



An exploratory study on grapsid crab zonation in Kenyan mangroves

F. Dahdouh-Guebas^{1,*}, M. Verneirt¹, S. Cannicci², J.G. Kairo³, J.F. Tack⁴ & N. Koedam¹

¹Laboratory of General Botany and Nature Management, Mangrove Management Group, Vrije Universiteit Brussel (VUB), Pleinlaan 2, B-1050 Brussels, Belgium; ²Dipartimento di Biologia Animale e Genetica 'Leo Pardi', Università degli Studi di Firenze, Via Romana 17, I-50125 Firenze, Italia; ³Kenya Marine and Fisheries Research Institute, PO Box 81651, Mombasa, Kenya; ⁴Belgian Biodiversity Platform, c/o Institute of Nature Conservation, Kliniekstraat 25, B-1070 Brussels, Belgium; *Author for correspondence: Tel: +32 02 629 34 22, Fax: 34 13, E-mail: fdahdouh@vub.ac.be

Key words: crab, Detrended Correspondence Analysis, Grapsidae, Kenya, mangrove, zonation

Abstract

Despite earlier efforts to understand the role played by grapsid crabs in mangroves, their importance in the structuring and functioning of such systems is fully appreciated, particularly with regard to small-scale studies. The present study provides some new data on the interaction between mangroves and crabs, namely the link between the distribution of particular mangrove tree species and the distribution of certain crab species at the assemblage level. Floristic and faunistic relevés were made in Gazi Bay (2 sites) and Mida Creek (3 sites), 140 km apart on the Kenyan coast, along five transects in a series of quadrats covering the width of the mangrove belts. Zonation of both mangrove vegetation and brachyuran fauna was described and height above datum and distance to the mainland (limit of non-flooded area) measured. The relationship between the presence and the absence of crabs and trees was analysed using detrended correspondence analysis.

Summarized, the mangrove tree zonation pattern contains four assemblages with a particular dominant species: first a landward *Avicennia marina* zone, followed by a mixed zone with *Ceriops tagal*, *Rhizophora mucronata* and *Bruguiera gymnorhiza*, and finally a *R. mucronata* zone and a *Sonneratia alba* zone, both of which can mix with seaward *A. marina*. Ordination results show that the distribution of *Neosarmatium meinerti* and *Sesarma ortmanni* is linked to the landward *A. marina* zone, that of *Neosarmatium smithii*, *Sesarma guttatum* and *Sesarma leptosoma* corresponds to the *R. mucronata* zone and that of *Metopograpsus thukuhar* and *Sesarma elongatum* to the seaward *A. marina* and *S. alba* zone. There appears to be one major underlying factor in the zonation of both crabs and trees, with most likely a complex multiple causality. In certain cases the association between crabs and trees are causal, whereas in other cases it can be the result of an independent restriction to the same zones by a common cause.

Introduction

Descriptions of mangrove vegetation structure are available for many regions worldwide. In East-Africa Graham (1929), Walter and Steiner (1936), Kokwaro (1985), Ruwa and Polk (1986), Gallin et al. (1989), Ruwa (1990; 1993), Gang and Agatsiva (1992) and Van Speybroeck (1992) have investigated the vegetation or zonation pattern in mangrove forests. Most of these studies put a strong emphasis on the vegetation or plant cover alone. The study of vegetation structure

or assemblages on the other hand, provides data that are important in a broader ecological framework and can also include for instance faunistic aspects.

A variety of mangrove fauna has been identified as consumers of mangrove propagules, but decapods have been reported world-wide to influence their recruitment to a large extent (Smith, 1987a, 1987b; Smith et al., 1989; Osborne and Smith, 1990; Anon., 1991; Weinstock, 1994; McKee, 1995; McGuinness, 1997; Dahdouh-Guebas, 2001). For Kenya in particular, Dahdouh-Guebas et al. (1997, 1998, 1999) have

shown that grapsid crabs feed on mangrove propagules and can possibly be a threat to the early development of mangrove seedlings.

In the present study the aims are to describe the zonation of mangrove trees and grapsid crabs in two Kenyan coastal creek systems about 140 km apart, to emphasize the variability of mangrove tree zonation patterns between sites and to investigate whether the distribution of certain crab species is linked to the distribution of particular mangrove tree species. The term 'zonation' is defined here as banding of vegetation types with a certain, often monospecific, floristic composition. Hypotheses on the correlation between crabs and trees are discussed.

Materials and methods

Description of the sites studied

The study areas were located in Gazi Bay (4°26' S, 39°30' E) and Mida Creek (3°20' S, 40°00' E), two well studied water bodies along the 570 km long Kenyan coast (Figure 1). Gazi Bay is an open creek located about 40 km South of Mombasa and fed by two seasonal rivers. Mida Creek, a creek with a narrow opening towards the ocean, is situated about 100 km North of Mombasa. Unlike Gazi Bay, Mida Creek has no overland freshwater input, but benefits from a high groundwater outflow (Tack and Polk, 1999).

All nine East-African mangrove species *sensu* Tomlinson (1986), as well as *Xylocarpus molluccensis* (Lamk.) Roem., occur along the Kenyan coast. In Gazi Bay two study sites were sampled, 'Gazi Covered' and 'Gazi Cleared', which correspond to two different forest types. The 'Covered' type is a natural, relatively undisturbed forest, whereas the 'Cleared' type is a forest with many marks of exploitation (Figure 1). In Mida Creek, the specific sites 'Mida', 'Sita' and 'Dabaso' were investigated (Figure 1). All study sites were chosen from aerial photographs in order to ascertain a fringing forest type (following Lugo and Snedaker, 1974) and to be representative for the wider area.

Methodology

All fieldwork was carried out between July and September 1993. Line transects were drawn down the slope covering the entire width of the mangrove belt in order to investigate the zonation of the mangrove

Table 1. Scale used to estimate the abundance of crab species based on *both* the frequency of individuals and burrows (see Figure 2). The 6 combinations were found to be realistic in the field.

Coefficient	individual frequency (m ⁻²)	burrow frequency (m ⁻²)
0	none	none
1	1 individual	none
2	< 10 individuals	none
3	> 10 individuals	< 10 burrows
4	> 10 individuals	10–20 burrows
5	> 10 individuals	> 20 burrows

trees and crabs. The line transects consisted of a sequence of evenly spread, but non-connected quadrats of 5 × 5 m with in-between spaces of 1 to 15 m depending on the length of the transect. The mangrove vegetation in each quadrat was described by means of the relevé method of Braun-Blanquet (Westhoff and Van der Maarel, 1978; Van der Maarel, 1979), which describes the vegetation according to number and/or coverage degree of species for four different vegetation layers. In the same quadrat crabs were sampled according to a similar method using the ordinal scale from 0 to 5 (Table 1), which is known to generate reliable population estimates (Frith and Frith, 1977; Frith and Brunenmeister, 1980; Macintosh, 1988; Bosire et al., 1999). The crabs considered were predominantly herbivorous species only (Dahdouh-Guebas et al., 1999), which are able to interfere with natural regeneration of mangroves. However, *Metopograpsus oceanicus* Jacquinot was omitted from the investigation because of its rarity in all sites and *Cardisoma carnifex* (Herbst) was not investigated. Occasional visual observations on the behaviour of the crabs were recorded to help formulating hypotheses on the causalities of their distribution. The 'phyto-' and 'zoosociological' sampling was augmented with the distance to the mainland (i.e. limit non-flooded area) and the local topography. The latter was measured by means of the line method of Dawes (1981), whereby the height above datum of a given high tide was taken as a reference. These topographic measurements were made on all sites within 24 hours. An observed tidal range within Mida Creek of more than 2.5 m, as compared to the reported 3.5 m outside the creek (Spalding et al., 1997), indicates that height differences between actual tidal amplitude and tide table predictions, known to

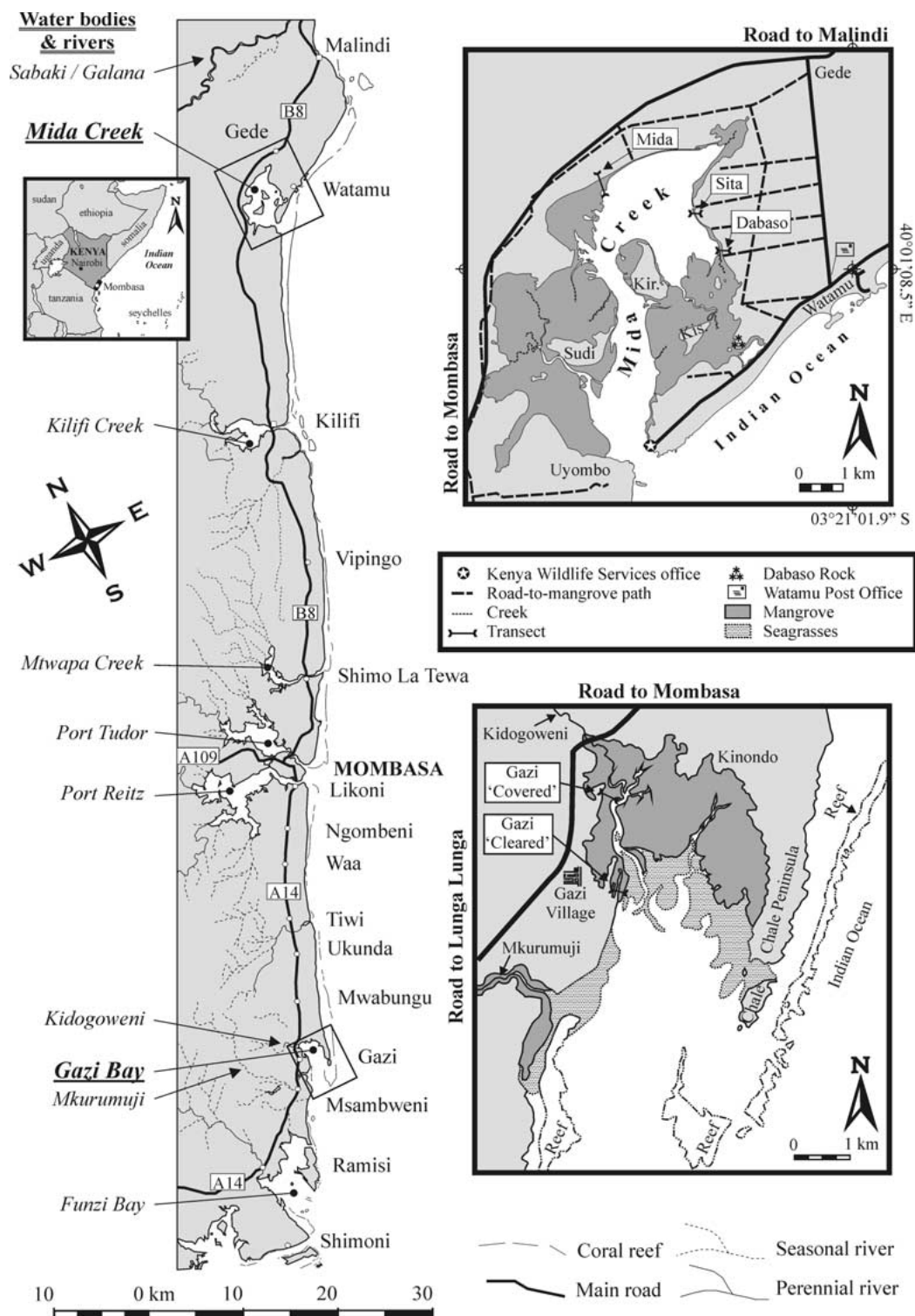


Figure 1. Map of the Kenyan coast showing details of the study areas Gazi Bay and Mida Creek (adapted from Dahdouh-Guebas et al., 2000), and the location of the specific study sites (transects). On the Mida Creek map: Kir. = Kirepwe, Kis. = Kisiwani.

Table 2. Comparison of the adult vegetation type of different transects between quadrats with a similar height above datum.

'Height above datum'-range	Adult vegetation in				
	Gazi 'Covered'	Gazi 'Cleared'	Mida	Dabaso	Sita
2.60 – 3.10 m	<i>C. tag.</i> + <i>B. gym.</i> + <i>X. gra.</i> + <i>A. mar</i>	<i>A. mar</i>	<i>A. mar.</i>	<i>A. mar</i>	<i>C. tag</i> + <i>A. mar</i> + <i>R. muc</i>
2.10 – 2.60 m	<i>C. tag.</i> + <i>B. gym.</i> + <i>R. muc.</i> + <i>A. mar</i>	<i>R. muc</i>	<i>A. mar</i>	<i>C. tag.</i> + <i>R. muc.</i>	no quadrat of similar height
1.50 – 2.00 m	<i>A. mar.</i> + <i>R. muc</i>	<i>R. muc</i> + <i>C. tag</i>	<i>A. mar</i> + <i>R. muc</i>	<i>R. muc</i>	<i>S. alb</i>

A. mar = *Avicennia marina*, *B. gym* = *Bruguiera gymnorrhiza*, *C. tag* = *Ceriops tagal*, *R. muc* = *Rhizophora mucronata*, *S. alb* = *Sonneratia alba*, *X. gra* = *Xylocarpus granatum*.

occur in some enclosed and shallow bay systems such as this one, were minimal.

The floristic and faunistic relevés were graphically fitted to the topographic measurements. The association between the presence or absence of each of the mangrove crabs and tree species was investigated using Detrended Correspondence Analysis (Hill and Gauch, 1980) using PC ORD for Windows (McCune and Mefford, 1997).

Results

The variability in mangrove zonation between the sites can be observed (Figure 2). Height above datum does not correspond with a certain mangrove assemblage (e.g. cf. *Rhizophora mucronata* Lamk. between Gazi 'Covered' and Mida, and *Avicennia marina* (Forsk.) Vierh. between all sites, Figure 2 and Table 2).

A synthesis of the zonation in our sites (Figure 2) would comprise four zones, each having a dominant species. The first and landward zone has *Avicennia marina* as a dominant species, occasionally mixed with *Heritiera littoralis* Dryand, *Bruguiera gymnorrhiza* (L.) Lamk. or *Ceriops tagal* (Perr.) C.B. Rob. The second zone is a mixed zone in which *Ceriops tagal* is always found to be present, but not necessarily as the dominant species. It is often mixed with *Rhizophora mucronata* and *Bruguiera gymnorrhiza*, with an occasional presence of *Xylocarpus granatum* König. The third zone is a *Rhizophora mucronata* zone, which is often monospecific, but which can be mixed with *Avicennia marina*. Sometimes *Ceriops tagal* thrives in the understorey of this zone (Figure 2d). The last and most seaward zone has *Sonneratia alba* J. Smith as the dominant species, but like the former zone, it is found to mix with *Avicennia marina*, which occurs in very different environments along the slope. As is

expected in the natural environment, the boundaries of these zones are not distinct but gradual.

Neosarmatium meinerti De Man and *Sesarma ortmanni* Crosnier are always restricted to the landward (*Avicennia*) zone and were observed in Mida, Gazi 'Covered' and Gazi 'Cleared' outside the range of the transect as a resident of the herbaceous vegetation on sandy substrate.

The ordination plot is shown in Figure 3 and the eigenvalues are 0.855, 0.369 and 0.169 for the first, second and third axis respectively. The variation explained by these first three axes are 55.0%, 8.9% and 0.6% respectively. Although field data were introduced as independent data, the general zonation pattern of mangrove trees and crabs can be clearly discerned as three clusters, typical for the lower-, mid- and upper-intertidal respectively.

As can be observed from the clusters within the ordination graph (Figure 3), the species scores (hereafter 'SS') of *Sesarma ortmanni* and *Heritiera littoralis* are within the same range according to the first axis (779–914), and the same is true for those of *Neosarmatium meinerti* (SS = 682) and the landward *Avicennia marina* fringe (SS = 623). *Bruguiera gymnorrhiza* (SS = 534) and *Ceriops tagal* (SS = 526) were not associated to any particular crab species. *Neosarmatium smithii* H. Milne-Edwards (SS = 327) was observed near *Rhizophora mucronata* trees (SS = 362), either in monospecific or mixed stands. *Sesarma guttatum* A. Milne-Edwards (SS = 400) was present in all sites and mostly over a wide range. However, like *N. smithii*, it seems to be associated with the *Rhizophora* zone. *Sesarma leptosoma* Hilgendorf (SS = 348) was found less frequently and over a slightly smaller range than *S. guttatum*, but nevertheless in the same forest zones. *Sesarma leptosoma* was observed to climb the canopies of *Rhizophora mucronata* only. Also the crab

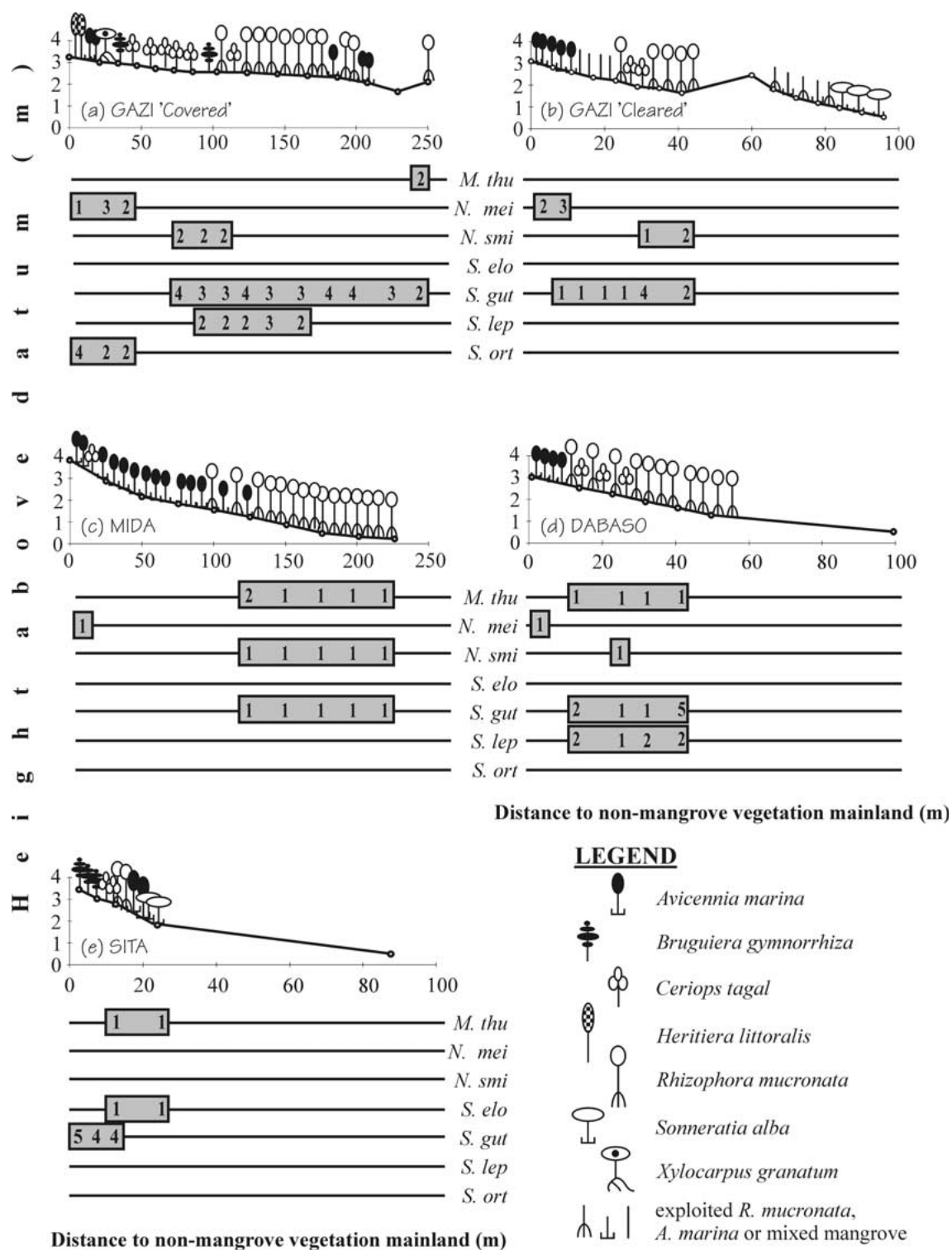


Figure 2. Topographic levels and schematic of the adult mangrove vegetation at the five study sites along the Kenyan coast. The distribution of the crabs along the transects is represented by the boxes on the lines, and the abundance values, based on both the number of individuals and the number of burrows (combinations as in table 1), are indicated within the boxes. *M. thu* = *Metopograpsus thukuhar*, *N. mei* = *Neosarmatium meinerti*, *N. smi* = *Neosarmatium smithii*, *S. gut* = *Sesarma guttatum*, *S. ort* = *Sesarma ortmanni*, *S. lep* = *Sesarma leptosoma* and *S. elo* = *Sesarma elongatum*.

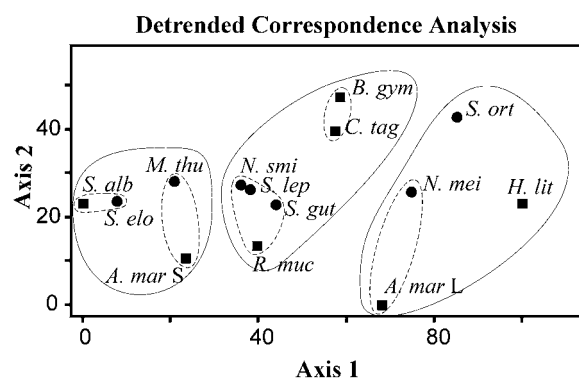


Figure 3. Results from the indirect species ordination (DCA) of the following presence/absence data in 43 sample points. The graph is scaled proportionate to the longest axis (% of maximum). Polygons, based on species scores (SS) with respect to the first axis, represent various degrees of species associations based on species scores, and were added to ease the visual interpretation (dashed lines represent higher degrees of association than full lines; see text for SS-details). Tree species (squares): *A. mar* = *Avicennia marina* (L = landward zone; S = seaward zone), *B. gym* = *Bruguiera gymnorhiza*, *C. tag* = *Ceriops tagal*, *H. lit* = *Heritiera littoralis*, *R. muc* = *Rhizophora mucronata*, *S. alb* = *Sonneratia alba*; Crab species (circles): abbreviations as in Figure 2.

Metopograpsus thukuhar (Owen) (SS = 190) was observed less frequently and *Sesarma elongatum* (SS = 69) was only observed in Sita, both of them near creeklets. However, near Dabaso these species were common in the *Rhizophora* zone fringing the creeks. *Avicennia marina* is present again as a seaward zone (SS = 214), which illustrates the disjunct zonation pattern of this species, together with other typical frontal mangrove species such as *Sonneratia alba* (SS = 0). Only the distribution of *Neosarmatium meinerti* correlated consistently with a restricted height above datum range (approx. 3 m and above).

Discussion

The schematic site description and the vegetation data (Figure 2) confirm the general zonation pattern of mangroves that exists along the Kenyan coast (Walter and Steiner, 1936; Gallin et al., 1989). However, a new observation with respect to the species assemblages, of less importance here but of major importance in sustainable mangrove management and restoration frameworks, is the presence of *Ceriops tagal* in the understorey of some *Rhizophora mucronata* dominated vegetation patches (cf. Kairo 2001). The importance lies in the fact that *R. mucronata* is a preferred species

for house construction in Kenya (Dahdouh-Guebas et al., 2000), and that this exploited species is therefore not necessarily the species that will regenerate.

Despite the common zonation, its variability can be striking and earlier hypotheses that the height above datum is the determining factor in mangrove zonation (Walter and Steiner, 1936; Clarke and Hannon, 1970) or that tree species position along such a topographic gradient is a useful predictive tool (Watson, 1928) must be limited to their indicative value. Different floristic compositions in quadrats with a similar height above datum (Table 2), together with emersion curves for Kilindini (Mombasa) as published by Brakel (1982), show that some mangrove species can survive in areas with very different emersion times (differences of 6 to 12 hours per tidal cycle within *A. marina*, *C. tagal* and *R. mucronata*), and display disjunct zonation patterns with striking morphometric differences (e.g. *A. marina* in Gazi 'Covered'; Dahdouh-Guebas et al., submitted).

Similarly, the zonation of herbivorous crabs does not seem to be correlated with height above datum either. This is particularly well illustrated by the distribution of *Sesarma guttatum* and *Metopograpsus thukuhar*. The occurrence of the former varies from the landward zone (Sita), over the middle zone (Gazi 'Cleared') to the more seaward zones (Gazi 'Covered' and Mida). In Gazi 'Covered', Sita and Dabaso, the abundance of *S. guttatum* does not increase or decrease gradually but instead jumps from many individuals and many burrows (coefficient 5, Figure 2) to no individuals and no burrows (coefficient 0, Figure 2). *Sesarma leptosoma* displays a true mangrove tree-dependence and has a typical vertical migrating behaviour – almost exclusively on *Rhizophora mucronata* – allowing them to feed on fresh leaves and water (Vannini and Ruwa, 1994; Cannicci et al., 1996a, 1996b; Vannini et al., 1997; personal observation). The presence of the same crab species in *Ceriops tagal* and *Rhizophora mucronata* zones, as suggested in general for Kenyan mangroves by Ruwa (1997), must be rejected based on the results of this study.

The results from the ordination (Figure 3) show that there is one main first axis explaining 55% of the variability, indicating that there is one main factor responsible or that a complex of factors exist for the observed distribution of tree and crab species. Mangrove tree species zonation has been correlated with different biotic and abiotic factors such as physiological adaptations to salinity and frequency of tidal inundation, tidal flow and geomorphology, nutrient availability,

salinity of the soil (Naidoo, 1985), soil sulphide and redox levels (Hart, 1959; McKee, 1993; Matthijs et al., 1999), competition between species (Clarke and Myerscough, 1993), tidal sorting of propagules (Clarke, 1993; Clarke and Myerscough, 1993), light availability to seedlings, and predation of seedlings (Dahdouh-Guebas et al., 1998; Dahdouh-Guebas, 2001), many of which are reviewed in more detail in Smith (1992). Clearly none of these hypotheses can be expected to adequately and solely account for the observed species distribution and it is increasingly clear that mangrove zonation is the result of a complex interaction between different biotic and abiotic environmental factors.

A causal relationship could be as a source of food for the crabs, whether direct or through mangrove-consuming intermediates, as a source of protection among the mangrove root complex, as differentially beneficial conditions created by the root complex, such as oxygen conditions in the soil, soil compaction and consolidation, or, crabs and trees might simply require similar environmental conditions, such as physico-chemical, tidal or edaphic conditions, restricting them to the same zones independently by a common cause. The results from the height above datum of species and the ordination results from our five sites (Figure 3) suggest that the distribution of the crab species correlates better with the mangrove tree species or assemblage present rather than with the height above datum, unlike Icely and Jones (1978) suggested for *Uca* species. However, on-going research by Ballerini et al. (2000) and Cannicci et al. (2000) reports no differential distribution in relation to mangrove tree species for sersarmid crabs within Mida Creek and suggests multivariate analysis to untangle the environmental factors such as temperature, salinity and soil granulometry that govern distribution of mangrove crabs.

The present study raises the question whether crabs influence the establishment of certain mangrove tree species. A dominance-predation hypothesis was proposed by Smith (1987b), who found an inverse relationship between seed predation and the dominance of a tree species in mangrove forest canopies. Although the above model was not supported for mangroves in Gazi Bay (Dahdouh-Guebas et al., 1997), crabs and other propagule predators might still contribute to the establishment of the vegetation structure, rather than the zonation, of mangroves. Especially in mixed zones, but sometimes even in zones where one species is dominant, succession and future vegetation structure depends on the abundance and diversity of species:

the species composition (and the dominance) in such a zone before and after a disturbance is not necessarily the same, but depends on the growing performance of the individuals in the understorey and their competitive capacity (Dahdouh-Guebas, 2001; Kairo, 2001). The investigation of a relationship between propagule predators and trees in mangroves in our opinion therefore necessitates an emphasis on the mixed nature or the assemblage where present, rather than the dominant species (cf. Walter and Steiner, 1936; Macnae, 1966).

Acknowledgements

We would like to thank Prof. Dr P. Polk (VUB) and Prof. Dr M. Vannini (Università degli Studi di Firenze) for support, Dr E. Okemwa (Kenya Marine and Fisheries Research Institute) and Mrs. Y. Vermeulen (Kenya Belgium Project in Marine Sciences) for logistics in Kenya, and Mr. Francis Ayimba for field assistance. A lot of gratitude is due to all the local people, in particular family Ba'alawy from Gazi for being such a fine host family. The first author is a Postdoctoral Researcher from the Fund for Scientific Research (FWO – Flanders). The research was also financed by the Fund for Collective Fundamental Research (FKFO) and with a specialisation fellowship of the Institute for the Promotion of Innovation by Science and Technology in Flanders (IWT).

References

- Ballerini, T., Macia, A. and Cannicci, S. 2000. Zonation of mangrove crabs at Inhaca Island (Mozambique): a new hypothesis. Abstract Volume of the Meeting on Mangrove Macrobenthos, 7–11 September, Mombasa, Kenya. pp. 9–10.
- Bosire, J., Dahdouh-Guebas, F., Kairo, J.G. and Koedam, N. 1999. Faunal and floral secondary succession in a restored mangrove system in Kenya. Personal communication on the 15th Biennial International Conference of the Estuarine Research Foundation 'Where THE River Meets the Sea', 25–30 Sept., New Orleans, U.S.A. (also submitted).
- Brakel, W.H. 1982. Tidal patterns on the East African coast and their implications for the littoral biota. Proceedings of the Symposium on the Coastal and Marine Environment of the Red Sea, Gulf of Aden and Tropical Western Indian Ocean 2: pp. 403–418.
- Cannicci, S., Skov, M.W. and Vannini, M. 2000. The influence of abiotic and biotic factors on the distribution of mangrove crabs at Mida Creek (Kenya): a multivariate approach. Abstract Volume of the Meeting on Mangrove Macrobenthos, 7–11 September, Mombasa, Kenya: pp. 20–21.
- Cannicci, S., Ritossa, S., Ruwa, R.K. and Vannini, M. 1996a. Tree fidelity and hole fidelity in the tree crab *Sesarma leptosoma*. J. Exp. Mar. Biol. Ecol. 196(1–2): 299–311.

- Cannicci, S., Ruwa, R.K., Ritossa, S. and Vannini, M. 1996b. Branch fidelity in the tree crab *Sesarma leptosoma*. J. Zool. 238(4): 795–801.
- Clarke, L.D. 1993. Dispersal of grey mangrove (*Avicennia marina*) propagules in south-eastern Australia. Aquat. Bot. 45: 195–204.
- Clarke, L.D. and Hannon, N.J. 1970. The mangrove swamp and salt marsh communities of the Sydney district. III. Plant growth in relation to salinity and waterlogging. J. Ecol. 58: 351–369.
- Clarke, L.D. and Myerscough, P.J. 1993. The intertidal distribution of the grey mangrove (*Avicennia marina*) in south-eastern Australia: the effects of physical conditions, interspecific competition and predation on propagule establishment and survival. Aust. J. Ecol. 18: 307–315.
- Dahdouh-Guebas, F. 2001. Mangrove Vegetation Structure Dynamics and Regeneration. PhD dissertation, Vrije Universiteit Brussel, Brussels, Belgium, 317 pp.
- Dahdouh-Guebas, F., Mathenge, C., Kairo, J.G. and Koedam, N. 2000. Exploitation of mangrove wood products from a subsistence perspective: a case-study in Mida Creek, Kenya. Economic Bot. 54(4): 513–527.
- Dahdouh-Guebas, F., Verneirt, M., Tack, J.F. and Koedam, N. 1997. Food preferences of *Neosarmatium meinerti* de Man (Decapoda: Sesarminae) and its possible effect on the regeneration of mangroves. Hydrobiologia 347: 83–89.
- Dahdouh-Guebas, F., Giuggioli, M., Oluoch, A., Vannini, M. and Cannicci, S. 1999. Feeding habits of non-ocypodid crabs from two mangrove forests in Kenya. Bull. Mar. Sci. 64(2): 291–297.
- Dahdouh-Guebas, F., Verneirt, M., Tack, J.F., Van Speybroeck, D. and Koedam, N. 1998. Propagule predators in Kenyan mangroves and their possible effect on regeneration. Mar. Freshw. Res. 49(4): 345–350.
- Dahdouh-Guebas, F., De Bondt, R., Abeysinghe, P., Kairo, J.G., Triest, L. and Koedam, N. 1999. Ecologic-comparative study of the disjunct zonation pattern of *Avicennia marina* (Forsk.) Vierh. in Gazi Bay (Kenya). Personal communication on the 15th Biennial International Conference of the Estuarine Research Foundation 'Where THE River Meets the Sea', 25–30 September 1999, New Orleans, U.S.A. (also submitted).
- Dawes, C.J. 1981. Marine Botany. John Wiley and sons, New York, USA.
- Frith, D. W. and C. B. Frith. 1977. Observations on fiddler crabs (Ocypodidae: Genus *Uca*) on Surin Island, Western Peninsular, Thailand, with special reference to *Uca tetragonon* (Herbst). Phuket Mar. biol. C. Res. Bull. 18: 1–14.
- Frith, D.W. and Brunenmeister, S. 1980. Ecological and population studies of fiddler crabs (Ocypodidae: Genus *Uca*) on a mangrove shore at Phuket Island, Western Peninsular, Thailand. Crustacea 39(2): 157–189.
- Frusher, S.D., Giddins, R.L. and Smith, T.J. III. 1994. Distribution and abundance of grapsid crabs (Grapsidae) in a mangrove estuary: effects of sediment characteristics, salinity tolerances, and osmoregulatory ability. Estuaries 17(3): 647–654.
- Gallin, E., Coppejans, E. and Beeckman, H. 1989. The mangrove vegetation of Gazi bay (Kenya). Bulletin de la Société Royale Botanique de Belgique 122: 197–207.
- Graham, R.M. 1929. Notes on the mangrove swamps of Kenya. J. East Afr. Nat. Hist. Soc. 36: 157–165.
- Hart, M.G.R. 1959. Sulphur oxidation in tidal mangrove soils. Plant & Soil 11(3): 215–236.
- Hill, M.O. and Gauch, H.G. 1980. Detrended correspondence analysis: an improved ordination technique. Vegetatio 42: 47–58.
- Icelly, J.D. and Jones, D.A. 1978. Factors affecting the distribution of the Genus *Uca* (Crustacea: Ocypodidae) on an East African shore. Est. Coast. Mar. Sci. 6: 315–325.
- Kairo, J.G. 2001. Ecology and Restoration of Mangrove Systems in Kenya. PhD dissertation, Vrije Universiteit Brussel, Brussels, Belgium, 110 pp.
- Kokwaro, J.O. 1985. The distribution and economic importance of the mangrove forests of Kenya. J. East Afr. Nat. Hist. Soc. Nat. Museum 75(188): 1–10.
- Lugo, A.E. and Snedaker, S.C. 1974. The ecology of mangroves. Ann. Rev. Ecol. Syst. 5: 39–64.
- Macintosh, D.J. 1988. The ecology and physiology of decapods of mangrove swamps. Symp. Zool. Soc. London 59: 315–341.
- Macnae, W. 1966. Mangroves in Eastern and Southern Australia. Aust. J. Bot. 14(1): 67–104.
- Malley, D.F. 1978. Degradation of mangrove leaf litter by the tropical sesarimid crab *Chiromanthes onychophorum*. Mar. Biol. 49: 377–386.
- Matthijs, S., Tack, J., Van Speybroeck, D. and Koedam, N. Mangrove species zonation and soil redox state, sulphide concentration and salinity in Gazi Bay (Kenya), a preliminary study. Mang. Salt Marsh. 3: 243–249.
- McCune, B. and Mefford, M.J. 1997. Multivariate Analysis of Ecological Data. Version 3.09. MjM Software, Gleneden Beach, Oregon, U.S.A.
- McGuinness, K.A. 1997. Seed predation in a tropical mangrove forest: a test of the dominance-predation model in northern Australia. J. Trop. Ecol. 13: 293–302.
- McKee, K.L. 1993. Soil physiochemical patterns and mangrove species distribution – reciprocal effects ? J. Ecol. 81: 477–487.
- McKee, K.L. 1995. Mangrove species distribution and propagule predation in Belize: an exception to the dominance-predation hypothesis. Biotropica 27(3): 334–345.
- Micheli, F. 1993. Feeding ecology of mangrove crabs in North Eastern Australia: mangrove litter consumption by *Sesarma messa* and *Sesarma smithii*. J. Exp. Mar. Biol. Ecol. 171: 165–186.
- Naidoo, G. 1985. Effects of waterlogging and salinity on plant – water relations and on the accumulation of solutes in three mangrove species. Aquat. Bot. 22: 133–143.
- Osborne, K. and Smith, T.J. III. 1990. Differential predation on mangrove propagules in open and closed canopy forest habitats. Vegetatio 89: 1–6.
- Ruwa, R.K. 1990. The effects of habitat complexities created by mangroves on macrofaunal composition in brackish water intertidal zones on the Kenyan coast. Disc. Innov. 2(1): 49–55.
- Ruwa, R.K. 1993. Zonation and distribution of creek and fringe mangroves on the semi-arid Kenyan coast. In: Lieth, H. and Al Masoom, A.A. (eds.), Towards the Rational Use of High Salinity Tolerant Plants. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Ruwa, R.K. 1997. Zonation of burrowing crabs in the mangroves of the east coast of Kenya. In: Kjerfve, B., de Lacerda, L.D. and Diop, E.H.S. (eds.), Mangrove Ecosystem Studies in Latin America and Africa, pp. 316–324. UNESCO, Paris, France.
- Ruwa, R.K. and Polk, P. 1986. Additional information on mangrove distribution in Kenya: some observations and remarks. Kenya J. Sci. Ser. B7(2): 41–45.
- Slim, F.J. 1993. Interlinkages between Eastern-African coastal ecosystems workshop, Zanzibar, Tanzania, 4 p.
- Smith III, T.J. 1987a. Effects of seed predators and light level on the distribution of *Avicennia marina* Forsk. in tropical tidal forests. Est. Coast. Shelf Sci. 25(1): 43–52.
- Smith III, T.J. 1987b. Seed predation in relation to tree dominance and distribution in mangrove forests. Ecology 68(2): 266–273.
- Smith III, T.J., Chan, H.T., McIvor, C.C. and Robblee, M.B. 1989. Comparisons of seed predation in tropical, tidal forests from three continents. Ecology 70(1): 146–151.

- Smith III, T.J. 1992. Forest structure. *In*: Robertson, A.I. and Alongi, D.M. (eds.), Tropical Mangrove Ecosystems. pp. 101–136. Washington D.C., USA.
- Spalding, M., Blasco, F. and Field, C. 1997. World Mangrove Atlas. The International Society for Mangrove Ecosystems, Okinawa, Japan. 178 pp.
- Tack, J.F. and Polk, P. 1999. Tropical catchments, their interaction with the coastal zone. *In*: Harper, D. and Brown, T. (eds.), Sustainable Management in Tropical Catchments. John Wiley and Sons Ltd., London, UK.
- Tomlinson, P.B. 1986. The Botany of Mangroves. Cambridge University Press, Cambridge, UK. 419 pp.
- Van der Maarel, E. 1979. Transformations of cover-abundance values in phytosociology and its effects on community similarity. *Vegetatio* 39: 97–114.
- Vannini, M. and Ruwa, R.K. 1994. Vertical migrations in the tree crab *Sesarma leptosoma* (Decapoda, Grapsidae). *Mar. Biol.* 118: 271–278.
- Vannini, M., Oluoch, A. and Ruwa, R.K. 1997. Tree-climbing decapods of Kenyan mangroves. *In*: Kjerfve, B., de Lacerda, L.D. and Diop, E.H.S. (eds.), Mangrove Ecosystem Studies in Latin America and Africa. pp. 325–338. UNESCO, Paris, France.
- Van Speybroeck, D. 1992. Regeneration strategy of mangroves along the Kenyan coast. *Hydrobiologia* 247: 243–251.
- Walter, H. and Steiner, M. 1936. Die Ökologie der Ost-Afrikanischen Mangroven. *Zeitschr. f. Botanik* 30: 65–193.
- Watson, J.G. 1928. Mangrove forests of the Malay Peninsula. *Malayan Forest Rec.* 6: 1–275.
- Weinstock, J.A. 1994. *Rhizophora* mangrove agroforestry. *Econ. Bot.* 48(2): 210–213.
- Westhoff, V. and Van der Maarel, E. 1978. The Braun-Blanquet approach. *In*: Whittaker, R.H. (ed.), Classification of Plant Communities. pp. 287–399. W. Junk Publishers, The Hague.

