

Litter degradation and CN dynamics in reforested mangrove plantations at Gazi Bay, Kenya

J.O. Bosire^{a,b,*}, F. Dahdouh-Guebas^a, J.G. Kairo^b,
J. Kazungu^b, F. Dehairs^c, N. Koedam^a

^a *Laboratory of General Botany and Nature Management, Mangrove Management Group, Vrije Universiteit Brussel, Pleinlaan 2, B-1050 Brussels, Belgium*

^b *Kenya Marine and Fisheries Research Institute (KMFRI), P.O. Box 81651, Mombasa, Kenya*

^c *Department of Analytical and Environmental Chemistry, Mangrove Management Group, Vrije Universiteit Brussel, Pleinlaan 2, B-1050 Brussels, Belgium*

Received 21 May 2004

Abstract

The main objective of this study was to assess how mangrove reforestation has influenced litter degradation and concomitant nutrient dynamics in previously deforested plantations. Dynamics of nutrients (carbon, nitrogen and C:N ratios) in decomposing leaves of conspecific species were investigated with litterbags in *Sonneratia alba* and *Rhizophora mucronata* reforested treatments using appropriate bare and natural less disturbed treatments as controls. Bare treatments had the lowest decay rates (Kd^{-1}) and thus the highest t_{50} values (when 50% of the original weight had been decomposed) for both species. The contrary was true for natural treatments, while both parameters were intermediate in reforested treatments, suggesting that other than direct litter input, reforestation has modified site conditions which have enhanced organic matter decomposition. There were significant seasonal differences in decay rates for treatments within the *R. mucronata* species, with rates being higher during the wet season with accompanying lower t_{50} values. Decay rates were overall higher ($P < 0.05$) in the *S. alba* species and as a result no litter was retrieved from its natural treatment by the 5th week. Higher amphipod colonisation was observed in reforested and natural treatments than bare treatments, which may have contributed to higher decay rates in the former. There were significant differences ($P < 0.05$) in N concentration among treatments with natural and reforested treatments having similarly higher concentrations than bare treatments in both seasons. C:N ratios (an important determinant of nutritional leaf quality) were also similarly low in natural and reforested treatments and higher in bare treatments. Mangrove reforestation thus seems to have enhanced litter degradation and concomitant nutrient remineralisation, suggesting that other than species litter quality, tidal inundation and seasonal factors, specific stand management regimes play an important role in determining the efficiency of these ecological processes in mangrove ecosystems. © 2005 Elsevier Ltd. All rights reserved.

Keywords: Mangrove reforestation; Litter degradation; Nutrient dynamics; Kenya

1. Introduction

Mangrove swamps are considered to be productive ecosystems, in which the rate of primary productivity is high (Heald, 1971; Odum and Heald, 1972; Boto

and Bunt, 1981). This high productivity is often attributed to high litter degradation rates and efficient recycling of nutrients, which are supplied by both autochthonous litter and allochthonous inputs from natural and anthropogenic sources (Lee, 1990; Kazungu et al., 1993; Bouillon et al., 2002). Usually less than 10% of litter material produced in mangrove forests is consumed alive (Heald, 1971; Odum et al., 1982). The bulk

* Corresponding author. Tel.: +254 11 475154; fax: +254 11 475157.
E-mail address: jbosire@kmfri.co.ke (J.O. Bosire).

of this primary production thus enters the system as detritus. Fresh detritus of low nutritive value is decomposed through a sequence of physical, chemical and biological processes (Lee, 1990; Ashton et al., 1999), thus making the subsequent organic material more nutritious by microbial enrichment processes (Odum and Heald, 1975; Alongi, 1998). The nutrients generated by remineralisation of this action are ultimately made available for primary production and this in turn supports a wide variety of consumers (Macintosh, 1984; Alongi and Sasekumar, 1992).

The rapid breakdown of organic material in the mangrove ecosystem seems to ensure that large proportions of organic matter production (mangrove leaves) are recycled within the forest and this initial retention of production most likely reduces tidal export from the mangroves (Hemminga et al., 1994; Lee, 1998) to the adjacent open water. This is complemented with additional organic carbon input into mangrove systems from either estuarine or marine sources (Jennerjahn and Ittekkot, 2002; Bouillon et al., 2002, 2003) to meet the system's internal requirements.

Most studies on mangrove litter degradation and concomitant nutrient dynamics have hitherto concentrated on differences among: tidal elevations (Twilley et al., 1986, 1997; Mfilinge et al., 2002), species and seasons (Tam et al., 1990; Alongi et al., 1992; Twilley et al., 1997; Woitchik et al., 1997; Mfilinge et al., 2002) and litter components (Steinke et al., 1983; Van der Valk and Attiwill, 1984; McKee and Faulkner, 2000). Specific stand management regimes, i.e., regulated exploitation versus excessive extractive pressure which leads to deforestation, and subsequent reforestation in areas where natural regeneration is impeded, do influence nutrient recycling (Ashton et al., 1999). Reforestation has been found to alter site physico-chemical conditions (McKee and Faulkner, 2000; Bosire et al., 2003) and is thus assumed to ultimately restore the functional importance of nutrient fluxes through it among other ecosystem functions. We had the opportunity to compare three conditions simultaneously, which allowed a systematic comparison of reforested treatments with natural mangroves as well as bare treatments using the well established litterbag technique (Steinke et al., 1983; Van der Valk and Attiwill, 1984; Tam et al., 1990) to assess variations in litter degradation and accompanying nutrient regeneration among these treatments. Such information is necessary to give more insight into nutrient recycling in mangrove systems undergoing different management regimes. The litterbag technique may underestimate actual decomposition rates due to reduced exposure to mechanical forces and exclusion of larger invertebrates (Wieder and Lang, 1982; Ashton et al., 1999), but it does reflect trends and thus provide for comparisons across treatments.

The main objective of this study was to investigate the impact of mangrove reforestation in previously

deforested treatments on litter degradation rates and nutrient dynamics as an important functional indicator of ecosystem recovery at Gazi Bay, Kenya, using appropriate deforested and natural less disturbed treatments as controls.

2. Materials and methods

2.1. Study area

The present study was conducted at Gazi Bay, Kenya in *Rhizophora mucronata* Lamk. and *Sonneratia alba* J. Smith reforested plantations, which were both 8 years old at the time of investigation. Deforested and natural treatments adjacent to the respective reforested treatments were used as controls. The replanted stands were part of the respective deforested treatments, but the latter have not been reforested, hence they had the same site history. The controls were also of the same inundation regime as the reforested treatments. The *S. alba* treatments were in the lower intertidal inundated during all high tides, while the *R. mucronata* treatments were in the higher intertidal inundated during spring tides. For more details on study area and treatment description, refer Bosire et al. (2003).

2.2. Leaf degradation experiments

Leaf decomposition rates in reforested mangrove treatments of *R. mucronata* and *S. alba* were compared with rates in natural and deforested treatments, which had a similar site history, inundation regime and proximally adjacent to the reforested treatments (Bosire et al., 2003). Litterbags were used to estimate the rates of mangrove leaf (*R. mucronata* and *S. alba* within respective treatments) breakdown. Senescent leaves which had turned yellowish were hand picked from the trees because these are normally the majority of the leaves on the forest floor and have already started their decomposition. The leaves were air dried for 24 h so that no surface water remained and then known weights (30 g for *R. mucronata* and 20 g for *S. alba*) placed into 20 cm × 20 cm nylon bags with a mesh size of 1 mm². A batch of four samples each weighing the respective weights above for each species was retained and oven dried at 80 °C to constant weight to get initial dry weight, and allow for initial carbon and nitrogen concentration analysis. The 1 mm mesh size is small for significant loss of small leaf particles, but large enough to allow microbial colonisation and entry of small benthic invertebrates. Twenty eight bags per treatment were securely tied to aerial roots of the reforested and natural mangrove treatments and pegs firmly driven into the soil for the bare controls giving a total of 168 litterbags. Four bags from each treatment were retrieved at weekly

intervals (except for the wet season when no sampling was done in the first week) and taken to the laboratory where they were washed on 1 mm sieve to remove sediments and separate macroinvertebrates colonising the litter. The macroinvertebrates were identified (under 25×) into taxonomic classes. The resulting litter after washing was oven dried at 80 °C and the final dry mass recorded. The degradation/nutrient regeneration experiments were done both during the dry season from February to March and wet season from May to June to assess spatial and temporal variations.

2.3. Nutrient analysis

For every harvest of litterbags, nutrient analysis for total carbon (C) and nitrogen (N) were done for every respective sample. To prepare samples for C and N analysis, the dried samples were pre-treated with inert liquid nitrogen to make them brittle and ground to a fine consistency using a pestle and mortar. Total carbon and nitrogen of pre-weighed samples were determined with a Carlo Erba NA 1500 Elemental Analyser using pre-weighed silver cups. Before analysis, 0.25 ml of 5% HCl was added to the samples to remove any carbonates and then oven dried overnight at 50 °C. Acetanilide (C = 71.03%, N = 10.36%) was used for standardisation (Woitchik et al., 1997).

2.4. Statistical analysis

Differences among species, seasons, time (weeks) and treatments were analysed using SPSS Univariate Anova, while multiple comparisons were done with the Tukeys test. All data sets were log (log 10) transformed for normalisation. To analyse for the time effect from weekly data, three time intervals were selected: ‘0’ for initial dry weights, C and N concentrations or C:N ratios; 2nd week to capture leaching effects and related rapid changes and 5th week because this is the last week material was recovered from the *S. alba* natural treatment. The relationship between percentage dry mass (*y*) remaining in litterbags at time *t*, for all treatments were fitted to a negative exponential model

$$y = x_0e^{-kt},$$

where *y* is the percentage of the initial dry weight *x*₀ remaining after time *t* (days), and *k* is a decay constant. Half times (*t*₅₀) of decomposing materials in respective treatments were calculated as *t*₅₀ = ln 2/*K* (Ashton et al., 1999).

3. Results

3.1. Litter degradation

Among species, dry weight loss was higher in *S. alba* than *R. mucronata*. Consequently no litter was harvested from the natural treatment of the former by the 5th week in both seasons, whereas the *R. mucronata* natural treatment had 22% and 8% of the original dry weight remaining by the 7th week during the dry and wet seasons, respectively (Table 1 and 2). For the *R. mucronata* species, weight loss rates were higher in the wet season as reflected from the higher wet season daily weight loss or *Kd*⁻¹ and lower half times or *t*₅₀ when 50% of the initial mass had been decomposed (Table 3). However, there was no significant seasonal variation (*P* = 0.245) among respective treatments within the *S. alba* species. Weekly weight loss was highest between initial dry weight and weight in the 2nd week across treatments. For instance during the wet season, dry weight in the *S. alba* natural treatment dropped from 100% or initial dry weight to 17% by the 2nd week (Table 2). Within species, natural treatments had the highest *Kd*⁻¹ values, reforested treatments intermediate, whereas the bare treatments had the least (Table 3). For instance within the *R. mucronata* species during the wet season, the bare treatment had a very low *Kd*⁻¹ of 0.03 and a *t*₅₀ of 164 days; a *Kd*⁻¹ of 0.19 and a *t*₅₀ of 26 days for the reforested and a *Kd*⁻¹ of 0.41 and a *t*₅₀ of 12 days for the natural treatments. Due to its low weight loss rate, the bare treatment of *R. mucronata* had a very poor fit to the exponential model (*R*² = 0.2964, *P* > 0.01) compared to the natural and reforested treatments (*R*² = 0.9406, *P* < 0.01; *R*² = 0.8195, *P* < 0.01, respectively). Leaves in the *R. mucronata* bare treatment thus remained fairly intact during the sampling period.

Table 1

Dry weight composition (as a percentage of the original dry weight) of litter in the different treatments of the two mangrove species over the sampling period (weeks) during the dry season

Species	Treatment	0	1	2	3	4	5	6	7
<i>S. alba</i>	Bare	100	48 ± 4	53 ± 10	42 ± 4	32 ± 4	24 ± 8	28 ± 6	25 ± 8
	Reforested	100	51 ± 7	12 ± 2	7 ± 2	6 ± 3	5 ± 3	2 ± 2	
	Natural	100	33 ± 9	10 ± 4	2 ± 1	1 ± 1	1 ± 0		
<i>R. mucronata</i>	Bare	100	88 ± 3	87 ± 2	95 ± 2	88 ± 6	82 ± 5	89 ± 3	88 ± 6
	Reforested	100	76 ± 3	74 ± 2	58 ± 4	58 ± 1	59 ± 7	45 ± 9	47 ± 10
	Natural	100	81 ± 7	71 ± 6	58 ± 6	54 ± 9	50 ± 14	29 ± 6	22 ± 6

Table 2

Dry weight composition (as a percentage of the original dry weight) of litter in the different treatments of the two mangrove species over the sampling period (weeks) during the wet season

Species	Treatment	0	2	3	4	5	6	7
<i>S. alba</i>	Bare	100	64 ± 2	46 ± 2	54 ± 3	38 ± 3	36 ± 4	36 ± 2
	Reforested	100	40 ± 3	25 ± 4	8 ± 1	3 ± 0.3	1 ± 0.2	1 ± 0.3
	Natural	100	17 ± 1	16 ± 2	2 ± 0.3			
<i>R. mucronata</i>	Bare	100	76 ± 0.3	76 ± 2	75 ± 1	68 ± 1	77 ± 1	78 ± 1
	Reforested	100	51 ± 1	50 ± 2	40 ± 3	48 ± 2	27 ± 1	27 ± 1
	Natural	100	49 ± 1	32 ± 2	16 ± 2	13 ± 2	13 ± 3	8 ± 2

Table 3

Decay constants (K), correlation coefficients (R^2) from exponential equations and calculated half lives (t_{50} expressed in days) of *S. alba* and *R. mucronata* bare, reforested and natural treatments during the dry and wet seasons

Stand	Treatment	Season	Kd^{-1}	R^2	t_{50}
<i>S. alba</i>	Bare	Dry	0.18	0.8312	27
		Wet	0.16	0.8194	31
	Reforested	Dry	0.59	0.9132	8
		Wet	0.85	0.978	6
	Natural	Dry	1.06	0.9536	5
		Wet	1.38	0.9703	3
<i>R. mucronata</i>	Bare	Dry	0.01	0.2743	379
		Wet	0.03	0.2964	164
	Reforested	Dry	0.10	0.8978	47
		Wet	0.19	0.8195	26
	Natural	Dry	0.18	0.7723	27
		Wet	0.41	0.9406	12

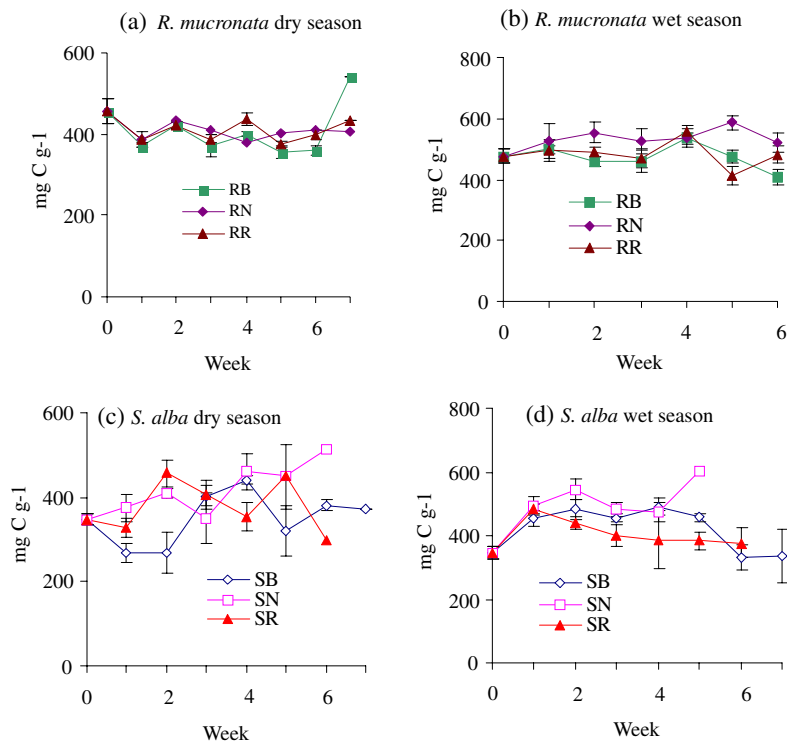


Fig. 1. Changes in C concentrations ($mg\ C\ g^{-1}$) during decomposition in the *R. mucronata* treatments (RB, bare; RN, natural; RR, reforested) during the (a) dry season; (b) wet season and *S. alba* treatments (SB, bare; SN, natural; SR, reforested) during the (c) dry season; (d) wet season (means ± se).

3.2. C and N concentrations

Among species, *S. alba* had lower C concentrations than *R. mucronata* (Fig. 1(a) and (b)). Inter-seasonal variations differed ($P < 0.01$) with the dry season having higher concentrations for both species. C concentrations remained fairly constant ($P = 0.896$) during the sampling period (Fig. 1(a)–(d)) with minor variations. For instance during the wet season, the initial C concentration in *R. mucronata* leaves was $477 \pm 25 \text{ mg C g}^{-1}$, while the concentration in its natural treatment by the 8th week was $474 \pm 49 \text{ mg C g}^{-1}$. For the *S. alba* leaf material with an initial C concentration of $348 \pm 13 \text{ mg C g}^{-1}$ in the dry season, concentration by the 7th week in the bare treatment was $373 \pm 46 \text{ mg C g}^{-1}$. C concentrations among treatments within species were similar ($P = 0.077$).

Sonneratia alba species had higher ($P < 0.01$) N concentrations than *R. mucronata* (Fig. 2(a)–(d)). The wet season had higher ($P < 0.01$) N concentrations across treatments than the dry season. For instance in the dry season, the *S. alba* species with an initial N concentration of 5 mg g^{-1} , its reforested treatment had $7 \pm 0.2 \text{ mg g}^{-1}$ at the end of the sampling period, while during the same period in the wet season it had

$10 \pm 1.7 \text{ mg g}^{-1}$. N concentrations increased throughout the sampling period in all treatments, with the exception of the *R. mucronata* bare treatment where N concentration remained fairly constant in the dry season (Fig. 2(a)). Within the *R. mucronata* species from an initial N concentration of 5 to $6 \pm 1 \text{ mg g}^{-1}$ in the bare, $13 \pm 0.6 \text{ mg g}^{-1}$ in the reforested and $12 \pm 1.7 \text{ mg g}^{-1}$ in the natural treatments in the wet season, the latter two treatments had similar and higher concentrations than the former. A similar trend was replicated during the dry season within this species. However, the *S. alba* treatments had similar N increases over time and in both seasons. Among species, C:N ratios (Fig. 3(a)–(d)) were higher ($P < 0.01$) in the *R. mucronata* species than in *S. alba*. Within *R. mucronata* species C:N ratios were similarly lower in natural and reforested treatments, than in the bare control. The *S. alba* treatments however had similar C:N ratios over the sampling period in both seasons. Total N remaining (%) decreased more rapidly in the *S. alba* species ($P < 0.01$) than in the *R. mucronata* species (Fig. 4(a)–(b)) following dry weight loss trends with rates being highest in natural treatments, intermediate in reforested treatments and least in bare treatments for both species. However, there were no significant seasonal variations ($P = 0.862$) in total N loss.

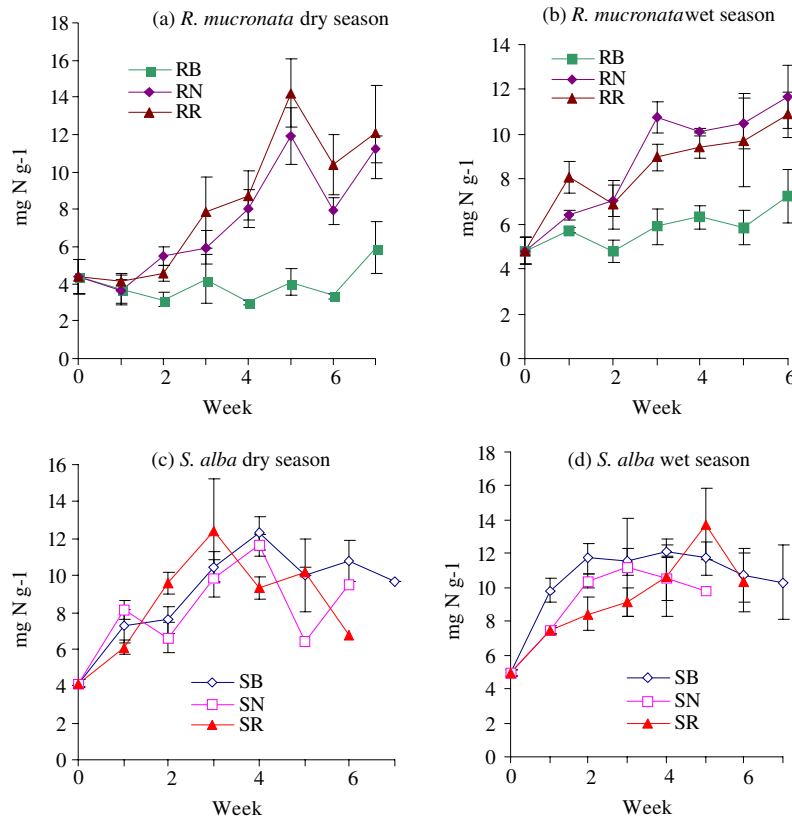


Fig. 2. Changes in N concentrations (mg N g^{-1}) during decomposition in the *R. mucronata* treatments (RB, bare; RN, natural; RR, reforested) during the (a) dry season; (b) wet season and *S. alba* treatments (SB, bare; SN, natural; SR, reforested) during the (c) dry season; (d) wet season (means \pm se).

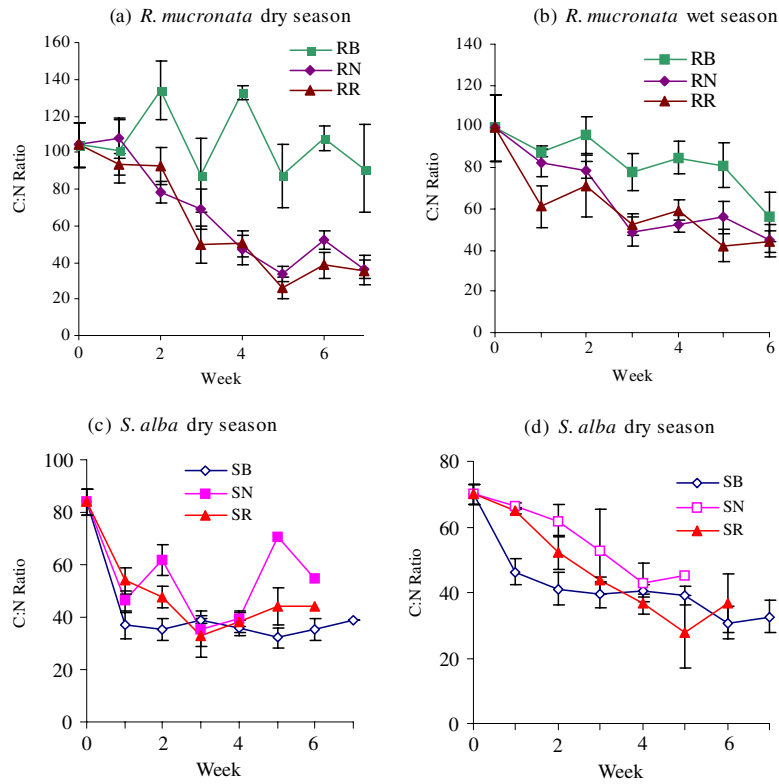


Fig. 3. Changes in C:N ratios during decomposition in the *R. mucronata* treatments (RB, bare; RN, natural; RR, reforested) during the (a) dry season; (b) wet season and *S. alba* treatments (SB, bare; SN, natural; SR, reforested) during the (c) dry season; (d) wet season (means \pm se).

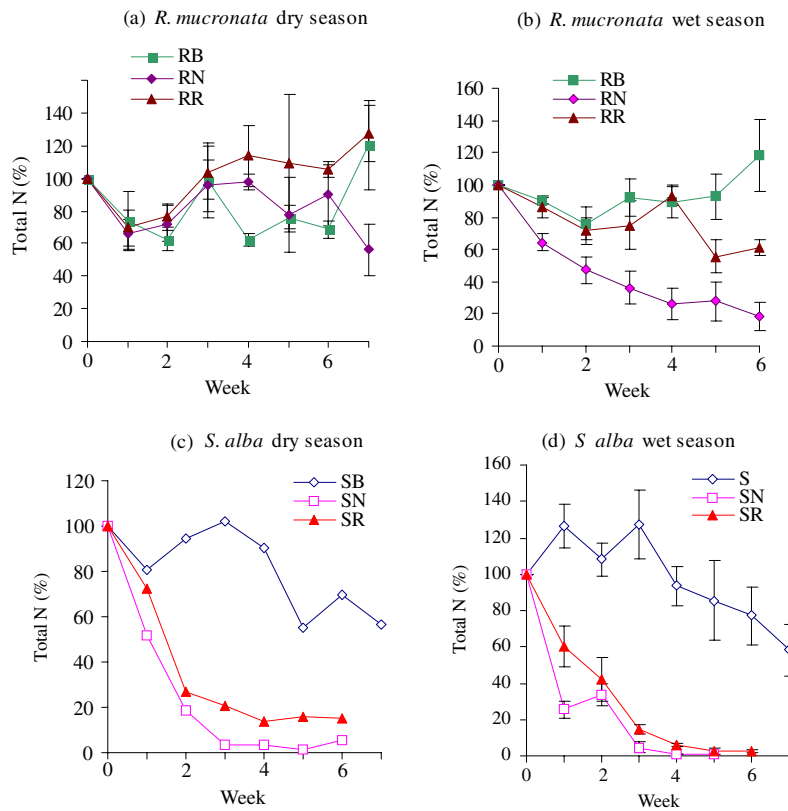


Fig. 4. Changes in total N% during in the *R. mucronata* treatments (RB, bare; RN, natural; RR, reforested) during the (a) dry season; (b) wet season and *S. alba* treatments (SB, bare; SN, natural; SR, reforested) during the (c) dry season; (d) wet season (means \pm se).

4. Discussion and conclusion

Decay rates within both species were highest in natural treatments, intermediate in reforested treatments and lowest in bare controls. Initial weight losses during the first two weeks were also more rapid in natural and reforested treatments emphasising the importance of mangrove cover in enhancing detrital material degradation in the system and concomitant nutrient regeneration. The initial rapid weight loss rates were most likely due to the fast release of non-structural carbohydrates such as sugars and starches (dissolved organic materials – DOM) easily utilised by microbes (Benner et al., 1988; Tam et al., 1990; Mfilinge et al., 2002), which subsequently colonised and initiated the breakdown of leaf material.

Amphipods, nematodes, turbellarians, isopods and polychaetes were found to colonise litter in natural and reforested treatments' litterbags in both species, which never occurred in bare treatments. Amphipods were the dominant group suggesting that they were relatively more important in enhancing litter breakdown. This faunal component has been found to enhance degradation by feeding directly on detritus (Camilleri, 1992; Poovachiranon et al., 1986) and this directly influences the rate of decomposition (Basaguren and Pozo, 1994). No amphipods were however observed in the *R. mucronata* bare treatment litter bags, which had the lowest decay rate. This corresponds to the findings of Bosire et al. (2004) who found this bare treatment to be the most impoverished in terms of faunal colonisation.

Crabs were found to tear litterbags and shred litter in *R. mucronata* natural and reforested treatments. Bosire et al. (2004) found sediment-infauna densities in these treatments (Table 4) to follow a similar trend (natural > reforested > bare), and recorded more sesarimid crab species in the natural and reforested treatments. Crab species composition was also similar among these treatments, while *Uca* spp. dominated the bare treatment. Thus, suggesting that faunal colonisation especially in reforested treatments (compared to bare treatments) is playing a significant role in litter breakdown and subsequent nutrient remineralisation. Sesarimid crabs (where they occur) initiate litter breakdown and thus enhance microbial processes in the detrital

food chain (Lee, 1998). Middleton and McKee (2001) found that exposure to crabs and amphipods tripled overall rates of leaf degradation. This suggests that the presence of herbivorous crabs in the *R. mucronata* reforested treatment, which did not occur in the bare control contributes to much higher decay rates in the former than observed in this study. Nevertheless, decay rates in the reforested treatment were still 10-fold higher (Table 3) than the bare treatment during the dry season. In the same season it could take at least 1 year for 50% of the original dry weight to be lost, while t_{50} in the same season in the reforested treatment was a comparably low 7 weeks.

Total canopy removal by clear-felling in the bare treatments has exposed the substrate to intense irradiation. Bosire et al. (2003) found significantly high interstitial water temperature and salinity in the *R. mucronata* bare treatment (compared to reforested and natural treatments), suggesting that desiccation coupled with impoverished faunal abundances could also be playing a role in retarding litter degradation/nutrient recycling. Drying of any kind kills or limits growth of microflora, removes water from plant cell cytoplasm and changes the chemical status of leaf material, which are important media for microbial growth (Mfilinge et al., 2002). Impeded microflora and macroinvertebrate colonisation due to deforestation subsequently impairs degradation processes. Mangroves modify physico-chemical parameters (Bosire et al., 2003) and create a variety of microhabitats besides providing many food materials, which encourage faunal colonisation (Macnae and Kalk, 1962; Macnae, 1968; Micheli et al., 1991; Dahdouh-Guebas et al., 1999). The modified physico-chemical conditions and macroinvertebrate colonisation seem to support higher weight loss rates in treatments with mangrove cover as compared to bare treatments (Camilleri, 1992; Benner and Hodson, 1985; Steinke et al., 1990).

Among species, decay rates were found to be higher in *S. alba*. Differential flooding (Ashton et al., 1999; Woitchik et al., 1997; Mfilinge et al., 2002) has been found to play a significant role in determining leaf detritus decay rates among lower and upper intertidal treatments. The *S. alba* treatments located at lower intertidal in this study are flooded during all high tides, whereas the *R. mucronata* treatments which were at the higher intertidal are flooded only during spring tides. Litter in the lower intertidal thus remained submerged in water for a longer time than those in the high intertidal. Litter in *R. mucronata* treatments was thus exposed to occasional drying during neap tides, which when compounded with less input of nutrients (especially N) from seawater (Gulis and Suberkropp, 2003), slowed down leaching and saprophytic decay more effective when leaves are wet (Robertson et al., 1992; Mfilinge et al., 2002). Water soaking causes leaching of labile materials and promotes microbial activity both of which

Table 4
The density of sediment infauna (macrobenthos) in the *S. alba* and *R. mucronata* treatments (Extracted from Bosire et al., 2004)

Species	Treatment	Density (n m ⁻²)
<i>S. alba</i>	Bare	7847
	Reforested	17,604
	Natural	94,757
<i>R. mucronata</i>	Bare	104
	Reforested	17,118
	Natural	18,348

increase decomposition rates (Tam et al., 1990; Ashton et al., 1999). Other than specific mangrove stand physical characteristics, differences in litter quality have also been found to be critical in influencing decay rates (Robertson, 1988; Steinke et al., 1990; Twilley et al., 1997). High tannin content is known to be aversive to detritivores and thus inhibit microbial activity (Steinke et al., 1990; Ashton et al., 1999), while nutritious leaf material with low C:N ratios have higher decay rates (Wieder and Lang, 1982). Though tannin concentrations in *Sonneratia* leaves have not been published, their lower initial C:N ratios (Rao et al., 1994) combined with high inundation frequency, may have enhanced leaf decay in this stand.

Nitrogen concentration increases over time were similar among the *S. alba* treatments. The similarity among these treatments was most likely due to frequent flooding and continuous nutrient input from the adjacent open water (Gulis and Suberkropp, 2003), which counteracted the effects of reduced nutrient supply and desiccation (due to clear felling) in the bare treatment. Within the *R. mucronata* species, increments were similar among the natural and reforested treatments, but significantly higher than in the bare treatment. N increase during the sampling period was most likely due to immobilisation (Middelburg et al., 1996) as a result of accumulation of microbial biomass and products of microbial activity, and their incorporation into humic compounds (Rice, 1982; Mfilinge et al., 2002). Melilo et al. (1984) suggested that conservation of N by decomposers throughout the sampling period may lead to N accumulation, also evident from the decreasing C:N ratios. During the wet season, lower C:N ratios, higher amphipod colonisation, moist conditions coupled with supply of inorganic nutrients through freshwater discharge (Kazungu et al., 1993; Woitchik et al., 1997) may have increased dry weight loss rates in *R. mucronata* natural and reforested treatments. There were no seasonal variations in the *S. alba* treatments probably because of the high frequency of inundation.

Generally *S. alba* treatments released more N to the surrounding (compared to *R. mucronata* treatments) most likely due to low C:N ratios, inundation frequency and accompanied nutrient supply in the former. Decomposing organic materials low in N tend to be “net immobilisers”, while materials rich in N are generally “net remineralisers”. But among treatments within each species, bare treatments were found to be the most conservative in releasing N, hence showed the slowest total N decrease. Therefore, the degree of nutrient remineralisation does not mainly depend on initial C:N ratios and tidal inundation, but also on specific site conservation status or management regimes.

Though there were differences among reforested and natural treatments in terms of dry weight loss rates which were also reflected in total N loss, N immobilisa-

tion and decrease in C:N ratios among these treatments were similar. The findings of this study suggest that other than direct litter input, mangrove reforestation modifies sites conditions in such a way that enhances the system's litter degradation and nutrient remineralisation efficiency. Coupled with this is recovery of the system's inherent ecological functions, e.g., faunal colonisation and natural revegetation, which have been found to be either impoverished or completely impaired in the bare treatments used in this study (Holmgren, 2002; Bosire et al., 2003, 2004). The findings seem to support a need for the retention of standards through selective logging to not only ensure seed availability for restocking the affected sites, but also to provide for continuity of inherent ecological functions, albeit at a potentially reduced scale. This will ensure sustainability of ecological services and economical benefits derived from concerned mangrove forests.

Acknowledgements

The efforts of KMFRI colleagues who were involved in both the fieldwork and labwork namely George Onduso, Alfred Obinga and Moses Orwenyi is highly appreciated. Much thanks are also due to Loreto De Brabandere and Steven Bouillon for assistance in C:N analysis. Jan Vermaat, Loreto De Brabandere and Steven Bouillon's review of the manuscript is highly appreciated. The first author is a VUBAROS scholarship holder, while the second author is a Postdoctoral Researcher of the Fund for Scientific Research (FWO – Vlaanderen). The International Foundation for Science (IFS) funded the work.

References

- Alongi, D.M., 1998. Coastal Ecosystem Processes. CRC Press, New York, USA.
- Alongi, D.M., Sasekumar, A., 1992. Benthic communities. In: Robertson, A.I., Alongi, D.M. (Eds.), Tropical Mangrove Ecosystems. American Geophysical Union, Washington, pp. 137–172.
- Alongi, D.M., Boto, K.G., Robertson, A.I., 1992. Nitrogen and phosphorous cycles. In: Robertson, A.I., Alongi, D.M. (Eds.), Tropical Mangrove Ecosystems. American Geophysical Union, Washington, pp. 251–292.
- Ashton, E.C., Hogarth, P.J., Ormond, R., 1999. Breakdown of mangrove litter in a managed mangrove forest in Peninsular Malaysia. In: Dodd, R.S. (Ed.), Diversity and Function in Mangrove Ecosystems, Hydrobiologia 413, 77–88.
- Basaguren, A., Pozo, J., 1994. Leaf litter processing of alder and eucalyptus in the Aguera stream system (Northern Spain) II Macroinvertebrates associated. Archive fur Hydrobiologia 132, 57–68.
- Benner, R., Hodson, R.E., 1985. Microbial degradation of the leachable and lignocellulose components of laves and wood from *Rhizophora* mangle in a tropical mangrove swamp. Marine Ecology Progress Series 23, 221–230.

- Benner, R., Hodson, R.E., Kirchman, D., 1988. Bacterial abundance and production on mangrove leaves during initial stages of leaching and biodegradation. *Archiv für Hydrobiologie* 31, 19–26.
- Bosire, J.O., Dahdouh-Guebas, F., Kairo, J.G., Koedam, N., 2003. Colonization of non-planted mangroves into reforested mangrove stands. *Aquatic Botany* 76, 267–279.
- Bosire, J.O., Dahdouh-Guebas, F., Kairo, J.G., Cannicci, S., Koedam, N., 2004. Spatial macrobenthic variations in a tropical mangrove Bay. *Biodiversity and Conservation* 13, 1059–1074.
- Boto, K.G., Bunt, J.S., 1981. Tidal export of particulate organic matter flow from a northern Australian mangrove system. *Estuarine Coastal and Shelf Science* 13, 247–255.
- Bouillon, S., Koedam, N., Raman, A.V., Dehairs, F., 2002. Primary producers sustaining macro-invertebrate communities in intertidal mangrove forests. *Oecologia* 130, 441–448.
- Bouillon, S., Dahdouh-Guebas, F., Rao, A.V.S., Koedam, N., Dehairs, F., 2003. Sources of organic carbon in mangrove sediments: variability and possible ecological implications. *Hydrobiologia* 495, 33–39.
- Camilleri, J.C., 1992. Leaf litter processing by invertebrates in a mangrove forest in Queensland. *Marine Biology* 114, 139–145.
- Dahdouh-Guebas, F., Giuggioli, M., Oluoch, A., Vannini, M., Cannicci, S., 1999. Feeding habits of non-ocypodid crabs from two mangrove forests in Kenya. *Bulletin of Marine Science* 64, 291–297.
- Gulis, V., Suberkropp, K., 2003. Interactions between stream fungi and bacteria associated with decomposing leaf litter at different levels of nutrient availability. *Aquatic Microbial Ecology* 30, 149–157.
- Heald, E.J., 1971. The productivity of organic detritus in a south Florida estuary. University of Miami Sea Grant Technical Bulletin No. 6, 110 pp.
- Hemminga, M., Slim, F.J., Kazungu, J., Ganssen, G.M., Nieuwenhuize, J., Kruij, N.M., 1994. Carbon outwelling from a mangrove forest with adjacent seagrass beds and coral reefs (Gazi Bay, Kenya). *Marine Ecology Progress Series* 106, 291–301.
- Holmgren, S., 2002. Re-establishment of algae and benthic fauna in replanted mangroves. MSc. Thesis, University of Stockholm, Stockholm, Sweden, 32 pp.
- Jennerjahn, T.C., Ittekkot, V., 2002. Relevance of mangroves for the production and deposition of organic matter along tropical continental margins. *Naturwissenschaften* 89, 23–30.
- Kazungu, J., Dehairs, F., Goeyens, L., 1993. Distribution of particulate and organic material in Gazi Bay. In: Woitichik, A.N. (Ed.), *Dynamics and Assessment of Kenyan Mangrove Ecosystems*, Commission of the European Communities, Project TS2-0240-C (GDF), Final Report, pp. 175–193.
- Lee, S.Y., 1990. Primary productivity and particulate organic matter flow in an estuarine mangrove-wetland in Hong Kong. *Marine Biology* 106, 453–463.
- Lee, S.Y., 1998. Ecological role of grapsid crabs in mangrove ecosystems: a review. *Marine and Freshwater Research* 49, 335–343.
- Macintosh, D.J., 1984. Ecology and productivity of Malaysian mangroves crab populations (Decapoda: Branchyura). In: Soepadimo, E., Rao, A.N., Macintosh, D.J. (Eds.), *Proceedings of the Asian Symposium on Mangrove Environment, Research and Management*. University of Malaya, Kuala Lumpur, Malaysia, pp. 354–377.
- Macnae, W., 1968. A general account of the fauna and flora of mangrove swamps and forests in the Indo-West Pacific region. *Advances in Marine Biology* 6, 72–270.
- Macnae, W., Kalk, M., 1962. The ecology of the mangrove swamps at Inhaca Island, Mozambique. *Journal of Ecology* 50, 19–34.
- McKee, K.L., Faulkner, P.L., 2000. Restoration of biogeochemical function in mangrove forests. *Restoration Ecology* 83, 247–259.
- Melilo, J.M., Naiman, R.J., Aber, J.D., Linkins, A.E., 1984. Factors controlling mass loss and nitrogen dynamics of plant litter decaying in northern streams. *Bulletin of Marine Science* 35, 341–356.
- Mfilinge, P.L., Atta, N., Tsuchiya, M., 2002. Nutrient dynamics and leaf litter decomposition in a subtropical mangrove forest at Ora Bay, Okinawa, Japan. *Trees* 16, 172–180.
- Micheli, F., Gherardi, F., Vannini, M., 1991. Feeding and burrowing ecology of two East African mangrove crabs. *Marine Biology* 111, 247–254.
- Middelburg, J.J., Nieuwenhuize, J., Slim, F.J., Ohowa, B., 1996. Sediment biogeochemistry in an East African mangrove forest (Gazi bay, Kenya). *Biogeochemistry* 34, 133–155.
- Middleton, B.A., McKee, K.L., 2001. Dégradation of mangrove tissues and implications for peat formation in Belizean island forests. *Journal of Ecology* 89, 818–828.
- Odum, W.E., Heald, E.J., 1972. Trophic analyses of an estuarine mangrove community. *Bulletin of Marine Science* 22, 671–738.
- Odum, W.E., Heald, E.J., 1975. The detritus-based food web of an estuarine mangrove community. In: Cronin, L.E. (Ed.), *Estuarine Research*. Academic Press, New York, pp. 265–286.
- Odum, W.E., Mcinvor, C.C., Smith III, T., 1982. *The Ecology of the Mangroves of South Florida: A Community Profile*. US Fish and Wildlife Services, Office of Biological Services, Washington (DC).
- Poovachiranon, S., Boto, K., Duke, N., 1986. Food preference studies and ingestion rate measurements of the mangrove amphipod *Parhyale hawaiiensis*. *Journal of Experimental Marine Biology and Ecology* 98, 129–140.
- Rao, R.G., Woitichik, A.F., Goeyens, L., Vanriet, A., Kazungu, J., Dehairs, F., 1994. Carbon, nitrogen and stable carbon-isotope abundance in mangrove leaves from an East Africa coastal lagoon (Kenya). *Aquatic Botany* 47, 175–183.
- Rice, D.L., 1982. The detritus nitrogen problem: new observations and perspectives from organic chemistry. *Marine Ecology Progress Series* 9, 153–162.
- Robertson, A.I., 1988. Decomposition of mangrove litter in tropical Australia. *Journal of Experimental Marine Biology and Ecology* 166, 235–247.
- Robertson, A.I., Alongi, D.M., Boto, K.G., 1992. Food chains and carbon fluxes. In: Robertson, A.I., Alongi, D.M. (Eds.), *Tropical Mangrove Ecosystems*. American Geophysical Union, Washington, pp. 293–326.
- Steinke, T.D., Naidoo, G., Charles, L.M., 1983. Degradation of mangrove leaf and stem tissues in situ in Mgeni estuary, South Africa. In: Teas, H.J. (Ed.), *Biology and Ecology of Mangroves*. Junk, The Hague, pp. 141–149.
- Steinke, T.D., Barnabas, A.D., Samuru, R., 1990. Structural changes and associated microbial activity accompanying decomposing of mangrove leaves in Mgeni Estuary. *South African Journal of Botany* 56, 39–48.
- Tam, N.F.Y., Vrijmoed, L., Wong, Y.S., 1990. Nutrient dynamics associated with leaf decomposition in a small mangrove community in Hong Kong. *Bulletin of Marine Science* 47, 68–78.
- Twilley, R.R., Lugo, A.E., Patterson-Zucca, C., 1986. Litter production and turnover in basin mangrove forests in southwest Florida. *Ecology* 67, 670–683.
- Twilley, R.R., Pozo, M., Garcia, V.H., 1997. Litter production in riverine mangrove forests in the Guayas River estuary, Ecuador. *Oecologia* 111, 109–122.
- Van der Valk, A.G., Attiwill, P.M., 1984. Decomposition of leaf and root litter of *Avicennia marina* at Westernport Bay, Victoria, Australia. *Aquatic Botany* 18, 205–221.
- Wieder, R.K., Lang, G.E., 1982. A critique of the analytical methods used in examining decomposition data obtained from litterbags. *Ecology* 63, 1636–1642.
- Woitichik, A.F., Ohowa, B., Kazungu, J.M., Rao, R.G., Goeyens, L., Dehairs, F., 1997. Nitrogen enrichment during decomposition of mangrove leaf litter in an east African coastal lagoon (Kenya): relative importance of biological nitrogen fixation. *Biogeochemistry* 39, 15–35.