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Mangrove species zonation and soil redox state, sulphide concentration and salinity in Gazi Bay (Kenya), a preliminary study

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Abstract

The relationship between soil redox state, sulphide concentration, salinity and spatial patterns of mangrove species distribution was investigated in the mangrove forest of Gazi Bay (Kenya). Field measurements were conducted to examine the relationship between species distribution along a band transect of 280 m and soil redox potential (Eh) and sulphide patterns, as well as the indirectly related (through flooding regimes) soil salinity. Of the three major species *Avicennia marina*, *Ceriops tagal* and *Rhizophora mucronata* present along the transect, only the distribution of the latter correlated with the measured soil variables, *R. mucronata* being absent from the less-reduced zone with high salinity. *Bruguiera gymnorhiza* and *Heritiera littoralis* occur in minor populations, they are restricted to the saline, sulphide-poor and less-reduced substrates. From the results it is concluded that soil redox potential (Eh), sulphide concentration and salinity may contribute to structure mangroves through the distribution of dominant species, however in combination with other environmental conditions and processes of vegetation dynamics.

Introduction

Zonation of mangrove species is a striking aspect of many mangroves. This spatial distribution is also observed in Kenya (East Africa), though it is not universal. The possible causes of the zonation pattern and of spatial distribution in general have been debated extensively in the literature (MacNae, 1968; Chapman, 1976; Snedaker, 1982; Tomlinson, 1986) and different causes have been hypothesized. In the Kenyan mangroves, *Sonneratia alba* Sm. often forms a rather narrow strip at the seaward forest margin, followed by pure or mixed stands of *Rhizophora mucronata* Lam. and *Avicennia marina* Forsk. Vierh., then followed by pure or mixed stands of *Ceriops tagal* (Perr.) C.B.Robinson and *A. marina*. *Bruguiera gymnorhiza* (L.) Lam. does not form a distinct zone but occurs scattered within *Avicennia*, *Rhizophora* and *Ceriops* stands. *Lumnitzera racemosa* Willd. occurs usually as a small, interrupted fringe, beyond the higher *A. marina* zone, but it is also encountered within this zone. *Xylocarpus granatum* Koen. and *Heritiera littoralis* Dryand. in Ailon occur in a more localised distribution and do not commonly contribute to the zonation pattern (Graham 1929; Walter and Steiner, 1936; Gallin et al., 1989; Beeckman et al., 1990; Ruwa, 1990; Van Speybroeck, 1992).

The hypothesis that different tolerance to flooded conditions may contribute to spatial patterns (McKee, 1993; Youssef and Saenger, 1996, 1998) has not been investigated physio-ecologically in the Kenyan mangroves, but it was suggested for this area from distribution patterns given in Beeckman et al., (1990). Waterlogging results in the virtual exclusion of free oxygen from the soil which becomes anoxic with an accompanying modification of soil-chemical processes. These effects include the production of various potentially toxic substances, such as sulphide. Thus, the growth of mangrove in a reduced soil depends not only on the capacity of the plant to maintain aerobic metabolism in its roots (which may in turn affect soil aeration status (McKee, 1993)), but also on mechanisms for detoxifying or adapting to soil phytotoxins.

The objective of this study was to investigate whether the soil redox state (Eh) and the soil sulphide concentration may cause or contribute to mangrove zonation in Kenya. Field measurements were conducted to examine whether Eh and sulphide concentration correlate with the presence or absence of particular mangrove species, as was observed for several mangrove species in a neotropical system (McKee, 1993).

Methods

Study site

Location

The study site is located in the mangrove forest of Gazi Bay (Kenya: 4° 25′ S, 39° 50′ E). The site is part of a more intensively studied part of the forest (Kairo, 1993; Dahdouh-Guebas, 1994; Verneirt, 1994; De Bondt, 1995; Middelburg, et al., 1996) of the well-studied Gazi Bay (Vanhove, 1990; Beeckman et al., 1990; Slim et al., 1996; Dahdouh-Guebas et al., 1997). The entire mangrove forest in the bay has an area of 6.61 km^2 (Middelburg and Hemminga, 1995) with a maximum width of 3.3 km (map 1).

Climate

The rainfall pattern is bimodal with a mean annual total of 1408 mm for Gazi (average for 1990–1995, for Gazi averages of longer periods are not available). The Southeast monsoon (April–October) brings the major rains which fall from April to June, with a peak in May. Most of the annual precipitation is received in this period. The minor rain period is from October to December (with a peak in November), mainly during the Northeast monsoon (November–March). The annual average of atmospheric temperature at Mombasa (50 km North) is around 27 °C and fairly even over the year. A full climate diagram of Mombasa may be found in Walter and Lieth (1967).

Field measurement

Field work was carried out in January and February 1995, corresponding to the dry season. A 280 m band transect, which ran from the coconut plantation–mangrove forest interface into the mangroves towards the border of the mangrove vegetation, was established perpendicular to the creek. Following the emersion curves for Kilindini (Mombasa), according to Brakel (1982), the upper part of this transect would approximately be emersed 10–12 h per tidal cycle, the lower part 4–6 h per tidal cycle. Quadrats of 5 m by 5 m with 5 m intervals were outlined. In each quadrat the vegetation was described (species cover and abundance) according to the adapted Braun-Blanquet method (Van Speybroeck, 1992) in order to determine species distribution along the transect. Seedling density was recorded separately in each quadrat. The seedling category was taken to comprise all plants shorter than 1 m. Herbaceous plants are absent from this mangrove area. Nomenclature of mangrove species is according to Tomlinson (1986), except for *Bruguiera gymnorhiza*.

The soil level elevation above datum in cm was measured at several points along the transect with a theodolite. Soil Eh and sulphide concentration were measured *in situ* in the respective quadrats at 10 cm depth during exposure to the atmosphere of the soil at low tide. Eh was measured after equilibration for 1 h with a platinum–Ag/AgCl redox electrode connected to a pH/mV/T meter (P 601, Eijkelkamp, Agrisearch Equipment). The same instrument with a sulphide electrode (Elit 225) and a double junction reference electrode (Schott-Geräte) was used for soil sulphide determinations. The sulphide reading was taken when the measurement was stable (after a few minutes). Interstitial water was collected with a slightly modified *in situ* interstitial water sampler as described in McKee et al., (1988). This simple apparatus consisted of a narrow diameter (3 mm) plastic tube, which was sealed at the lower end, connected to a 50-ml capacity syringe. The plastic tube was, starting from the lower end, perforated over a length of 10 cm by 20–30 small holes. The holes were covered with three layers of a 149 μm meshed nylon gauze to prevent the entering of sediment. The plastic tube was inserted slowly into the soil to a depth of 13 cm and suction was applied by the 50-ml syringe. In sandy soils the collection of 50 ml sample was fast (5 min), in muddy soils it could take up to half an hour. Sediment and air were expelled from the sample by a 3-way valve, inserted between the collection tube and the syringe. The first 10–20 ml of each sample were discarded through the 3-way valve. The pH of the interstitial water was measured with a glass Ag/AgCl pH electrode (Schott-Geräte) connected to the same pH/mV/T meter. The NaCl content was determined with a refractometer (Atago S-10). Both pH and salinity of the intersti-

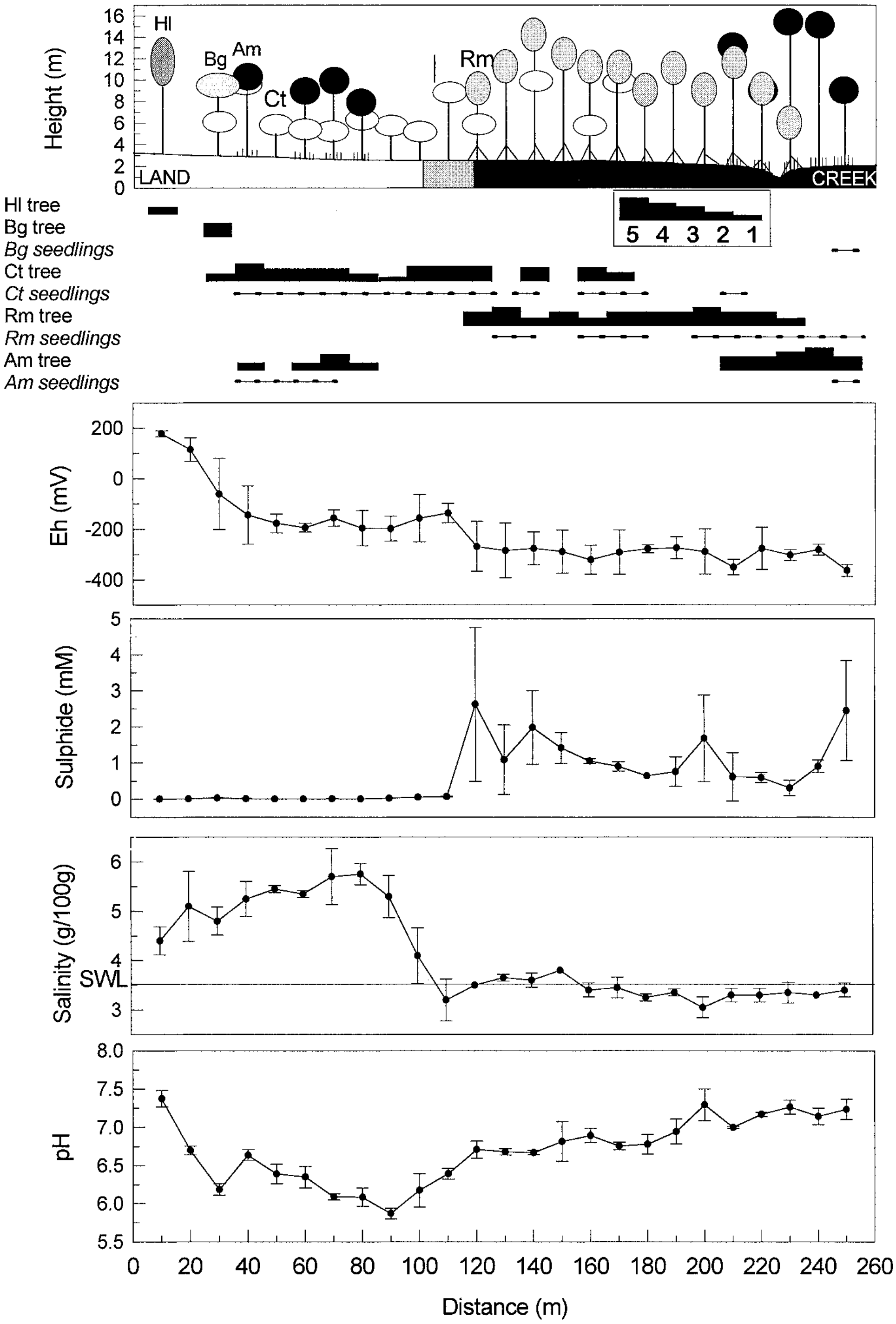


Figure 1. Distribution of the vegetation and soil variables (soil redox potential [mV] and sulphide concentration [mM], interstitial water salinity [g/100 g] and pH) measured along a perpendicular transect from the coconut plantation–mangrove interface to the creek (distance from the interface in m). The thickness of the lines in the second figure reflects the cover to the adapted Braun-Blanquet scale (5 = 76–100% cover, 4 = 51–75% cover, 3 = 26–50% cover, 2 = 6–25% cover, 1 = 1–5% cover). Hl: *Heritiera littoralis*, Bg: *Bruguiera gymnorhiza*, Ct: *Ceriops tagal*, Rm: *Rhizophora mucronata*, Am: *Avicennia marina*, SWL: Sea Water Salinity Level. Bars indicate standard deviation.

tial water sample were measured after arrival in the laboratory.

Results

The higher intertidal was occupied by a mixed zone of *C. tagal* and *A. marina* with a few *B. gymnorhiza* individuals present, followed by a mixed zone of *R. mucronata* and *C. tagal* and then followed by pure stands of *R. mucronata* which partly overlapped seaward *A. marina* individuals. One *H. littoralis* tree was present at the coconut plantation–mangrove interface. Seedlings, with the sole exception of *B. gymnorhiza*, followed the distribution pattern of the parental tree (Figure 1).

The change from *Ceriops–Avicennia* to the *Rhizophora–Ceriops* zone coincided with a drastic change in soil characteristics. The landward *Ceriops–Avicennia* zone was characterised by a sandy substrate, but over a 20 m interval (the transition zone) it changed into a dark grey coloured muddy soil. This soil type was present until the creek. In Gazi Bay a soil textural gradient towards an increasing loam fraction at the seaward side was observed (Vanhove, 1990).

Soil Eh after the coconut plantation–mangrove forest interface decreased abruptly from $+175 \pm 16$ mV to a moderately reduced soil (-182 ± 74 mV). It did not change significantly in the *Ceriops–Avicennia* zone. It decreased again abruptly in the transition zone to a very low value (-284 ± 38 mV) and then remained at this level in the *Rhizophora–Ceriops* and the overlapping *Rhizophora–Avicennia* stands. The strongly reduced soil was associated with a very high sulphide concentration (0.3–4.6 mM), the moderately reduced soil with a very low sulphide concentration ($<$ 1–75 μM). The sulphide measurements showed a high variability between replicates and between neighbouring sampling sites. The values however clearly differentiate a high sulphide (mM level) zone and a low sulphide zone (μM level) with a stepped transition. Interstitial water salinity was high in the landward *Ceriops–Avicennia* zone with a maximum of 6.1%. In the transition zone the salinity decreased to a value close to sea water salinity (3.4 ± 0.2%) and remained at this level in the seaward *Rhizophora–Ceriops* and *Rhizophora-Avicennia* zones. The higher interstitial water salinity in the higher, less frequently flooded landward zone may be attributed to the effects of evapotranspiration, restricted exchange between tidal water and interstitial water or lack of groundwater inflow. The pH showed a gradual change, it declined gradually from pH 7.4 after the coconut plantation–mangrove forest interface to pH 5.9 in the transition zone, after which it increased gradually to pH 7.5 at the creek. The level of Eh, sulphide concentration and salinity were associated with the change in apparent soil type (sandy–muddy soil).

Discussion

Of the three major species (*A. marina*, *R. mucronata* and *C. tagal*) present along the transect, only the distribution of *R. mucronata* reflects changes in Eh, sulphide and salinity (Figure 1, Table 1). *R. mucronata* is present in the seaward zone characterised by a strongly reduced substrate, a high sulphide concentration and seawater salinity. According to MacNae and Kalk (1962) and Naidoo (1985), *Rhizophora* requires a soft, water-saturated substrate but cannot tolerate strongly saline soil. This is in agreement with the absence of *R. mucronata* from the more saline landward zone.

The distribution of either *C. tagal* or *A. marina* cannot be correlated with the distribution of Eh values, the sulphide concentration nor the salinity. *C. tagal* was present in the landward zone, which is characterised by a moderately reduced soil, a low sulphide concentration and a high salinity, and then continued over a strongly reduced soil with a very high sulphide concentration and seawater salinity levels. In general, there was no growth difference observed for *C. tagal*, but a few dwarf individuals were present at the landward side of the zone. *A. marina* demonstrated a bimodal distribution: a mixed landward zone with *C. tagal* which is characterised by a moderately reduced substrate and a low sulphide concentration and a seaward zone overlapping with the seaward end of the *R. mucronata* zone characterised by a strongly reduced soil and a very high sulphide concentration. Also a great difference in salinity between the two zones was measured, the landward zone was associated with a high salinity and the seaward zone with sea water strength salinity. A difference in growth was observed, seaward *Avicennia* individuals being more robust and taller than the landward individuals. According to Ruwa (1990) this difference is due to the higher salinity in the landward zone. It should, however be noted that seaward *A. marina* individuals grow on a lower level with respect to datum. Although the more stunted growth of *A. marina* in the landward

Table 1. Soil redox potential Eh (mV), sulphide concentration (μM), interstitial water salinity (g/100 g) and pH for every mangrove species stand (*Avicennia* separated into landward and seaward zones): maximum, minimum, median and number of measured samples (*n*)

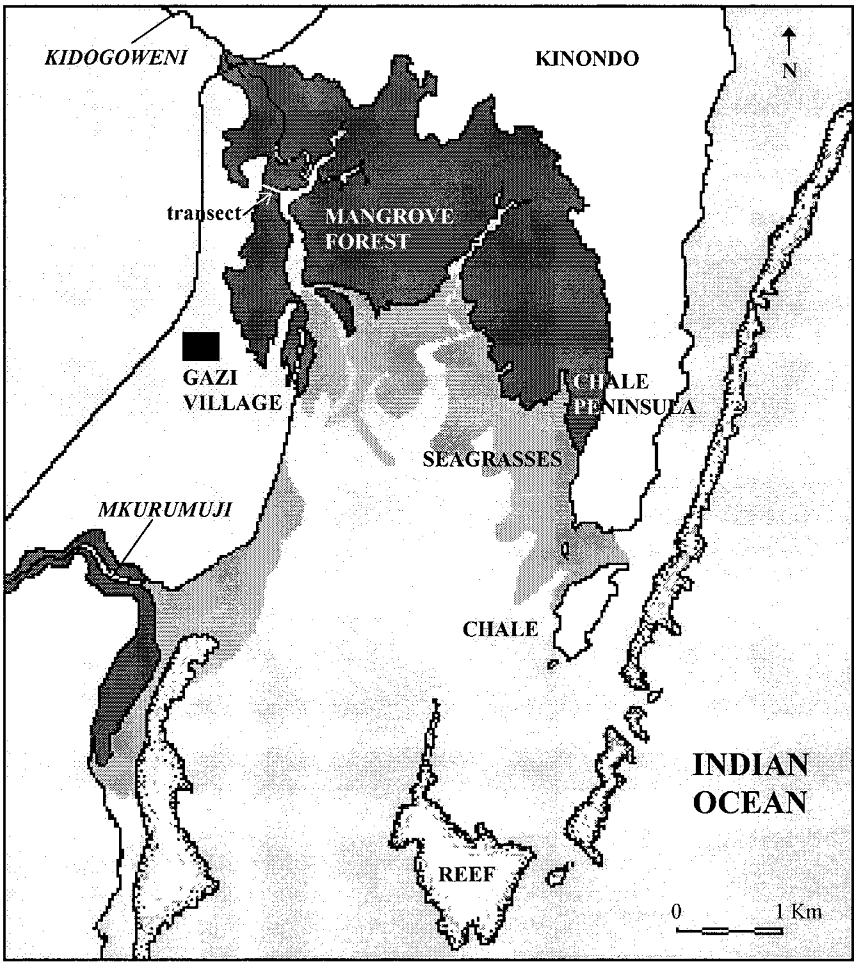
Soil variables	Mangrove species stand					
	Heritiera littoralis	*Bruguiera gymnorhiza*	*Ceriops tagal*	*Rhizophora mucronata*	Landward *Avicennia marina*	Seaward *Avicennia marina*
Eh (mV)						
Max	+186	+67	+67	−144	−130	−152
Min	+168	−211	−414	−400	−275	−405
Median	+182	−42	−204	−288	−182	−302
n	3	4	84	64	24	25
S^{2-} (μM)						
Max	–	27	5200	5100	48	4700
Min	–	5	2	2	1	200
Median	7	23	76	900	7	800
n	1	3	31	31	15	15
NaCl (g/100 g)						
Max	4.6	5.0	6.1	3.8	6.1	3.5
Min	4.4	4.6	2.9	2.9	5.2	3.2
Median	4.5	4.8	4.4	3.4	5.3	3.3
n	2	2	20	24	10	10
pH						
Max	7.45	6.74	7.00	7.44	6.69	7.44
Min	7.15	6.66	5.82	6.34	6.33	7.08
Median	7.30	6.70	6.44	6.84	6.41	7.17
n	2	2	30	24	10	10

mangrove zone may be due to adverse soil conditions (e.g. very high salinities), trees or shrubs in this zone do not have to cope with the problem of longer and deeper tidal inundation.

Apparently, not one set of environmental factors is causing the global mangrove zonation. The mangrove species which, in this mangrove area, constitute only a minor and local zone component, *Heritiera littoralis* and *Bruguiera gymnorhiza*, were restricted to the saline, less reduced and low sulphide landward zone. Though these soil factors might set some physiological limits to their success, other factors certainly restrict them further. Abiotic factors like water flow dynamics and waves, seedling predation and/or competition have been suggested as causing an important role in the establishment of the observed zonal distribution (Ball, 1980; Smith, 1987).

Salinity, though unrelated to the aeration status of the soil, was a function, at least in the dry season, of the flooding regime as well. The measurements were taken in the dry season and can only be seen as representative for this period. Several soil properties can be different in the wet season, rendering the differences between the seaward and landward zones less acute. During the wet season, the salinity levels in the landward zone can be expected to be lower. Also, rainfall might decrease Eh values in the landward zone due to water saturation.

Reciprocal effects of plant presence and soil aeration were amongst others observed by McKee (1993) and this precludes simple analysis of causal relations. Also, field investigations in a correlative approach will not yield conclusive results as to the environmental causes of the zonation, yet the data led us to reject a role of soil redox potential and sulphide concentration for the position of *A. marina* and *C. tagal*, both species that contribute considerably to the floristic composition and zonation. We cannot refute for *R. mucronata* the hypothesis regarding a role of soil redox status and related factors in spatially structuring mangroves, as expressed by McKee (1993) in another floristic context. For *R. mangle* L. and *A. germinans*



Map 1. Map showing the location of the transect (arrow) within the study site at Gazi Bay mangrove forest (Kenya). Figure adapted from Middelburg et al. (1996).

(L.) Stearn. seedling performance was shown to be dependent on flooding regime, Eh and sulphide levels (McKee, 1993). Propagule and seedling distributions follow parental zonation in Gazi Bay, as was observed by Van Speybroeck (1992), with the sole exception of *B. gymnorhiza*. This indicates that seedlings, except for those of *B. gymnorhiza*, are subject to the same environmental conditions as the respective adult trees. In Gazi Bay, soil factors related to flooding can contribute to the global zonation pattern in the mangrove forest through the establishment of the dominant *R. mucronata*. The global zonation is further caused by as yet unestablished factors.

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