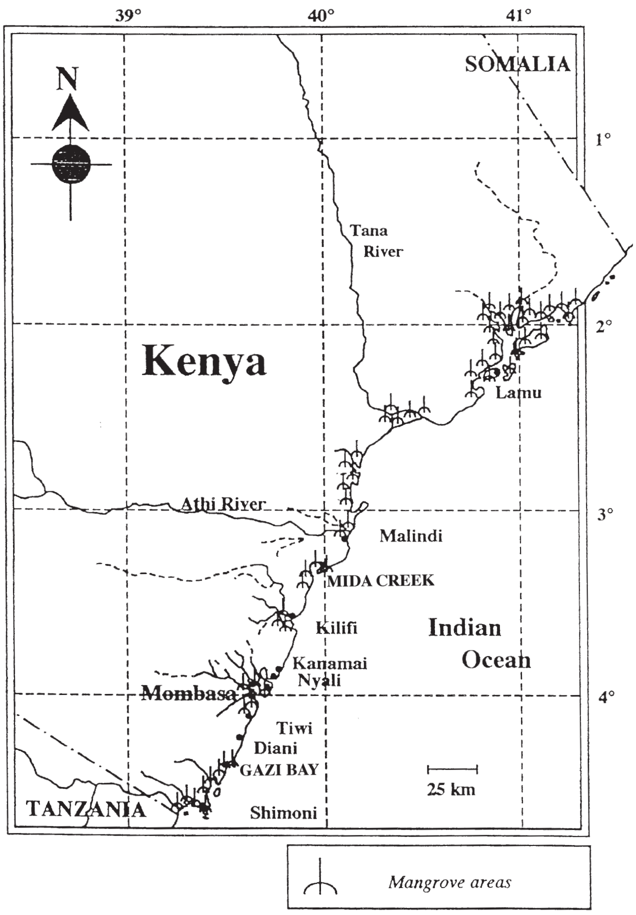

Fig. 1. Kenya coastline showing the mangrove areas (after Tack and Polk 1998). Study sites indicated in uppercase.

Predation by gastropods

In Mida Creek the snail *Terebralia palustris* L. is present in large numbers and was observed preying on mangrove propagules. Therefore, a preliminary experiment was designed to investigate the impact of this gastropod on the propagule-producing mangrove species present: *Bruguiera gymnorrhiza*, *Ceriops tagal* and *Rhizophora mucronata*. In total, 33 propagules (9, 12 and 12 respectively) were planted in a plot in the mangrove forest and monitored for three days. For the first 5 h, the propagules were photographed at 1-h intervals. The experiment was repeated with 33 peeled propagules.

Results

Predation by crabs

Both in the disturbed and the undisturbed area, predation and washing away occurred (Fig. 2).

In the disturbed area propagule loss was high in three segments along the transect: propagules were washed away in the seaward section and predated in the other two segments (Fig. 2*a*). The same two predation segments could be recognized in the undisturbed area (Fig. 2*b*); in one, the crab *Neosarmatium meinerti* de Man was present and in the other the crabs *Neosarmatium smithii* H. Milne-Edwards and *Sesarma guttatum* A. Milne-Edwards were present. In the plots where predation was heavy (plots 1, 2 and 6 in Fig. 2*a*; plots 2, 3 and 7 in Fig. 2*b*), for both the disturbed and undisturbed mangrove area, the plateau in the rate of predation (Fig. 3*a* and Fig. 3*b* respectively) was reached within 10 days after the propagules were planted. In one of the plots in the disturbed area, predation was already 80% within 2 days (Fig. 3*a*). The juvenile mangrove trees survived if they reached 25 days after plantation, i.e. no more juveniles were predated. *Rhizophora mucronata* was the only species for which there existed a significant difference between horizontally and vertically placed propagules after 14 days ($r_p = 0.42$; $t = 2.43$; $P < 0.05$). However, this was only the case for the transect in the undisturbed mangrove area, and after 23 days no significant

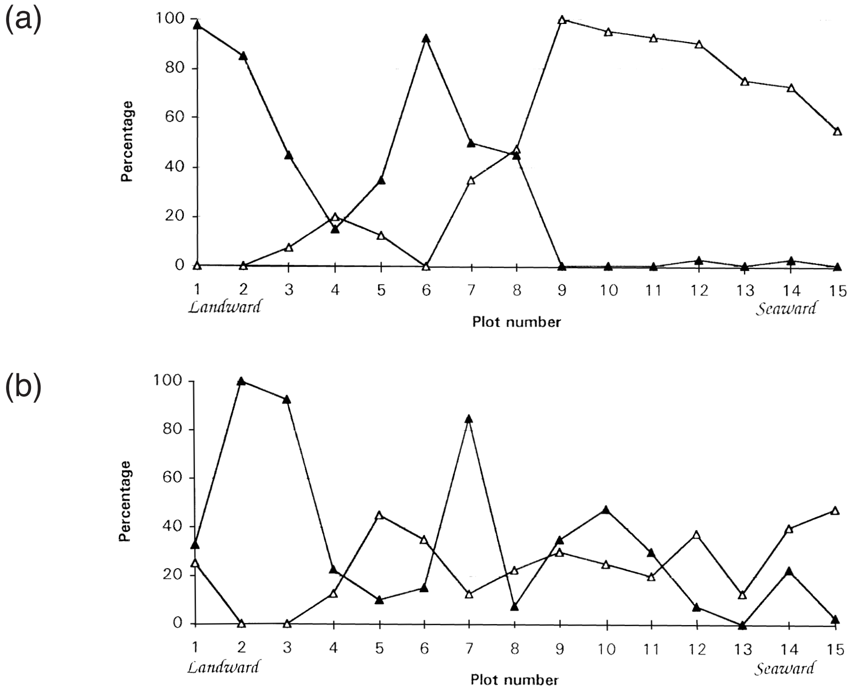

Fig. 2. Propagule loss (%) due to washing away and predation in *(a)* disturbed and *(b)* undisturbed mangrove forest after 48 and 47 days of monitoring respectively (Gazi Bay): △, washed away; ▲, predated.

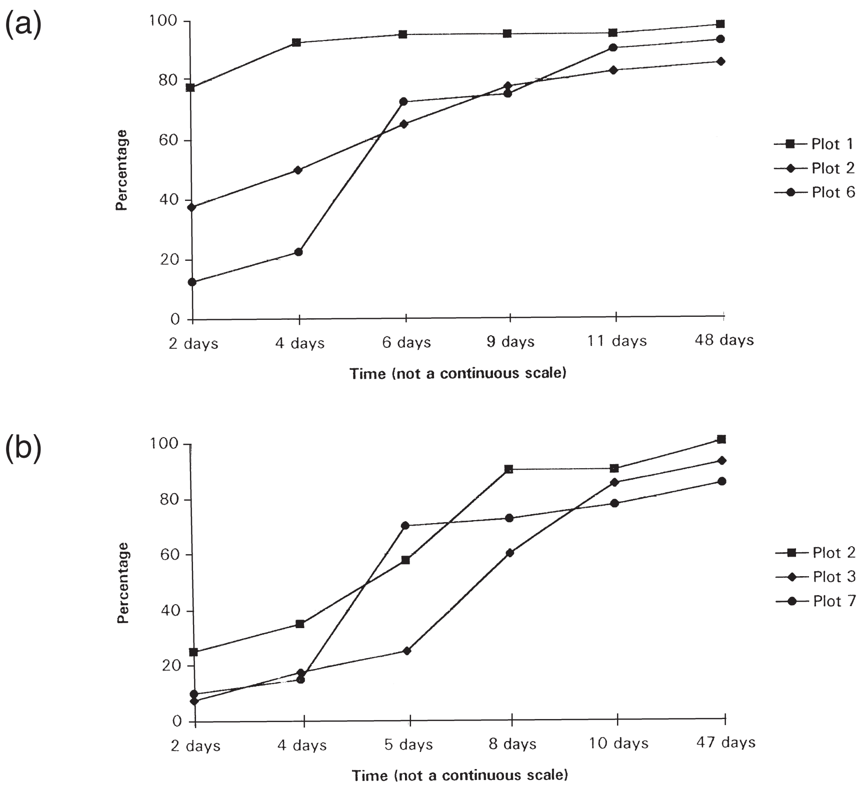

Fig. 3. Rate of predation in the plots with high propagule loss due to predation (Fig. 2) in *(a)* disturbed and *(b)* undisturbed mangrove forest (Gazi Bay).

difference was observed. Visual observations have pointed out that crabs may drag a horizontally placed propagule to their burrows before eating it, whereas predation on vertical propagules often occurred on the surface where the propagules were planted. However, when competition was too high the crabs tried to lift the propagule out of the substratum and drag it away.

In tests of the dominance–predation hypothesis, predation of propagules of a particular mangrove species was not correlated with the presence of an adult tree of the same species in one plot. The only exception was predation on *Rhizophora mucronata*. However, even for this species the correlation was only significant for the observations after 32 days ($r_p = 1.77$; $t = 2.27$; $P < 0.05$).

The ANOVA for the comparison between propagule predation in the disturbed and undisturbed forest showed that there is no difference between them ($F = 0.11$, d.f. 1; n.s.). Statistics for the comparison between propagule loss by predation and by being washed away and between propagule predation of horizontally and vertically placed juveniles have been summarized in Table 1. The significant differences between predation and washing away in each of the zones in the disturbed forest (Table 1*a*) indicate that it is either washing away or predation which is the main cause for propagule loss rather than a combination of the two. This can also be observed from Fig. 2*a*. As could have been expected already from Fig. 1*b*, the above-mentioned difference is not found in the undisturbed forest, but for the most seaward zone (Table 1*a*), and between-zone differences are absent. The global propagule loss is thus due to a synergism between predation and washing away, which is similar throughout the different zones, with some exceptions (Fig. 2*b*). None of the tests comparing propagule predation among species showed significant differences within any of the zones (results not shown).

Predation by gastropods

After 3 days, one *B. gymnorrhiza* and four *R. mucronata* propagules had been predated from the total of 33. The predation pressure in Mida Creek was clearly lower than that of the crabs in Gazi Bay. When the experiment was repeated with 33 peeled propagules, six propagules of each of the three species were predated, this representing a total predation of 54% (Table 2).

Discussion

In the disturbed mangrove area in Gazi Bay, the high disappearance rate of juveniles from the seaward section due to washing away (Fig. 2*a*) was expected, since they were exposed to wave action.

In plot number 1, which was in a landward zone dominated by *Neosarmatium meinerti*, the rapid predation by this sesarmid crab (Dahdouh-Guebas *et al.* 1997) is confirmed. Dahdouh-Guebas *et al.* (1997) observed a 50% propagule clearance in less than 2 h and 85% after 24 h in plots where almost full elimination of propagules occurred. The initial significant difference in predation for horizontal and vertical *Rhizophora* propagules in the present study can be explained by the weight and size of the propagules which make vertically planted ones difficult to handle for the crabs. Once the horizontal lying propagules are cleared the crabs

Table 1. Differences *(a)* in propagule loss for predation and for being washed away and *(b)* in propagule predation between horizontal and vertical placed juveniles, after 32 or 34 days of monitoring (Gazi Bay)

Refer to 'Materials and methods' for the number of plots in each of the zones

Source of variation	Undisturbed forest			Disturbed forest		
	t	d.f.	*P*	*t*	d.f.	*P*
(a) predated *v.* washed away						
Avicennia zone	1.043	2	n.s.	4.743	4	< 0.01
Mixed zone	1.624	2	n.s.	–	–	–
Ceriops/Rhizophora zone	0.785	12	n.s.	3.172	10	< 0.01
Clearcut zone	–	–	–	64.086	4	< 0.01
Avicennia/Rhizophora/Sonneratia zone	3.334	6	< 0.02	10.505	4	< 0.01
Predation between zones	$F = 2.69$, d.f. 3, n.s.			$F = 8.38$, d.f. 3, $P < 0.005$		
Washing away between zones	$F = 2.81$, d.f. 3, n.s.			$F = 54.83$, d.f. 3, $P < 0.001$		
(b) horizontal *v.* vertical						
Avicennia zone	0.447	2	n.s.	0.177	4	n.s.
Mixed zone	1.193	2	n.s.	–	–	–
Ceriops/Rhizophora zone	0.753	12	n.s.	0.61	10	n.s.
Clearcut zone	–	–	–	0	4	n.s.
Avicennia/Rhizophora/Sonneratia zone	1	6	n.s.	1	4	n.s.
Horizontal propagules between zones	$F = 5.81$, d.f. 3, $P < 0.01$			$F = 5.76$, d.f. 3, $P < 0.01$		
Vertical propagules between zones	$F = 1.3$, d.f. 3, n.s.			$F = 3.6$, d.f. 3, $P < 0.025$		

Table 2. Preliminary observations of the cumulative number of propagules predated by snails after 1, 2 and 3 days (Mida Creek)

Species	Unpeeled propagules (n = 33)			Peeled propagules (n = 33)		
	Day 1	Day 2	Day 3	Day 1	Day 2	Day 3
Rhizophora mucronata	0	3	4	6	6	6
Bruguiera gymnorrhiza	0	1	1	3	5	6
Ceriops tagal	0	0	0	1	4	6

can switch to the vertical planted ones. Between-zone differences are probably due to differences in predator abundance in each of the zones; in zones where propagule predators are abundant, significant differences between the predation of horizontal and vertical propagules would be less likely since high competition results in a quick clearing of the experimental plantation. This can also explain why in the undisturbed forest there is a significant difference in predation on horizontal propagules between the zones, due to different predator abundances, whereas there is none for the vertical propagules (Table 1*b*), because predators are not excessively abundant in the undisturbed forest or they have more background input (non-experimental) from stranding propagules. Although absence of specificity in feeding behaviour was observed before (Dahdouh-Guebas *et al.* 1997), the lack of significance for the differences on the predation among species in the present study may be due to the small sample sizes.

The dominance–predation hypothesis cannot be supported in the present study, since predation levels in forest plots where certain adult mangrove tree species are dominant are not significantly different from the predation levels in forest plots where the trees do not occur. McGuinness (1997) has come to similar conclusions when investigating seed predation in a northern Australian mangrove forest. One may assume that under natural conditions a sufficient number of tree juveniles escapes predation. However, in artificial regeneration plots predation is a serious threat. An alternative hypothesis to explain how mangrove trees could overcome high predation rates follows from a personal observation on *Ceriops tagal* in Gazi Bay. Observations of over 500 mature propagules per tree at one time suggest that in natural conditions this mangrove tree might saturate the crabs by dropping a large number of propagules in a short period. Hence, the saturation method is a possible way to protect artificial regeneration plots. In Sulawesi, although standard re-afforestation methods require less dense plantation (50-cm intervals) the people prefer dense plantation (25-cm intervals) of *Rhizophora mucronata* in order to saturate predators (Weinstock 1994). Knowledge about the zones in which predation is highest (this study), particularly in a disturbed forest which may need artificial regeneration, and about the abundances of crabs in the different zones (the subject of further studies) will improve the choice of location for artificial plantations and their survival.

In Mida Creek the difference between peeled and unpeeled propagules in degree of predation by snails might suggest a possible toxicity, unpalatability or presence of an antinutritional factor in the peel. However, further research is required to investigate an actual preference as was observed for crabs (Dahdouh-Guebas *et al.* 1997). Although this study is preliminary, it suggests that crabs may not be the only invertebrates preying on mangrove propagules in Kenya and affecting their survival.

The effect of predation on natural regeneration in Kenya cannot yet be ascertained. Understanding the links between the zonation of brachyuran predators and the zonation of the mangrove tree species is a necessary step in understanding their ecological interactions.

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