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Source: *Ambio*, Vol. 24, No. 7/8, Research and Capacity Building for Sustainable Coastal Management (Dec., 1995), pp. 492-496
Published by: Springer on behalf of Royal Swedish Academy of Sciences
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John F. Machiwa and Rolf O. Hallberg

Flora and Crabs in a Mangrove Forest Partly Distorted by Human Activities, Zanzibar

A preliminary study on flora and fauna in a disturbed mangrove ecosystem is presented. The zonation of mangrove flora in the forest is clearly displayed by two dominant species, *Avicennia marina* and *Sonneratia alba*. *A. marina* forms an almost pure stand at the terrestrial edge of the forest, however, the species is ubiquitous in the area. *S. alba* almost exclusively occupies the marine fringe of the forest. The grapsid crabs occupy the terrestrial edge of the mangrove area, which has a relatively well-consolidated substrate. The ocypodid crabs, on the other hand, occur in mixed associations in sandy/muddy locations, mainly free of dense cover of mangrove trees and also in swampy open areas. The ocypodids are occasionally seen in areas with sandy bottoms at the edge of the terrestrial fringe mangroves. The mollusk *Cerithidea decollata* is ubiquitous in the *A. marina* zone, whereas in the marine-fringe and the shoreline-zone mangroves several other species of mollusks are represented. A conceptualized model for organic-carbon flux in the ecosystem is proposed based on distribution of mangrove flora and litter as well as the grapsid crabs.

INTRODUCTION

Mangroves are salt-tolerant trees or shrubs colonizing sheltered shores and estuaries of tropical areas. They occupy an area between the high-tide mark and just below the mid-tide level. Approximately 16 mangrove families are known comprising 53 species (1). Their distribution and growth success is dependent on climatic, hydrographic, and edaphic factors. However, climate is most important, because temperature controls seed germination (2, 3). Even though mangroves are halophytes, it is most likely that salinity has no physiological function. Their adaptation to saline conditions ensures no competition from other terrestrial vascular plants (4). Material import and export to adjacent open waters are mainly by tidal flows (5–11). However, particulate matter and mangrove litter dynamics in the marine area close to a mangrove forest are influenced by the hydrodynamics and geomorphology of the shore. The ecological significance of mangrove areas as breeding, nursery or feeding grounds for fish and crustaceans, is well documented. The environmental importance of forests in the protection of beaches against erosion is known, and the role of the forests as buffer zones for protecting nearshore marine ecosystems from excessive terrigenous particle loading is obvious.

The mangrove forest adjacent to the city of Zanzibar is an example of a mangrove community that is in daily contact with people. To our knowledge, no quantitative studies exist, on the influence of human activities on organic-matter budget and fluxes in these important nearshore ecosystems. Cuff et al. (5) and Hopkinson and Hoffman (12), have reported such budget studies, but their work did not cover the mangroves. Another study by Van der Valk and Attiwill (13), considered such a budget for a mangrove community. Their investigation, however, included only a few organic-carbon compartments in a mangrove forest. Because of the frequent interaction between people and mangrove communities, especially the human activities relating to growing cities, the natural balance of materials in mangrove communities is being disturbed. Budget studies are, therefore, necessary for the sustainable management of these important areas of the coastal zone. The aim of this study was to determine the organic-carbon budget in Maruhubi forest. Future presentations will include the identification and quantification of the organic carbon flux in the area. The work of this preliminary study was carried out during 1994, and constitutes an inventory of mangrove flora and the macrofauna that directly feed on large particle litter.

STUDY AREA

The climate of the coral island of Zanzibar can be described as tropical marine, with rainfall between 400 and 800 mm per year. The rainy season is between March and May, when about 50% of the annual rainfall is recorded. Of the total amount of precipitation 25% takes place from October through December and approximately another quarter of the rainfall is distributed among the remaining months. The temperature range is narrow (27° to 30°C), and the average monthly relative humidity varies from 85% in April to about 75% in November. The winds are northeast (October to March) and southeast (March to October) monsoons, with short intermediate periods. The main water current is predominantly and permanently northbound, although very localized patterns do exist (14).

The Maruhubi mangrove forest lies within the city of Zanzibar (Fig. 1). The forest is composed of six species, *Sonneratia alba; Avecinnia marina* (Forsk.) Vierh., *Ceriops tagal* (Perr.) C.B.Rob., *Bruguiera gymnorrhiza* (L.) Lamk., *Rhizophora mucronata* Lamk., and *Lumnitzera racemosa* (L.) Gaertn., possibly, with a few *Xylocarpus and Heritiera* trees present. The mangrove area considered in this study covers approximately 30 ha. The terrestrial edge of this mangrove forest forms a border with human settlements. According to the 1988 census, the town inhabitants are estimated at 160 000 and the annual population growth rate is about 4%. The forest is also in the vicinity of a port (about 3 km to the south), a soft drink plant, and a tobacco factory. Most of the domestic solid refuse is dumped close to the forest. The major environmental concern was related to discharge by trucks of untreated sewage at the forest edge. Emptying of raw sewage in the area was stopped in March 1994.

Two streams open into the mangrove forest. These streams drain through residential areas and can thus be another source of domestic waste in the mangroves. During rainy weather a considerable amount of sewage is transported to the coastal waters off the city of Zanzibar by storm-water runoff.

The Maruhubi mangrove stand does not support significant fishery. The trees are considerably exploited by neighboring

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people for fish-trap construction or repair of fishing canoes, and dry branches are collected for firewood.

MATERIALS AND METHODS

Flora Studies

Mangrove plants of different sizes were counted. A total of 18 belt transects running perpendicular to the shoreline were selected for the entire forest. On each transect, several quadrants of 100 m^2 (10 m x 10 m) were constructed by using a rope and pegs. A hand magnetic compass was used for determining the direction of a transect. Mangrove plants with diameters greater than 2.5 cm at approximately 1.3 m. above ground were recorded as trees. An intact plant was classified as a seedling if it was shorter than 50 cm, and the intermediate plants were counted as saplings. The mangrove floor standing crop was determined by collecting and sorting all litter material in a 1 m^2 area. The dry weight of the litter was estimated after drying the litter at 80°C for four days.

Fauna Studies

Mangrove crabs and snails that permanently inhabit the forest were recorded during vegetation study. The crabs were randomly sampled using a 1 m^2 or a 0.25 m^2 quadrant. The number of holes was assumed to be equivalent to the abundance of crabs. Tree dwelling grapsid crabs and the snails were physically counted in the field. The nature of the substrate was determined by visual inspection.

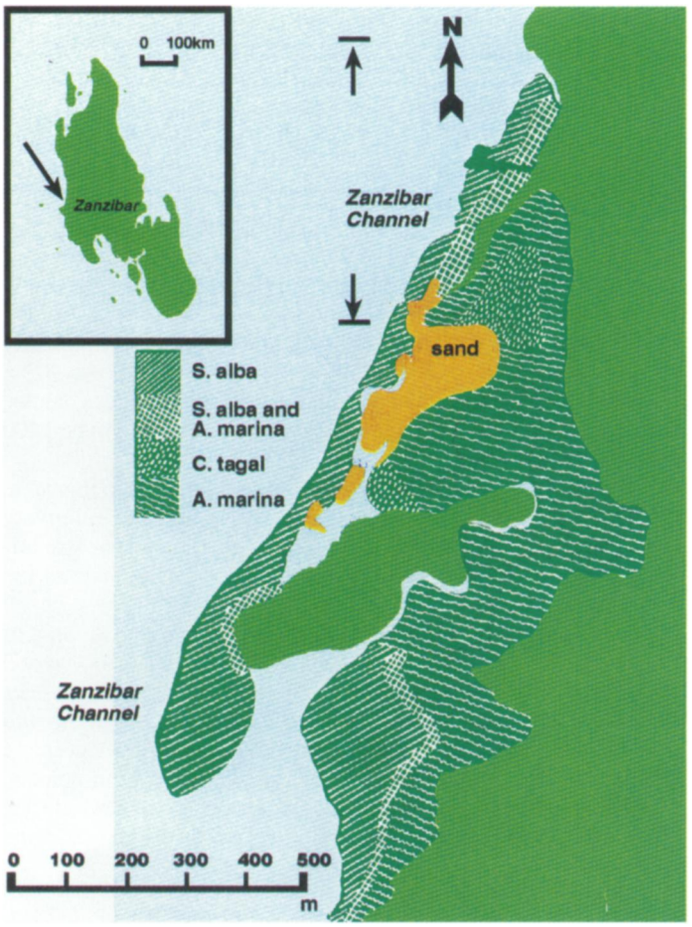


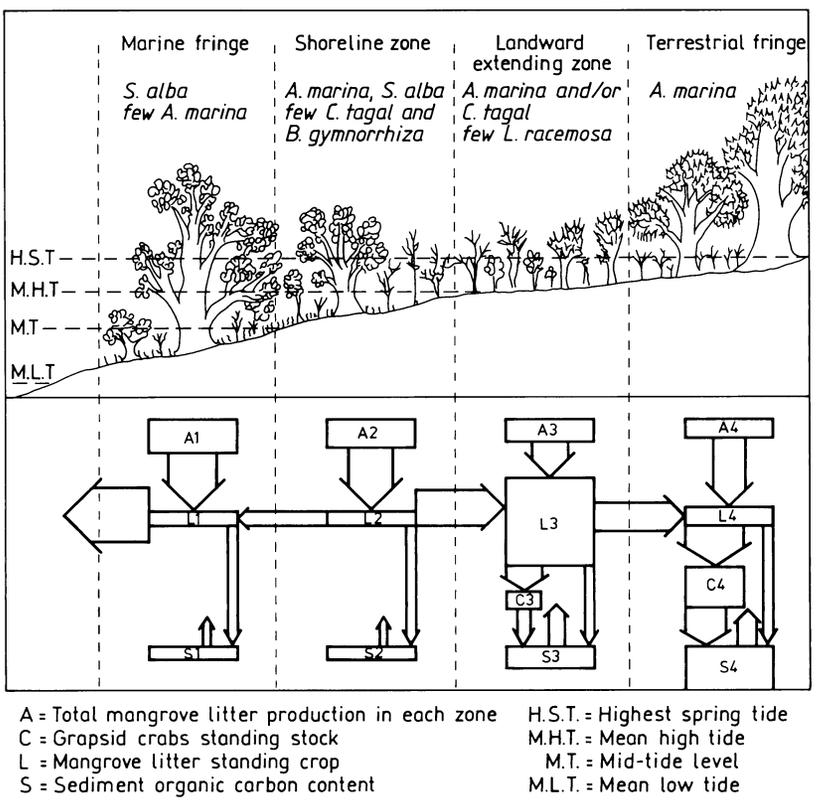
Figure 1. Zonation of Maruhubi mangrove forest.

RESULTS

The zonation of mangroves and mangrove fauna is often dependent on the geomorphology and hydrodynamics of a swamp. The presence of tidal channels, deep mud banks and semi-stagnant lagoons greatly influences and modifies the species distribution in a mangal. At Maruhubi, apart from the presence of tidal channels, freshwater streams and semi-stagnant lagoons, there is a high area where only terrestrial plants and animals can survive. Based on the distribution of flora presented in Table 1, the study area was partitioned into the marine fringe (MF), shoreline (SL), landward extending (LW) and the terrestrial fringe (TF) zones (Figs 1 and 2).

There are relatively few species of grapsid crabs in the mangroves and they exhibit a certain degree of zonation. The ocypodid crabs on the other hand occur in mixed associations in sandy/muddy locations, mainly free of a dense cover of mangrove trees, and also in swampy open areas. A zonation of species could not be found for the ocypodid crabs.

Figure 2. Generalized section of the study area and a conceptual model of organic carbon fluxes.



The Marine-fringe Zone

In Maruhubi forest, *S. alba* has entirely colonized the marine fringe, which lies between the high water (neap tide) and the mid-tide level (Fig. 1). *S. alba* trees are few, but of large size, on the marine fringe (Table 1), and their relative density decreases towards the shoreline. However, in the channels and creek area, *S. alba* extends as far as the seawater can reach. *S. alba* is sparsely distributed in the northern portion of the forest, where growth is about 1990 plants per ha. This area has the largest and oldest trees. In the MF zone, *S. alba* seedlings and saplings are 200 ± 165 (mean ± 1 standard deviation) and 953 ± 139 plants per ha respectively. *A. marina* seedlings are relatively

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abundant, there are 1020 ± 911 seedlings and 222 ± 193 saplings per ha. In the southern portion of the forest, *S. alba* and *A. marina* germinals are found growing in an area extending 30 m seaward from the marine-fringe mangroves. This extension can also be verified from old maps. Most likely, if the forest could be left undisturbed for a long period of time, it would extend seaward.

The conspicuous allochthonous litter in the marine fringe, especially in the northern and southern parts is algae and seagrass. The presence of materials that are not of mangrove-plant origin in these locations is evidence of organic carbon import into the forest. However, not all of the imported litter is permanently retained in the forest. The standing crop of litter is about 8.3 ± 5.2 g m^{-2} (dry weight), which includes mangrove leaves, sticks, and propagules. The production of litter was estimated to be 1400 g m^{-2} y^{-1}.

The ocypodid crabs are about 55.2 ± 27.2 ind. m^{-2} in this area. It was noted that the ocypodid crabs prefer areas of relatively clear, sandy floor in the sparsely growing mangroves. A maximum of 100 crabs m^{-2} was observed in the marine fringe of the southern portion.

About 10 tree climbing grapsids are found in a 100 m^2 area of the marine fringe, mainly on decaying parts of mangrove wood and prop roots, they represent the species *Metapograpsus messor, M. thukuhar* and *M. oceanicus*. *S. alba* and *A. marina* at the marine fringe and in the shoreline zone host a variety of snails. For example, *Littorina scabra* is found on leaves, whereas *Morula sp. Cerithium sp. Turbo coronotus,* and several other unidentified species are present on decaying parts of stems or branches of *S. alba. Terebralia palustris* is not represented in this zone.

The Shoreline Zone

The shoreline zone is colonized by *S. alba, A. marina* trees, saplings and seedlings. Occasionally, *C. tagal, B. gymnorrhiza,* and *R. mucronata* saplings and seedlings may occur. *A. marina* is the relatively dominant species (Table 1).

Mangrove leaf litter abundance is relatively low in this zone compared to the marine fringe. The total plant litter standing crop is about 4.6 ± 4.3 g m^{-2} (dry weight) and production is estimated to 1190 g m^{-2} y^{-1}.

The grapsid crabs are only about 1 ind. m^{-2} in this zone usually *Metapograpsus* spp. The ocypodid population, mainly *Uca* and *Dotila* spp., however, is more or less comparable to that of the MF. About 58.3 ± 18.8 ind. m^{-2} are found in the area, except at the supralittoral sands where the *Ocypode* spp. are found (about one ind. m^{-2}). The snail, *T. palustris* is found in sandy areas with decaying mangrove leaves.

The Landward Extending Zone

The landward extending mangrove zone is dominated by *A. marina.* There are also few isolated areas in the northern portion of the forest where *C. tagal* forms almost pure stands (Fig. 1). Occasionally, *L. racemosa* and *B. gymnorrhiza* are represented in this zone. *S. alba* is found only where the tidal channels extend to the landward extending (LW) zone in the central and southern parts of the forest. In the areas where *C. tagal* is densely growing, the seedlings are scarce (less than 1 per m^2) under the canopy.

There is a wide variation in the distribution of plants in the three portions of the forest at the LW zone. For example, *S. alba* grows only along the tidal creeks in the southern portion but is unrepresented in the northern and central portions.

Litter standing crop in this zone is high (Table 1) and production about 1000 g m^{-2} yr^{-1}. Tidal deposition of leaf litter takes place at the mean high tide mark.

The crab population in the area is predominantly the burrowing grapsids of the species *Sesarma impressum, S. meinerti* and unidentified *Sesarma* sp. and *Grapsus* sp. Only small to moderately large grapsids (carapace width < 50 mm) are represented in the LW zone, where about 9.6 ± 8.9 ind. m^{-2} are found on the forest floor. The ocypodid crabs are found in few isolated sandy areas and along the tidal channels.

The snail *Cerithidea decollata* is found in aggregations of between 5 and 20 snails on branches of *A. marina* trees, and on *A. marina* and *C. tagal* saplings.

The Terrestrial-fringe Zone

A. marina forms almost a pure stand at the terrestrial fringe. The trees grow luxuriantly despite the previous dumping of sewage waste in the area. Seedlings of this species are also abundant in the wet soft muddy areas of the terrestrial fringe. Up to 11 seedlings per m^2 were recorded in some areas in the MF zone.

Table 1. Distribution of mangrove flora and crabs at Maruhubi.

Variables	Mangrove zone			
	MF	SL	LW	TF
Number of trees (X ± 1 SD) ha^{-1}				
S. alba	4207 ± 2296	3405 ± 2042	850 ± 353	0
A. marina	628 ± 467	4596 ± 3039	11898 ± 2443	11220 ± 2599
C. tagal	0	100 ± 84	924 ± 191	0
B. gymnorrhiza	0	20 ± 6	1000 ± 721	0
R. mucronata	0	127 ± 89	0	0
L. racemosa	0	0	40	0
Number of saplings (X ± 1 SD) ha^{-1}				
S. alba	953 ± 139	289 ± 243	210 ± 14	0
A. marina	222 ± 193	1164 ± 986	2458 ± 2202	3653 ± 301
C. tagal	0	540 ± 396	4327 ± 3897	1390 ± 240
B. gymnorrhiza	0	20	206 ± 110	0
R. mucronata	0	0	40	0
L. racemosa	0	0	160	0
Number of seedlings (X ± 1 SD) ha^{-1}				
S. alba	200 ± 165	957 ± 924	130 ± 99	0
A. marina	1020 ± 911	2556 ± 2173	27993 ± 27654	74900 ± 32494
C. tagal	20	1700 ± 995	8761 ± 6133	0
B. gymnorrhiza	0	40	510 ± 316	0
R. mucronata	0	90 ± 14	0	0
L. racemosa	0	0	0	0
Number of crabs (X ± 1 SD) m^{-2}				
Ocypodids	55 ± 27	58 ± 19	28 ± 20	11 ± 5
Grapsids	< 1	1	14 ± 8	21 ± 8
Litter abundance (X ± 1 SD) gm^{-2}(d.w.)	8.3 ± 5.2	6. ± 4.5	69.8 ± 35.5	8.6 ± 1.3
Nature of substrate	sandy/sandy/ muddy-sand	muddy-sand	sandy/mudy-sand/ muddy-sand/ soft mudwith sewage with sewagedeposit deposit	stiff mud

MF = Marine fringe
SL = Shoreline
LW = Landward extending
TF = Terrestrial fringe

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The grapsids are mainly *Sesarma meinerti*. These areas with soft muddy substrates are occupied by small grapsid crabs (carapace width < 20 mm), which probably do not consume the *A. marina* propagules. Small grapsids occur in numbers of up to 20 ind. m^{-2}. In areas that are occupied by the big grapsids (carapace width > 20 – < 50 mm), not more than 10 individuals are accommo-dated in a 1 m^2 area. Only one large grapsid, usually with a carapace width of about 70 mm, can be accommodated with other crabs in a 1 m^2 area. The burrows of the largest grapsids can penetrate vertically down to 50 cm, before extending several centimetres horizontally. The big grapsids prefer the outer edge mangroves where the substrate is relatively consolidated compared to the soft muddy inner-mangrove areas. The presence of sewage deposits in the sediments of the forest does not affect the abundance of grapsid crabs. Generally, it was observed that the variation in abundance of the grapsid crabs at the terrestrial edge in the northern, central and the southern parts of the forest reflected the differences in consolidation of the substrate. The northern part of the forest which has a relatively stable substrate, has correspondingly many bigger grapsids per unit area.

Ocypodid crabs are weakly represented in the terrestrial edge mangroves (Table 1).

Mangrove leaf litter is generally low in the terrestrial fringe. About 35.8 ± 17.1g m^{-2} of leaf litter is found in the LW zone compared with only 1.9 ± 0.9g m^{-2} (d.w.) in the TF zone. The production of litter was estimated to 950 g m^{-2} yr^{-1}. In areas with large grapsids the floor is normally clear of most mangrove leaf litter and propagules.

The mollusk *Cerithidea decollata* is abundant in the TF zone. The northern part of the forest has relatively many large *A. marina* trees. In this area, more than 200 snails can occupy a single branch of an old mangrove tree.



Mangroves are still common habitats particularly in Mozambique and Southern Tanzania. Photo: O. Lindén.

DISCUSSION

The mangrove flora and macrofauna of Maruhubi forest clearly show some zonation patterns (Table 1). For the mangrove plants, for instance, the MF is mainly occupied by *S. alba*, and the SL zone is cohabited by *S. alba* and *A. marina*. The LW zone is colonized by *A. marina*, *C. tagal,* and occasionally by *B. gymnorrhiza* and *L. racemosa*. The TF zone, on the other hand, is almost a pure stand of *A. marina.* The zonation of mangroves is probably related to hydrodynamic, geomorphic and edaphic factors of the shore. Human interference has caused no effect on the zonation pattern, but has severely affected the expansion of the forest in areas used for boat anchorage. The seedlings are also missing in areas excavated for worm collection. On the other hand, the propagules show good germination, even in areas that have sewage deposits. Most likely, cutting of *S. alba* for boat repair distorts the natural trend of litter dynamics in the forest. The big branches are taken by fishermen, and the trimmings are collected for firewood.

Generally, the ocypodid and the tree-climbing grapsid crab populations decrease towards the land. The burrowing grapsids are only found in the landwards extending zone and in the terrestrial fringe. A similar distribution pattern has been described in other locations, for instance, in the Jamaican mangrove swamp (17). Two main factors influence the distribution of crabs in a mangal. First, zonation of mangrove crabs according to their dietary habits. This behavior has been observed in several locations (18–21). Second, and probably the most important factor, is their degree of adaptation to withstand desiccation stress (22–24). At Maruhubi, for example, the bigger grapsids occupy the exposed locations in sparsely growing mangroves. The young grapsids, on the other hand, prefer to live within shade areas of the young densely crowded mangroves. In the big and probably older mangroves, the substrate is relatively more consolidated than in areas with young plants. Therefore, the biggest grapsids are restricted at the edge mangroves where the substrate is stable. Presence of sewage deposit in the sediment does not deter the grapsids from colonizing the area. It was observed that the largest grapsids are mostly found at the former sewage-dump location.

A conceptual model for the flux of organic carbon in the Maruhubi area can be proposed based on distribution and production of mangrove litter and grapsid crabs. Knowledge of the food and feeding habits of the grapsid crabs in the LW and TF zones is essential for the organic carbon model. We observed that the grapsids are the most important low-tide mangrove-litter feeders of the forest (15). It has been calculated that the sesamid crabs can consume up to 79% of the total annual litter fall in the forest (25). This figure is more than double the amount suggested by Leh and Sasekumar (26), who reported that crabs consume between 20 and 30% of the average litter fall in the landward edge mangroves. Probably, the species types, distribution, and size groups of crabs in the two forests are different. Wide variations in consumption rates for crabs can exist even within a forest. The grapsids quickly grab and drag some fallen propagules, twigs of green leaves or freshly shed leaves into their burrows. It is not clear whether this food is immediately consumed or is stored for future consumption. The crabs do not immediately resurface after carrying the food item into their holes. This suggests, that the meal is, possibly, immediately shredded or that the crabs spend some time to store the food items in proper locations. Other studies (15, 16) have suggested that the leaves are stored for a sufficient period to allow them to age and to acquire a rich microbial population. Such leaves have improved palatability for crab consumption and high nutritional value. A typical vegetarian diet for the Sesarmid crabs has been reported (15), where more than 95% by volume of the gut content were leaf fragments. It was also observed that the crabs can eat other plants besides those of mangroves.

At Maruhubi, the large grapsids are voracious herbivores (15, 25). The grapsids rush for cut twigs of green *A. marina* leaves or fallen *C. tagal* fruits. The grapsids eat their meals inside their hideaway. Our laboratory data suggest that the grapsids with carapace width of about 70 mm fed almost continuously. They can consume 1000 mg (d.w.) of leaves (equivalent to about 13 mature green leaves of *A. marina*) in 24 hrs. The small grapsids

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(carapace width 10 to 50 mm), on the other hand, consumed between 0.4 and 178 mg (d.w.) of leaves, under the same conditions. The bigger grapsids do not store leaves for food for any length of time in their burrows. It is most likely, therefore, that the bigger grapsids consume their meals immediately after collection. The small ones, however, can store food for a relatively long period. Because of their greater consumption, big grapsids exhibit a limited choice for the type of leaves consumed. For instance, both the green and the brown leaves are equally selected, unlike the findings of laboratory observations by Camilleri (16). The big grapsid would rush for a twig of leaves rather than for a single leaf. The body size of the grapsids is probably critical in the selection of food items. Common grapsids in the terrestrial fringe are *Sesarma guttatum, S. impressum, S. meinerti* and several *Grapsus* spp.

The grapsid crabs in the MF and SL zones (e.g. *Metopograpsus* sp.), are apparently less adapted to desiccation stress, they occupy positions submerged by high tide, and where decaying mangrove litter is easily available.

In our model, we have used the numbers for mangrove-litter production, standing stock of grapsid crabs, litter consumption by grapsid crabs, and standing crop of mangrove litter presented in the text and in Table 1. The outflow of organic carbon from the sediment is supposed to be proportional to the inflow. We have assumed a steady-state situation and our model is, thus, representative of our sampling period, which was outside the rainy season. Our preliminary field observations suggest that there is a net outward flux of litter from the forest to the adjacent sea and there is no flux of litter between the LW and TF compartments. The input and output of carbon are balanced between the four compartments depicted in Figure 2.

Both the litter, particulate, dissolved, and volatile forms of organic carbon are mobilized by tidal flow. The litter that falls in the MF zone will probably be exported to the sea. Most leaf litter in the SL zone will be transported shorewards rather than seawards. Most of the mangrove leaf litter at the supralittoral fringe and in the LW zone probably undergo *in situ* decomposition. A small fraction of the litter is consumed by the grapsid crabs of the LW zone. Most of the litter that falls in the TF zone is retained. The leaves are largely eaten by the grapsid crabs of the TF zone. Mangrove leaf processing and leaf burying by crabs ensure a faster turnover rate for the leaf litter. These two activities by the crabs probably cause a high organic carbon content in the sediments of the LW and TF zones. The model suggests that the sediment at the TF zone should build up more organic carbon than any of the other compartments.

Other detritivores that visit mangrove forests during high tide, e.g. fish and several portunid crabs (20, 21), were not studied because of their low abundance in the area and their effect on the flux of organic carbon in the Maruhubi mangal is considered to be of minor importance.

CONCLUSIONS

The mangrove flora and macrofauna of Maruhubi mangrove forest clearly show zonation patterns that are not affected by human interference. The Maruhubi mangrove forest has the potential to expand in the northern and southern portions if boat anchorage and other destructive types of human interference are limited. The zonation of mangroves is probably related to both hydrodynamic, geomorphic, and edaphic factors of the shore.

Generally, the ocypodid and the tree-climbing grapsid crab populations decrease towards land. The burrowing grapsids are only found in the landward extending zone and in the terrestrial fringe.

The conceptual model for fluxes of organic carbon suggests that the sediment in the TF zone should build up more organic carbon than any of the other compartments.

References

1. Odum, W.E., McIvor, C.C. and Smith III, Y.J. 1988. *Ecology of the Mangroves of South Florida, A Community Profile.* US Fish and Wildlife Service. Office of Biological Service, Washington D.C. FWS/OBS - 81/24, pp. 1–144.
2. McMillan, C. 1971. Environmental factors affecting seedling establishment in the black mangrove on the central Texas coast. *Ecology 52,* 927–930.
3. Waisel, Y. 1972. *Biology of Halophytes.* Academic Press, New York, 395 pp.
4. Kunzler, E.J. 1974. Mangrove swamp systems. In: *Coastal Ecological Systems of United States I.* Odum, H.T., Copland, B.J. and MacMahan, E.A. (eds). The Conservation Foundation, Washington DC, pp. 1–533.
5. Cuff, W.R., Sinclair, R.E., Parker, R.R., Tranter, D., Bulleid, N.C., Giles, M.S., Godfrey, J.S., Griffiths, F.B., Higgins, H.W., Kirkman, H., Rainer, S.F. and Scott, B.D. 1983. A carbon budget for south west arm, Port Hacking. In: *Synthesis and Modelling of Intermittent Estuaries.* Cuff, W.R. and Tomezak, Jr (eds). Springer, Berlin, pp. 193–232.
6. Alongi, D.M., Boto, K.G. and Tirendi, F. 1989. Effects of exported mangrove litter on bacterial productivity and dissolved organic carbon fluxes in adjacent tropical nearshore sediments. *Mar. Ecol. Prog. Ser.* 56, 133–144.
7. Rezende, C.E., Lacerda, L.D., Ovalle, A.R.C., Silva, C.A.R. and Martinelli, L.A. 1990. Nature of POC transport in a mangrove ecosystem: A carbon stable isotopic study. *Estuar. Coast. Shelf Sci. 30,* 641–645.
8. Alongi, D.M. 1990. Effect of mangroves detrital outwelling on the nutrient regeneration and oxygen fluxes in coastal sediments of the central Great Barrier Reef Lagoon. *Estuar. Coast. Shelf Sci. 31,* 581–598.
9. Lee, S.Y. 1990. Primary productivity and particulate organic matter flow in an eastuarine mangrove-wetland in Hong Kong. *Mar. Biol. 106,* 453–463.
10. Gong, W.K. and Ong, J.E. 1990. Plant biomass and nutrient flux in a managed mangrove forest in Malaysia. *Estuar. Coast. Shelf Sci. 31,* 519–530.
11. Heminga, M.A., Slim, F.J., Kazungu, J., Ganssen, G.M., Nieuwenhuize, J. and Kruyt, N.M. 1984. Carbon outwelling form mangrove forest with adjacent seagrass beds and coral reefs (Gazi Bay, Kenya). *Mar. Ecol. Prog. Ser. 106,* 291–301.
12. Hopkinson Jr., C.S. and Hoffman, F.A. 1984. The estuary extended—A recipient-system study of estuarine outwelling in Georgia. In: *The Estuary as a Filter.* Kennedy, V.S. (ed.) Academic Press, London, pp. 313–330.
13. Van der Valk, A.G. and Attiwill, P.M. 1984. Decomposition of leaf and root litter of *Avicennia marina* at Westernport bay, Victoria, Australia. *Aquat. Bot. 18,* 205–221.
14. McClanahan, I.R. 1988. Seasonality in East Africa's coastal waters. *Mar. Ecol. Prog. Ser. 44,* 191–199.
15. Malley, D.F. 1978. Degradation of Mangrove leaf litter by the tropical sesarmid crab *Chiromantes onychophorum. Mar. Biol. 49,* 377–386.
16. Camilleri, J. 1989. Leaf choice by crustaceans in a mangrove forest in Queensland. *Mar. Biol. 102,* 453–459.
17. Waner, G.F. 1969. The occurrence and distribution of crabs in a Jamaican mangrove swamp. *J. Anim. Ecol. 38,* 379–389.
18. Hill, B.J. 1976. Natural food, foregut clearance rate and activity of the crab *Scylla serrata. Mar. Biol. 34,* 109–166.
19. Beever III., J.W., Simberloff, D. and King, L.L. 1979. Herbivor and predation by the mangrove tree crab *Aratus pisonii. Oecologia 43,* 317–328.
20. Paul, R.K.G. 1981. Natural diet feeding and predatory activity of the crab *Callinectes arcuatus* and *C. toxotes* (Decapoda, Brachyura, Portunidae). *Mar. Ecol. Prog. Ser. 6,* 91–99.
21. Williams, M.J. 1981. Methods for analysis of natural diets in portunid crabs (Crustacea: Decapoda: Portunidae). *J. Exp. Mar. Biol. Ecol. 52,* 103–113.
22. Malley, D.F. 1977. Adaptation of decapod crustaceans to life in mangrove swamp. *Mar. Res. Indonesia 18,* 63–72.
23. Jones, D.A. 1984. Crabs of the Mangal ecosystem. In: *Hydrobiology of the Mangal.* Por, F.D. and Dor, I. (eds). Dr.W.Junk Publ., The Hague, pp. 89–109.
24. Kyomo, J. 1992. Variation in the feeding habits of males and females of the crab *Sesarma intermedia. Mar. Ecol. Prog. Ser. 83,* 151–155.
25. Robertson, A.I. and Daniel, P.A. 1989. The influence of crabs on litter processing in high intertidal mangrove forests in tropical Australia. *Oecologia 78,* 191–198.
26. Leh, C.M.U and Sasekumar, A. 1985. The food of sesarmid crabs in Malaysian mangrove forest. *Malay. Nat. J. 39,* 135–145.

27. The reviewer is thanked for critical comments. C. Mhando of I.M.S. Museum identified some crab and snail specimens. J. Shunula provided data on litter production and M. Mwadini gave field assistance. We gratefully acknowledge their help. We also acknowledge the logistical support kindly offered by the Institute of Marine Science, Zanzibar. This research is funded by the Swedish Agency for Research Cooperation with Developing Countries (SAREC).

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