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Lateral fluxes of organic carbon in a mangrove forest partly contaminated with sewage wastes

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Abstract

Lateral fluxes of macrodetritus, particulate matter and dissolved organic carbon were determined. Samples were collected monthly at the mangrove forest–inshore water boundary and within the forest. Floating macrodetritus (mainly mangrove leaves) was collected by a net (2 mm mesh size). Dissolved and particulate matter were separated by filtration (0.45 μm filter) and centrifugation. Dissolved and particulate carbon were determined by a total organic carbon analyser (SHIMADZU model TOC-5000). There was a significant export of mangrove litter to the adjacent marine environment during spring tides. Rates of import and export of particulate matter in the forest were not statistically different. Trans-location of material within the forest was clearly demonstrated. A relatively high export of macrodetritus was recorded at the marine fringe (mainly colonised by *Sonneratia alba*). There was low export of litter in the terrestrial fringe zone, a mono-specific stand occupied by *Avicennia marina* (Forsk) Vierh. Net organic carbon export from the entire forest was 79×10^6g C y^{-1}, dissolved organic carbon accounted for about 78% of the total export.

Introduction

Mangrove ecosystems are among the most productive areas of coastal zones (e.g. Macnae, 1974). They provide nutrients for phytoplankton growth, thus enhancing secondary production and promotion of commercial fisheries. The forests also provide refugia and nourishment to a variety of resident heterotrophs and a large number of tidal migrant species (Robertson and Duke, 1987). Apart from the internal sources of nutrients, external supply of organic matter to mangrove areas through runoff is common. Such inputs include natural products decay of terrestrial plants and anthropogenic sources. The advantage, mangrove forests have over terrestrial forests, is that they have no large grazers. Hence, under natural conditions, mangroves can form continuous thickets. These forests are connected to the marine trophodynamic system by natural decomposition and tidal mobilization of large quantities of dissolved and suspended matter (Nixon, 1980; Boto and Bunt, 1981; Boto and Wellington, 1988; Alongi et al., 1989; Wattayakorn et al., 1990; Hemminga et al., 1994). The decay process involves leaching and fragmentation, performed mechanically by wave action and biologically by resident grazers and detritivores. During feeding, crabs and snails reduce whole mangrove leaves into small particles (Robertson, 1986; Twilley et al., 1986; Robertson and Daniel, 1989), which are favored by microbiota (Camilleri and Ribi, 1986). Microbial colonization, on the other hand, encourages litter consumption by the detritivores due to the enhanced palatability and the increased nutritional value of detritus (Camilleri, 1989).

The effects of the tidal regime on litter dynamics in mangrove forests has been addressed by several workers (e.g. Boto and Bunt, 1981). However, aspects of ecosystem energy flow in such environments are still poorly understood. Smalley (1960), for example, proposed that more than 90% of wetland primary productivity entered the litter mainly as leaves and propagules. Similar results have been re-

ported by Shunula (1996). Golley et al. (1962) used mass balance approach to estimate tidal exchange of material between a mangrove stand and adjacent marine biotopes. Their findings, however, needed more data to be more conclusive. In order to accurately assess material transport, Twilley (1985) modified the approach for studying tidally driven exchange of material. He sampled right at the forest–inshore water boundary. Lee (1990) was able to show that, despite a large litter component in a mangrove system, inundation frequency greatly controlled the net flux of material. Less frequent flooding can cause a net import of organic matter in a mangal regardless of the magnitude of the litter standing crop. Under favorable tidal conditions, the amount which is available to the coastal and offshore higher trophic level is dependent on the sum of production, leaching, decomposition and detrital storage in a mangrove system (Cundell et al., 1979; Robertson, 1988). The resident herbivores, mainly invertebrates, play a major role in regulating the magnitude of litter export by removing a large amount of it (Robertson, 1986; Lee, 1989; Robertson and Daniel, 1989; Robertson et al., 1990; Camilleri,1992; Emerson and McGwyne, 1992). The rate of litter turnover by sesarmid crabs is far more important than the microbial decay process in retaining autochthonous organic matter (Macnae, 1968; Leh and Sasekumar, 1985; Robertson, 1986, 1988). Other factors that control the amount of outwelled litter to the adjacent marine environment include the size of the mangrove forest in relation to the immediate open ocean. Geomorphology of the basin, amplitude of the tide, motion of the tidal water and inundation frequency are also important factors (Lugo et al., 1976; Alongi et al., 1989). In the Klong Ngao mangrove system, for instance, the mean net export of carbon on spring tides was almost twenty times the amount on neap tides (Wattayakorn et al., 1990).

Flood frequency is one of several factors which influence mangrove interstitial water salinity (Ball, 1988). Soil salinity is an important factor in regulating forest structure. It affects litter export by controlling leaf senescence and rate of abscission. The frequency of tidal flushing also influences litter removal by macrofauna (Robertson, 1986). The grapsid crabs at Maruhubi, for instance, fed during low tide mainly in daylight (Machiwa and Hallberg, 1995). More than 60% of litterfall was exported in the low to mid-intertidal forests which were regularly flushed, and crabs removed less than 30% (Robertson, 1986). The rate of microbial decay, however, was enhanced by the higher tidal activity and large water turnover (Odum et al., 1982; Twilley, 1985; Twilley, et al., 1986). In contrast, in the high intertidal mangroves that were occasionally flooded, the crabs removed more than 75% of the total litterfall (Robertson and Daniel, 1989). In general, large and frequent tidal flooding enhance litterfall and favors export (Pool et al., 1975) rather than *in situ* decomposition (Twilley, 1985; Lee, 1989). The extreme condition can be met in estuarine mangroves, where most of the litter is flushed, and the decay process may possibly start in the adjacent subtidal environment (e.g. Heald, 1971; Odum, 1971; Lugo and Snedenkar, 1974).

The behavior of dissolved organic carbon (DOC) in a mangrove ecosystem is less documented. Some of the few literature examples include Twilley (1985), who observed that DOC forms a significant fraction of material export from forest areas with low water turnover, where bacterial and fungal decay is a major pathway of litter removal. Because the within mangrove system cycling of material is closely coupled to the biotic component and the hydrodynamics of the area, Odum et al., (1979) have encouraged site specific investigations of system processes rather than extrapolation of results from one area to the other. This study investigated the effect of tidal inundation on mangrove litter standing stock and lateral fluxes of floating litter (macrodetritus), suspended particulate matter and DOC in a west Indian ocean mangrove forest.

Materials and methods

The study site

A 36.8 ha mangrove forest at Maruhubi and Kinazini (6°10′ S and 39°12′ E) was studied (referred to as Maruhubi). Maruhubi is in Unguja, the main island of Zanzibar in the western Indian ocean (Figure 1). The vegetated area is small compared to the adjacent open inshore marine area, because of the open geomorphology of the shoreline. The area experiences semi-diurnal tides, having a minimum depth at the mangrove forest–inshore water (MI) boundary of less than 1 m during the neap high tide and a maximum depth of 2.6 m during high spring tides. The entire forest is inundated by only 23% of the flood tides per annum. Mean (± standard deviation) salinity and temperature of the flood (33.0 ± 1.9‰; 31.5 ± 2.8 °C) and the ebb (33.6 ± 1.9‰; 30.7 ± 2.7 °C) flows

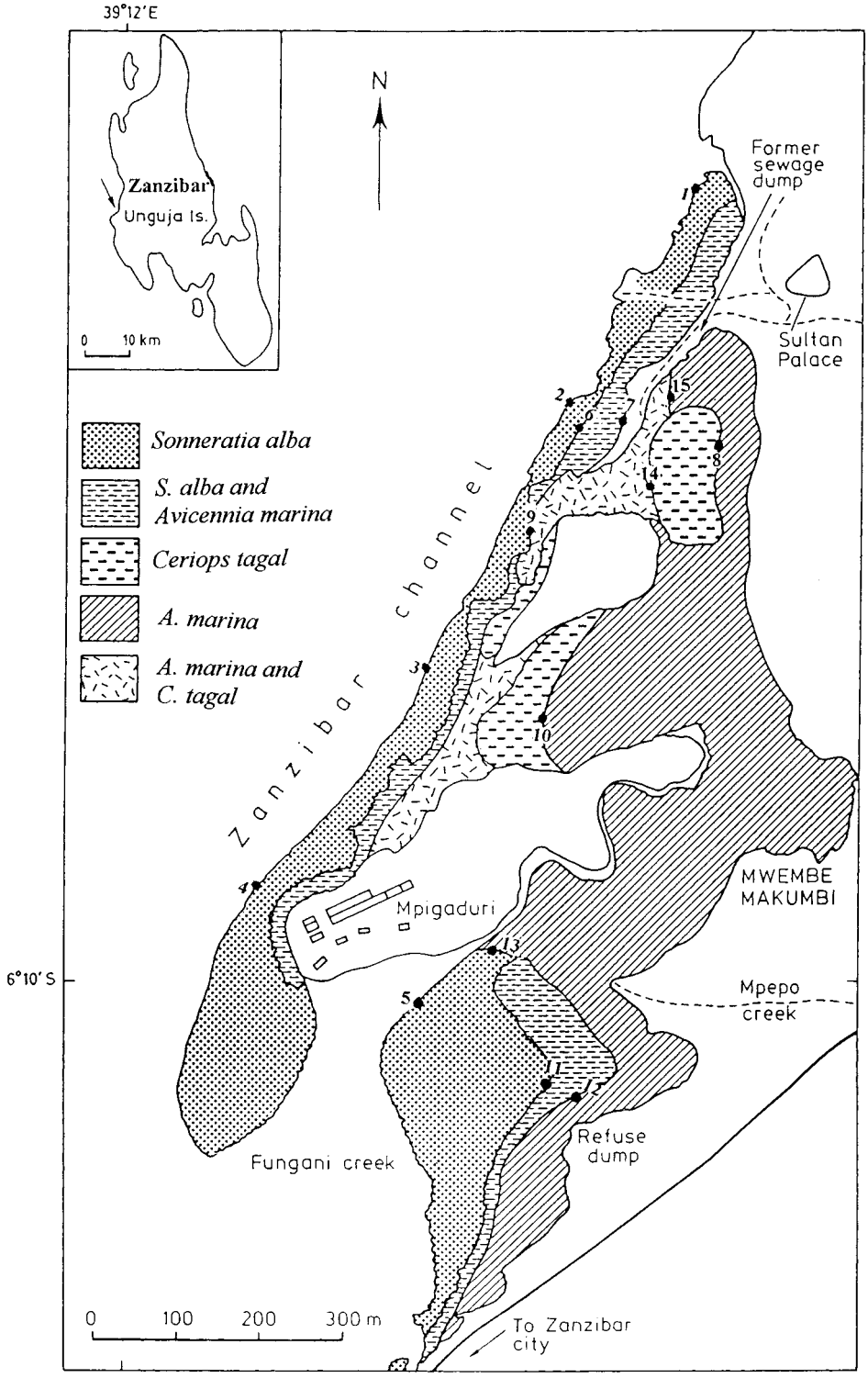


Figure 1. Location map for the Maruhubi mangrove area, showing the sampling stations in the mangrove forest zones.

(measured at the mangrove–inshore interface) are not significantly different between wet and dry weather.

Flora and fauna of the forest have been considered elsewhere (Machiwa and Hallberg, 1995; Shunula, 1996). Four zones of the forest were mapped (Figure 1). The zones of the forest included the marine fringe (MF) mainly comprising *Sonneratia alba* and the shoreline (SL) with mixed species, *S. alba* and *A. marina*. Zones, which were inundated by high spring tides, were the landward extending (LE) and terrestrial fringe (TF) areas. LE was subdivided into an area with a mixed association of *A. marina* and *Ceriops tagal* (LEA) and an almost mono-specific stand of *C. tagal* (LEB). The TF zone had an almost pure stand of *A. marina*, was subdivided into an area that had been used for sewage disposal (TF_s) and an area without sewage exposure (TF_{ns}). The sewage dump-site operated between 1980 and 1993.

Fifteen stations were established along the mangrove–inshore boundary and inside the forest. Stations 1–5 were at the mangrove–inshore boundary. Stations 6, 7, 9, 11 and 13 were in the shoreline area (MF and SL zones). Stations 8, 10, 12, 14 and 15 were at the landward extending area (LEA, LEB and TF). Locations of the stations in the forest were mainly governed by navigational constraints.

Mangrove litter production and litter standing crop

Litter production was measured using 36 litter traps made of a square wooden frame (0.25 m^2) and a tapering net (mesh size 2 mm.). The traps were suspended under the forest canopy just above the highest level of water. Traps were deployed in the zones of the forest (6 traps per area) and monthly collections were conducted. Litter was sorted into leaf, reproductive, and woody material, and all were dried to constant weight at 80 °C.

The aboveground standing litter biomass in the forest subecological zones was estimated by collecting all the surface litter in 1 m^2 quadrats that were constructed adjacent to the traps. The quadrats were permanently fixed using polyester twine mounted on four wooden pegs that were inserted in the ground. Surface litter was collected when the litter traps were being emptied. Litter was washed, partitioned into mangrove components, marine weeds and miscellaneous (mainly terrigenous) material, and dried and weighed as above.

Sampling of floating mangrove macrodetritus litter

Floating mangrove litter was collected by a net (2 mm. mesh size) that was set against the direction of the tidal flow. The net was kept above the water surface by closely fastened buoys. Weights were attached at the foot of the net to keep it anchored on the bottom. Two round bars (12 mm diameter) which were fixed 2 m. apart, allowing the net to oscillate up and down with waves and depth of water by means of metal rings that were attached on the vertical sides of the net. Macrodetritus was collected during both flood and ebb tides at stations 1–5. Flood and ebb currents were not exactly oppositely directed, due to the presence of obstacles. Where necessary, position of nets was altered between flood and ebb flows. Nets were deployed at least once monthly for the mangrove-inshore stations. Litter was washed, sorted into mangrove, seagrass, macrophytic algae, and miscellaneous (usually land derived debris) material. The plant material was then dried to constant weight at 80 °C. The mangrove components included leaves, propagules, stipules, flowers, calyces, and stem material (mainly small terminal twigs, and flakes of the bark).

Sampling and analysis of water samples

Sampling was conducted from September 1995 to August 1996. Hydrographic measurements of water depth were done manually or with a hand-held pressure sensor. Surface water samples at the mangrove–inshore boundary were collected at fixed depth intervals (0.25, 0.5, 1.0, 1.5 and 2.0 m.) during flood and ebb flows. Flood tides typically lasted for 3 hours and the ebb tides for 4 hours. Water samples were also collected from the forest zones at fixed depth intervals (0.25, 0.5 and 1.0 m.). Within the forest the flood flow ranged between 1 and 2 h and the ebb tide was between 1.5 and 3.5 h.

Water samples were analyzed for suspended particulate matter (SPM) by immediate centrifugation (3500 rpm, for 10 min). The SPM was washed with distilled water and kept frozen until freeze-dried and the weight was determined gravimetrically. Samples for DOC analysis were filtered through a 0.45 μm membrane filter (Schleicher & Schuell®) in the field and stored frozen in clean 25 ml. brown glass bottles with screw caps until analysis. To avoid contamination from the glassware, the new bottles were soaked overnight in 6M Nitric acid and rinsed six times with distilled and MilliQ® water. Total organic carbon

(TOC) content of the samples was determined with a Shimadzu® TOC analyser (model TOC-5000). The DOC was determined as non-purgeable organic carbon (NPOC) using a Shimadzu Autosampler (ASI-5000). POC was checked with a Shimadzu Solid Sample Module (SSM-5000A). Precautions for quality control included replication of samples and repetition of measurements. The coefficient of variation (c.v.) for six determinations of NPOC samples was better than 2.4%, and for the POC samples was less than 0.9%.

Computation of the field measurements

As the area of Maruhubi forest system is relatively open to tidal flushing, mass balance studies are complicated by accuracy in estimation of discharge rates. Per tidal cycle POC and DOC fluxes were calculated by multiplying average concentration with estimated water discharge. Values were integrated over a complete tidal cycle to obtain net material transport (Spurrier and Kjerfve, 1988). The discharge was estimated by multiplying the area of the forest with the mean depth of each respective forest zone. Within the forest standing stock of DOC and POC was calculated by multiplying the concentration per unit volume with total volume of water within a given forest zone.

Flow dynamics within the forest were mainly dominated by tidal forcing, which exhibited a distinct flood-ebb inequality. In order to calculate the resultant litter transport in and out of the forest, it was necessary to sample over a complete tidal cycle. Tidal cycles were assumed to last from the time the flood water reached the mangrove–inshore boundary until all the water had left the same location (normally about 8 h). This approach ignored the effect of flood-ebb velocity asymmetry in the forest. Tidal cycles lasted less than three hours in the TF zone. The tidal current energy was low in the forest due to frictional damping over the shallow bottom, as well as obstruction by mangrove trees. The residual litter loading was calculated by multiplying the mass of trapped litter per unit length of net, with the length of the coastline at the respective boundary of the mangrove zone. It was assumed that cross-sectional variability in litter transport within given boundaries remained small.

Statistical analyses

Mean, standard deviation (s.d.) and standard error (SE) were calculated from appropriate number of replicate samples. Litter fall and litter standing crop data were analyzed using a parametric one-way analysis of variance (ANOVA) to test the significant difference between the forest zones. Sample means were compared using the Tukey test.

Results and discussion

Mangrove litter production

Litterfall rates were statistically different (one-way ANOVA, $F = 9.19$, $P < 0.0001$) between the forest zones (Table 1). Leaf litter production (mean ± s.d. g m^{-2} d^{-1}) was higher (1.2 ± 0.7) for *A. Marina* growing in the area influenced by sewage than in the area without sewage exposure (1.05 ± 0.35). However, total litterfall (including reproductive parts) was low in the TF_s (2.0 ± 1.2) compared to the TF_{ns} area (2.3 ± 1.4). *A. marina* trees in the northern part of the TF zone, however, generally appeared large and probably older than the central and southern ones (Machiwa and Hallberg, 1995). *A. Marina* propagules were abundant in the litter from February–April. The peaks for litterfall varied between the species and were different for leaves and propagules (Shunula, 1996). Leaf litterfall was highest in June and July as well as in September, October and November, partly corresponding with dry weather (Figure 2). Reproductive parts were shed seasonally, except for *C. tagal*. Similar trends have been observed in Australia (Duke et al., 1984; Robertson Daniel, 1989) and other places (e.g. Day et al., 1987; Lee, 1989). Peak *A. marina* propagule production was from February–April, coinciding with the warmer wet season, and for *C. tagal*, it was spread throughout the year. Highest values of litter production occurred from February–April for *A. marina* and from September–November for *S.alba*. During the reproductive seasons, propagules made the highest proportion of litter yield. Total litterfall was 633 g dry weight (dw) m^{-2} y^{-1} in the MF and 298 g

Table 1. Litter production (mean ± s.d. g dw m^{-2} d^{-1}), standing crop (mean ± s.d.g dw m^{-2}), area (ha) and volume of water (m^3) in mangrove forest zones

Zone	Litterfall	Standing crop	Area	Volume
MF	1.7 ± 1.1	3.0 ± 1.7	11.3	214659
SL	1.6 ± 0.9	8.2 ± 6.3	4.5	49780
LEA	1.0 ± 0.8	32.4 ± 26.0	2.4	14608
LEB	0.6 ± 0.5	8.3 ± 3.6	2.6	15825
TF_s	2.0 ± 1.2	4.5 ± 7.2	2.6	15560
TF_{ns}	2.3 ± 1.4	10.3 ± 3.2	13.4	64633

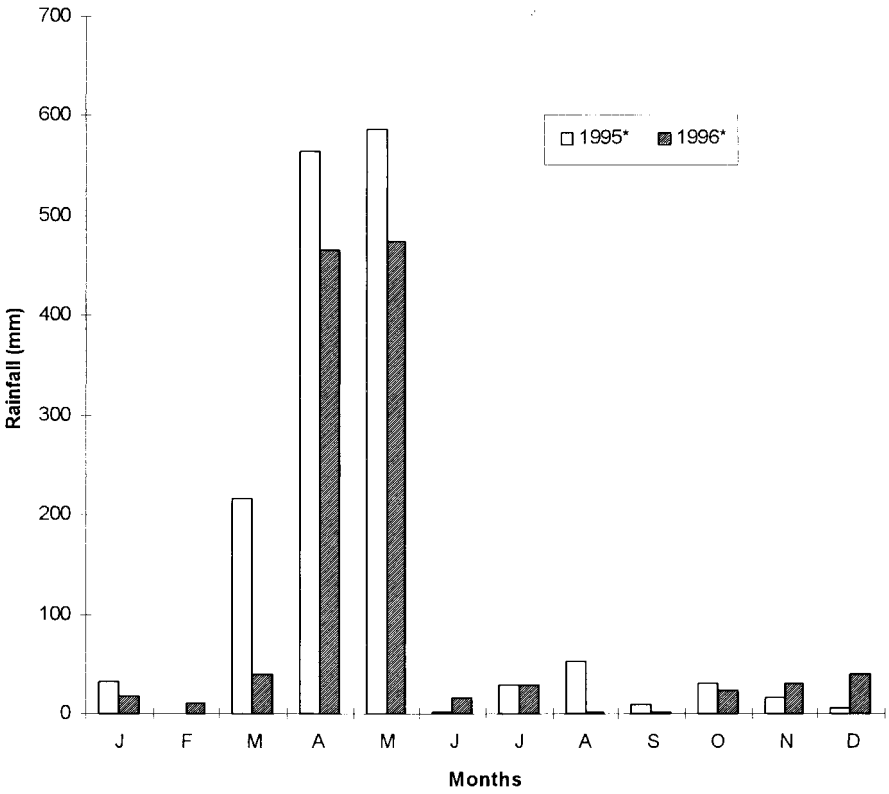


Figure 2. Monthly variation of rainfall in Zanzibar, for 1995 and 1996 (Source: Directorate of Meteology, Zanzibar zonal office).

dw m^{-2} y^{-1}, in the SL. The LEA and LEB zones had rates of 185 and 199.3 g dw m^{-2} y^{-1}, respectively and in the TF zone was 729 g dw m^{-2} y^{-1}. The mean litter production ($\pm$ 1 s.d.) for the entire forest was 461 $\pm$ 261 g dw m^{-2} y^{-1}. Leaves contributed between 60% and 75% of the annual total litter fall in the forest overall. At the TF zone, *A. Marina* produced the highest proportion of leaf litter (74.3%).

Pool et al. (1975) as well as Anderson and Christensen (1978) have argued that increased porewater salinity lead to increased leaf senescence, and consequently to increased litter fall. High salinity caused physiological responses that were analogous to those of terrestrial macrophytes under drought stress. Porewater salinity was comparatively high in the TF zone, where the leaves contributed the highest amount of the annual litter fall. Similar results have been reported by Shunula (1996), that leaves contributed between 50% and 80% of the monthly litterfall in the species at Maruhubi. Francisco et al (1987) reported an 89% contribution of leaves in Mexico, and Steinke and Ward (1990) recorded a 72% contribution of leaves in mangroves of South Africa. This study shows that litter yield in the Maruhubi forest generally well compared with results from other tropical forests (Saenger and Snedaker, 1993). The sparse canopy of this forest, as indicated by the overall lower tree density (Machiwa and Hallberg, 1995), resulted in lower litter production.

Mangrove litter standing crop

Mean ($\pm$s.d.) instantaneous standing crop of litter in the entire forest was 11.1 $\pm$ 10.8 g dw m^{-2}. Some areas of the forest had hardly any litter on the forest floor. Mean values for MF, SL, LE and TF zones were significantly different (one-way ANOVA, $F = 12.49$, $P < 0.0001$). Highest litter standing stock (32.4 $\pm$ 26.0 g dw m^{-2}) was recorded in the LE zone (Table 1). Aboveground litter mass in the four mangrove zones varied by zone: LEA > TF_{ns} > LEB > SL > TF_s > MF. Despite high litter production in the MF and TF zones, litter standing crops were comparatively low. *S. alba* leaves formed the highest proportion of litter biomass at the LEA zone, probably as a result of lateral transport by tidal flow (Figure 3). High tidal amplitude, frequent inundation, and high tidal flow velocity likely contributed to the low litter

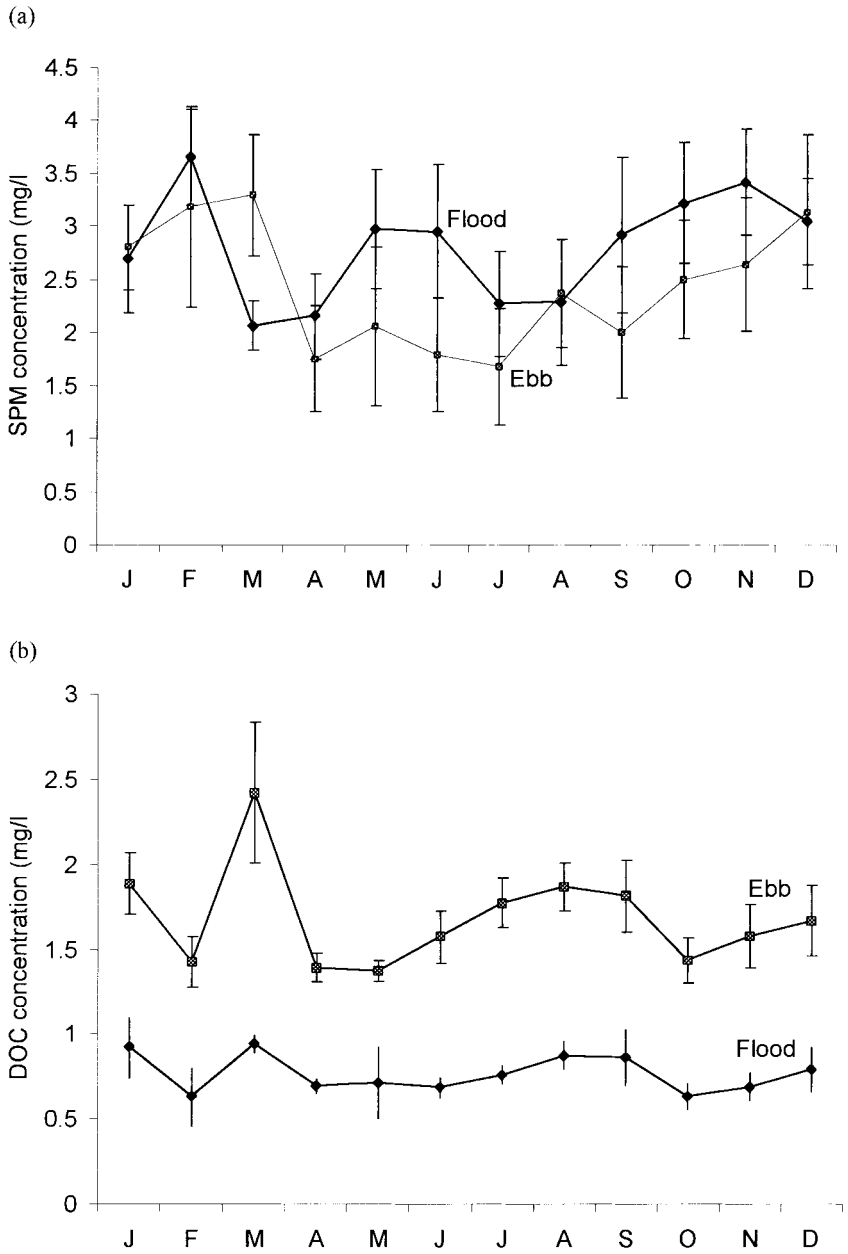


Figure 3. Monthly variations (mean ± SE) of flood and ebb tide concentrations of (a) suspended particulate matter and (b) dissolved organic carbon at the forest–inshore water boundary.

abundance on the floor of the MF zone. At the TF zone litter standing crop was likely also influenced by the abundance of the crabs. Density of crabs at the TF_s zone was higher than that of the TF_{ns} zone (Machiwa and Hallberg, 1995). Generally, peak periods of litterfall corresponded well with maxima for the forest floor litter biomass. Litter turnover time was longest in the landward-extending zone of the forest.

Lateral fluxes of macrodetritus

A high proportion of litterfall in the MF zone was exported, and only a small amount of mangrove litter remained on the forest floor. *S. alba* leaves composed the bulk of the outwelled material (over 90%). The tidally driven export of macrodetritus out of the mangrove stand was about 1×10^6 g dw ha^{-1} y^{-1}. This

was equivalent to approximately 22.4% of the annual litter production for the entire forest. The amount of mangrove litter that was exported varied with tidal amplitude, and the neap tide mean values were generally lower than the spring tide values. A few incidents, such as strong onshore winds and hurricane events, modified the net flux of macrodetritus from the forest. For example, hurricane Dolores (19 February, 1996) caused a major import of seagrass and seaweed into the mangrove stand. Most of this litter was outwelled during subsequent ebb flows. Litter transport, therefore, facilitated net nutrient and organic carbon outwelling from the Maruhubi forest. *S. alba* leaves formed the bulk of the exported material because of the predominance of *S. alba* trees in the MF zone. *S. alba* litter received maximum exposure to tidal flushing.

Another possibility, according to Steinke et al. (1983), concerns buoyancy. Leaves of *A. marina* do not remain buoyant for long, and are thus less likely to be lost compared to *S. alba* leaves, which float for a longer time. In the MF zone, where: (1) litter production was high; (2) litter standing-stock was low, and; (3) the grapsid crab population was low (Machiwa and Hallberg, 1995), a large proportion of the leaf fall was exported. Within the forest there was a net export of 18.4×10^6 g dw y^{-1} of mangrove litter from TF zone to the LE and SL zones. 2.8×10^6 g dw y^{-1} of mangrove litter was also exported from the MF zone to the SL zone via flood flow.

According to Twilley (1985), litter export controls the patterns of turnover times of mangrove floor biomass in the tidally dominated forest settings. Wattayakorn et al. (1990) reported leaf litter export of 0.06 kg dw litter ha^{-1} d^{-1} using a net with large mesh, with maximum values of 0.25 kg ha^{-1} d^{-1} during spring tides. Their estimates were low compared with those of Boto and Bunt (1981). The latter workers reported export up to 19.5 kg dw litter ha^{-1} d^{-1} at Coral Creek, Australia. Unlike Wattayakorn et al. (1990), this value included total litterfall from mangroves. Robertson and Daniel (1989) estimated tidal export of litter to be 107, 194, and 252 g m^{-2} y^{-1} for *Avicennia*, *Ceriops* and *Bruguiera* forests, respectively. These amounts were equivalent to 21%, 24%, and 25% of annual litterfall, respectively. The present results of mangrove macrodetritus outwelling (1029 kg dw ha^{-1} y^{-1} or 22.4% of annual litter fall) compared favorably with these literature values.

Dissolved organic carbon and suspended particulate matter

DOC concentration in the forest increased landward from the MI boundary during flood and ebb flows. The concentration of the ebb tide DOC varied from 0.8 to 1.4 mg C l^{-1}. Higher values coincided with the onset of late March rains, which followed a period of relatively dry, hot (28–32 °C) weather in January and February (Figure 2). In March, the ebb concentration was almost double the flood amount (Figure 3). At the mangrove–inshore boundary, the DOC concentration was highest ($>$ 1 mg l^{-1}) at stations 1 and 5 that were exposed to human interference and had consistently high levels of DOC. There was export of DOC seaward from the TF and LE zones. High levels of DOC in the TF zone of the northern part of the forest suggested a significant contribution from sewage waste. At the sewage site (station 15), maximum DOC concentration in ebb flow was 3.9 mg l^{-1} in March and the minimum was 2.6 mg l^{-1} in February. The estimated flux of DOC from TF to LE zone was 8.6×10^6 g y^{-1} and from LE to SL area was 11.2×10^6 g y^{-1}. Flux estimate of DOC from SL to MF zone was 25.4×10^6 g y^{-1} and from MF to the adjacent inshore water was 61.6×10^6 g y^{-1}. According to Twilley (1985), the export of organic carbon from mangroves is associated with the extent of tidal activity. He concluded that export was highest in mangroves that are frequently inundated by higher tides. Similar outwelling behavior of dissolved nitrogen (mostly in the organic form) was reported by Thong et al. (1993) in a mangrove area in Malaysia. Boto and Bunt (1981) suggested that undisturbed mangrove water channels might contain up to 40 mg l^{-1} DOC and 3 mg l^{-1} POC. High DOC concentrations were reported by Twilley (1985). He noted a sharp rise in the level of DOC following a rain event, from 13 to 20 mg l^{-1} the next day.

SPM at the MI boundary ranged between 1.6 and 3.4 mg l^{-1} (Figure 3). High concentration of SPM was generally obtained during windy days. Strong wind waves influenced particle re-suspension through scouring of bottom sediments. Suspended solids were also high at sites that were more exposed to human activities. The onset of long rains in March caused higher mobilization of particulate matter in ebb flow. Storm water mobilized particulate matter from the land. As the rain season progressed the SPM load decreased. Rivera-Monroy et al. (1995) similarly showed that maximum values of SPM (0.26 mg l^{-1}) occurred

during rainy season in September and October. The annual range of SPM was from 0.056 to 0.26 mg l^{-1} at the Terminos Lagoon forest, Mexico.

Net import of SPM to the Maruhubi stand was observed during all months except in January, March, August, and December, mostly in response to a storm following dry weather. The obstruction of ebb tidal flow by the mangrove trees retarded outwelling of suspended sediments. Short, shrubby mangroves in the SL and LE zones effectively increased the vertical settling velocity of the particles. The larger MF mangroves allowed relatively easy exchange of material between the stand and the adjacent inshore water, though. Within the forest the organic carbon content of the SPM ranged between 12% and 18%, whereas at the mangrove–inshore boundary it was between 6% and 7%. The high organic carbon content of the SPM in the TF zone was probably partly due to contributions from sewage and the fecal material of the crabs and molluscs, which were abundant in the TF zone.

The importance of macrodetritus, POC, and DOC fluxes in mangrove organic carbon dynamics were compared. Mean values of SPM revealed a net import of SPM in the forest. The ebb flow mobilized relatively low levels of SPM of high organic carbon content, while the flood tide SPM level was relatively high but of poor organic carbon content. Results suggested, therefore, that the mangrove system was a sink for marine derived SPM of low organic carbon content and a source of the organic rich SPM. Despite the low levels, DOC at Maruhubi contributed about 78% to the TOC export from the forest. The proportion of sewage-derived DOC was low, because the area experiencing sewage was less than 7% of the total forest area. Amount of export of DOC compared well with previous findings. Twilley (1985), for example, found that up to 75% of TOC flux from a mangrove forest was DOC.

Conclusions

In the Maruhubi mangrove system the major energy source for the resident detritivores was the landward extending mangroves. The present study further illustrated the importance of within-forest transportation of material. *In situ* biotic and hydrodynamic factors led to effective retention of mangrove litter. Pathways of material loss from the forest were mainly through DOC and floating macrodetritus export by ebb flows. However, the contribution of the forest to the energy budget of the adjacent inshore communities was largely through dissolved material. The importance of the landward extending mangrove area as a producer of DOC was emphasized. It was not possible to estimate the amount of mangrove material that was exported via consumption by tidal immigrants.

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