

Characterization of Forest Structure and an Assessment of Litter Production, Accumulation and Litter-associated Invertebrates in Two Naturally Occurring *Rhizophora mucronata* Stands in Mauritius (Indian Ocean)

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Abstract

Many studies have cited mangroves as being among the most productive ecosystems of the world in terms of gross primary productivity and litter turnover, which forms a major food source for most estuarine animals. The present study aimed at characterizing the forest structure and assessing litter production, accumulation and litter-associated invertebrates at two naturally occurring *Rhizophora mucronata* stands in Mauritius, namely Macondé and Bambous Virieux, found respectively in the south-western and south-eastern part of the island. Comparatively with Bambous Virieux, Macondé has a taller and denser population of *Rhizophora mucronata* trees with heights ranging from 4.8 to 9.0 m and a stand density of 14622 trees per/ha. Litter fall rates at Macondé averaged at 4.63 g DW m⁻² day⁻¹ and 4.74 g DW m⁻² day⁻¹ at Bambous Virieux. Peak litter fall rates occurred at the beginning of March coinciding with strong windy period. At both sites, leaves were the most important contributors in the total litter fall: 54.2% and 42.7% at Macondé and Bambous Virieux respectively. There was a positive correlation between litter fall rate and wind speed. No site difference was found in litter production and accumulation, but there was a significant difference in litter fall rates among samplings. At Macondé, litter accumulated at an average of 780.48 g m⁻² and 649.0 g m⁻² at Bambous Virieux; the turnover rates of leaf litter were 0.12 g DW m⁻² day⁻¹ and 0.14 g DW m⁻² day⁻¹ respectively. Litter fall and turnover rates at the two sites are discussed in relation to the structural

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characteristics of the mangrove stands and to the hydrology and meteorology of the sites. The study also showed that litter forms a microhabitat to a rich diversity of species; litter-associated invertebrates comprised mainly of three Phyla: Arthropoda, Mollusca and Annelida.

Keywords: Mangroves, litter production, accumulation, turnover rates, invertebrates.

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INTRODUCTION

Mangroves are among the most productive ecosystems of the world in terms of gross primary productivity and litter production (Sessegolo & Lana, 1991). Litterfall, consisting of both vegetative and reproductive structures, represents a fraction of net primary production that can be accumulated on the forest floor, remineralized through decomposition or exported to nearby ecosystems (Brown, 1984). Decomposition of mangrove litter and detritus recycling are of major importance in mangrove ecosystems as the products from these processes make a significant contribution to the food chain of the estuarine fauna thriving the mangrove ecosystem (Snedaker & Snedaker, 1984) in which sesarmid crabs are considered to be the keystone species with regard to nutrient recycling (Kristensen *et al.*, 2008). Sesarmids can therefore be used as biological indicators for the productivity of mangrove forests. The influence of the organic matter provided by the mangrove litter is not just restricted to the coastal line, but extends beyond it and reaches the coral reef areas (Flemming *et al.*, 1990).

Litter dynamics in mangroves involve measurements of components such as production rates, decomposition rates, standing stock and turnover of litter; and these represent a major step in understanding the structure and function of the ecosystem. Litter fall is the shedding of vegetation and reproductive plant structures that may be caused by senescence or stress; by mechanical factors, for example wind; by a combination of all these; or by death and weathering of the whole plant (Brown, 1984). Litter fall is an important index of potential carbon transport to coastal ecosystems (Twilley *et al.*, 1997) and the activity of macro-litter decomposers such as sesarmid crabs (Woodroffe, 1982). Mangroves are widely recognized as important sources of organic carbon which enter estuaries in the form of fallen leaves, twigs and reproductive structures. In this respect, because it is an important component of productivity and because methods of directly measuring primary productivity in mangrove forests are technically difficult (Tam *et al.*, 1998), litter fall measurement is a commonly measured functional aspect of mangrove forests (May, 1999). As for leaf litter turnover, all aspects of ecological processes of leaf loss from the mangrove forest floor are integrated in its measurement. These processes include degradation, tidal export and crab consumption of the accumulated litter (Twilley *et al.*, 1997). In this same study, greater leaf litter turnover was associated with increased soil fertility, greater removal by crabs, increased tidal frequency and with the rainy season which in turn corresponds to higher export due to the effect of tides on the transport of leaf litter from the forest floor.

By 1993, the extent of mangroves in Mauritius was estimated to be up to 200 hectares (Kelleher *et al.*, 1995). Mangroves are mainly encountered on the east coast of the island, namely Trou d'Eau Douce, Pointe d'Esny, Poste Lafayette, Poste de Flacq and other islets such as Illot Brocus and Ile aux Cerfs (Proag, 1995). In Mauritius, only two species of mangroves occur, both of the Family Rhizophoraceae: *Bruguiera gymnorrhiza* and *Rhizophora mucronata* (Fagoonee, 1989; Appadoo, 2003); the latter species being the dominant one throughout the island (Fagoonee, 1989). Studies on mangrove ecosystems in Mauritius are rare with some recent studies focusing on mangrove-associated fungi (Poonyth *et al.*,

1999), molluscs (Appadoo & Romaldawo, 2005) and zooplanktons (Gunoo & Appadoo, 2004).

The aim of the present study is to provide information on the forest structure in two naturally occurring mangrove sites, Macondé and Bambous Virieux. The study also investigates on litter production, accumulation and assesses the productivity of the mangrove ecosystems in terms of the rates at which litter is entering the ecosystem; it aims at providing quantitative data on the litter that is available for local recycling by the benthos. This paper also reports the species richness of the invertebrate fauna associated with the mangrove litter.

MATERIALS AND METHODS

Study Areas

Two mangrove study sites were chosen: Macondé in the South-Western (20.45°S, 57.34°E) and Bambous Virieux, in the South-Eastern (20.33°S, 57.76°E) part of Mauritius. The sites were chosen according to the type of mangrove stands present there: at both sites, there were naturally occurring mangroves which had suffered little or no damage (e.g. from felling) and the mangrove stands were located far from residential areas. At both sites, there was a river flowing through the mangrove forest into the lagoon.

Macondé is composed of an approximate area of 0.6 hectare of a natural dense adult population of *Rhizophora mucronata*. The mangroves trees grow in sediment which is principally made up of a very fine sand of grain size of 106µm (Marooty, unpublished). The crab burrow density which is also an indication of the population density of crabs, was estimated to be 1.188×10^6 per hectare (Marooty, unpublished). Macondé is a sloppy area where the mangrove ground is partly inundated at high tides. Based on classification by Lugo and Snedaker (1974) mangroves of Macondé may be described as a fringing forest as it consists of a shoreline which is higher to the mean high tide. The reef is found at approximately 1 km from the shoreline. The adult trees formed a non-uniform band of an approximate length of 70 m along the coastline. Data obtained from the Mauritius Meteorological Services showed that during the study period, the maximum amount of rainfall was 140mm; this amount was recorded in the month of January. The wind speed varied from 1.9 to 43.8 km/h, while the range of atmospheric temperature was between 23.3 °C and 29.9 °C. Macondé is found in a characteristically dry and arid area of Mauritius.

At Bambous Virieux, the mangrove formation consisted of a mixed stand of *Rhizophora mucronata* and *Bruguiera gymnorrhiza* species; with *R. mucronata* being the dominant species. The total mangrove area in Bambous Virieux is 1.5 hectare. *Bruguiera gymnorrhiza* accounts about 1.0% of the total mangrove trees at Bambous Virieux and therefore this mangrove species has minimal contribution to the litter in the ecosystem. According to Lugo and Snedaker (1974) Bambous Virieux may be defined as an overwash forest that is frequently inundated and

flushed by the tides. Similarly to Macondé, the site at Bambous-Virieux was made up of a major portion of very fine sand of grain size 106 μm . The area adjacent to the mangrove forest is used for agricultural purposes. The number of crab holes at this study site was estimated to be 2.76×10^5 per hectare (Marooty, unpublished). The meteorology at Bambous Virieux showed that during the study period, the maximum amount of rainfall was 407.2 mm; this amount was recorded in the month of February. The wind speed ranged from 5.6 to 29.3 km/h, while the range of atmospheric temperature varied between 22.1 °C and 28.6°C. It is important to note that South-East Trade Winds blow over the island all over the year except when Mauritius is under the influence of tropical depressions or cyclones. The mangrove site at Macondé, being sheltered by mountains, suffers less from wind action as compared to Bambous Virieux which is directly influenced by the South-East Trade Winds. The lagoon at Bambous Virieux is approximately 5 km large.

Both study sites are influenced by diurnal tides, with two low tides and two high tides daily and both sites are protected by high wave action by the large lagoon area. Tides are on average 0.6m high; neap tides and spring tides are approximately 0.5m and 0.7m high respectively (Fagoonee, 1989). Freshwater input at both mangrove sites is quite important because of the steep topography of the island, thus influencing the biochemical constitution of the sediment in which the mangrove trees dwell.

The study was carried out from November 2005 until the end of March 2006. Sampling was performed twice monthly. Results provided here can therefore be viewed as preliminary providing a base for more detailed productivity study on mangroves of Mauritius.

Assessment of the forest structures

At each site, an approximate plot of 40 m x 50 m was studied, representing a sampling intensity of 33% and 13% at Macondé and Bambous Virieux respectively. The structure of the mangrove forests was assessed using a systematic design involving 5 m x 5 m quadrats spaced at 5 m (from one edge of the quadrat to the other edge of a quadrat) apart in the studied plot area. This design is used in areas where an obvious heterogeneity can be represented (Myers & Bazely, 2003), which is the case of the mangrove forests being studied. A total of 9 permanent quadrats at each study site were sampled. In each quadrat, diameter of all the stems greater than 2.5cm was measured at 1.3m above ground (elsewhere referred to as dbh – diameter at breast height). All trees whose dbh were less than 2.5cm and height less than 3.0m were classified as juvenile (Kairo *et al.*, 2002). Dispersion of juveniles was calculated using the Morisita's Index, I_o (Morisita, 1959) as given by Sukardjo (1987) and Kairo *et al.* (2002).

$$I_o = q \sum_{i=1}^q \frac{n_i(n_i - 1)}{N(N-1)}$$

Where, q is the number of quadrats, n_i is the number of individuals per species in the i th plot and N is the total number of individuals in all q quadrats. If $I_o > 1$, the population is described as being clustered, if $I_o = 1$, the population is randomly clustered and if $I_o < 1$, the population is evenly dispersed.

In order to calculate the mean dominant height (MDH), the heights of five tallest trees were taken with the use of a graduated telescopic rod as suggested by Cintron and Novelli (1984). The canopy cover of the study areas was measured using a spherical densiometer.

Sampling of mangrove litter fall

Litter fall production in mangrove ecosystems is usually assessed through the use of litter baskets or traps (Brown, 1984). For the present study, litter traps were constructed with a circular frame of 10m diameter and a depth of 75cm. This yielded an interception area of 0.785 m² for litter. The bottom of the trap was covered with a nylon fabric with a mesh size of approximately 1.0mm² as suggested by Brown (1984). Fifteen traps were installed in each study site. The number of traps was decided with reference to the study performed by Sukardjo and Yamada (1992), where one litter trap was placed in every 10m x 10m subplot with 10m interval among the traps. Each trap was suspended to the canopy trees above the high tide mark, that is, approximately 50 cm from the ground, with the use of solid nylon strings. Litter was collected from each trap at two weeks interval and was processed in the laboratory. Two samplings were done per months, except for December and March, for which only one sampling had been performed.

In parallel to the litter fall collection from the traps, litter from the surface of the forest floor was also collected in order to determine the accumulation rate of litter on the mangrove ground floor. For this purpose, a 25cm² square quadrat was placed randomly on the ground between 3 and 10 m from each trap as suggested by Conacher *et al.* (1996) and litter was collected from the quadrats.

At each sampling station environmental parameters such as; salinity, temperature, Dissolved Oxygen (DO), conductivity and pH of water were measured *in situ* at three permanent stations in each study site. Climatic parameters such as rainfall, wind speed and atmospheric temperature during the study period were obtained from the local meteorological station.

Litter processing

In the laboratory, litter collected from each trap was oven-dried to constant weight at 70°C (Day *et al.*, 1996), sorted into leaves, stipules, woody materials, flowers, fruits and “others” (debris from plants other than the mangrove trees) and weighed to the nearest 0.1 g (Twilley, 1997). The ground-litter samples used for the determination of litter accumulation rate, were processed in the same manner as the litter fall.

Saenger and Snedaker (1993) present a predictive equation for the expected mangrove litter fall rate. The equation uses the linear regression of litterfall against

the ratio of latitude and height:

$$\text{Litterfall (t.ha}^{-1}\text{)} = 10.366 - \log_e (\text{Latitude/Height})$$

The expected litterfall for Macondé and Bambous Virieux was calculated using the above equation and compared with the true litterfall rate obtained in the present study.

The turnover rate of leaf litter on the floor of the forest was estimated using the equation developed by Olson (1963):

$$k = L / X_{ss}$$

Where, L: input or leaf litter fall production

X_{ss} : steady-state content of leaf litter accumulated on the forest floor

k: turnover rate

Litter-Associated Invertebrate Fauna

The samples collected from the forest floor were used for the study of the litter-associated macro-organisms (≥ 2.0 mm). The litter was sorted and the organisms collected were preserved in 5% formaldehyde for later identification.

Statistical Analyses

Data for litter production rates, accumulated litter, physical and climatic parameters and abundance of invertebrate fauna were tested for normality by the Shapiro-Wilk test. Two-way ANOVA was used to test for any difference ($p < 0.05$) in litter fall and accumulation rates between the sites and among the samplings. Regression analysis was used to relate physical and climatic parameters (rainfall, wind speed, air temperature, water temperature, salinity, pH, DO, conductivity) to the amount of litter falling into the mangrove ecosystem. All statistical analyses were run with SPSS (SPSS Inc., 2004).

RESULTS

Structural characteristics of the mangrove forests

At Macondé, the total number of mangrove trees surveyed in all the nine quadrats, which covered an area of 225 m², amounted to 329 (Table 1). Tree height ranged from 4.8 m to 9.0m, with the Mean Dominant Height (MDH) of 6.8 ± 0.9m. Stem diameters of adult mangrove trees ranged from 2.5 cm to 11.4 cm (mean: 4.8 ± 1.9 cm). The basal area of the mangrove stand at Macondé was 30.8 m² per hectare of ground area. The density of juveniles was 6.58 x 10⁴ trees/ha and according to the Morisita's dispersion index, they were evenly dispersed across the mangrove site ($I_0 < 1$). The mangrove tree density was 14622 trees/ha with a canopy cover of 81.7%.

Attribute	Site	
	Macondé	Bambous Virieux
Height range (m)	4.8 - 9.0	3.8 - 7.5
MDH * (m)	6.8 ± 0.9	5.2 ± 1.0
Canopy cover (%)	81.7	74.6
Basal Area (m² per hectare)	30.8	17.6
Stand Density (trees per hectare)	1.46 x 10 ⁴	9.6 x 10 ³
DBH range (cm)	2.5 - 11.4	2.5 - 8.9
Juveniles (per hectare)	6.58 x 10 ⁴	1.17 x 10 ⁵

Table 1. Structural characteristics of the mangrove stands at Macondé and Bambous Virieux

At Bambous Virieux, tree height ranged 3.8 m to 7.0 m, with the MDH of 5.2 ± 1.0m. As for the dbh range of mangrove trees in Bambous Virieux, it varied from 2.5 cm to 8.9 cm (mean: 4.3 ± 1.4cm). The basal area of the mangrove stand at Bambous Virieux was 17.6 m²/ha. The number of juveniles was 1.17 x 10⁵/ha of mangrove area. According to the Morisita's Index, the juvenile trees were regularly dispersed throughout the site ($I_0 < 1$). The mangrove tree density was 9636 trees per hectare and the canopy cover was 74.6%.

Litter production

The mean bimonthly litter fall rate at Macondé was 4.6 ± 2.5 g DW m⁻² day⁻¹ (Fig. 1). There was a variation in the litter fall rates among the samplings, with the highest peak (10.3 g DW m⁻² day⁻¹) occurring in the month of March. The mean bimonthly litter fall rate at Bambous Virieux was 4.7 ± 3.5 g DW m⁻² day⁻¹.

Similarly to Macondé, there was a variation in the litter fall rates among the samplings, with the highest peak ($13.1 \text{ g DW m}^{-2} \text{ day}^{-1}$) also occurring in the month of March. The highest standard error for litter fall rate at both study sites occurred in the month of March. The two-factor ANOVA revealed no significant difference ($p = 0.84$, $F = 0.04$, $df = 1$) in the mean bimonthly litter fall rates between the two sites. However, a significant difference ($p = 0.001$, $F = 17.79$, $df = 7$) in litter fall rates among sampling dates was noted. According to Saenger and Snedaker (1993) equation the expected mangrove litterfall rate at Macondé and Bambous Virieux should have been 9.340 t.ha^{-1} ($9.340 \times 10^2 \text{ g/m}^2$) and 9.378 t.ha^{-1} ($9.378 \times 10^2 \text{ g/m}^2$), which is well above the true rate obtained in the present study.

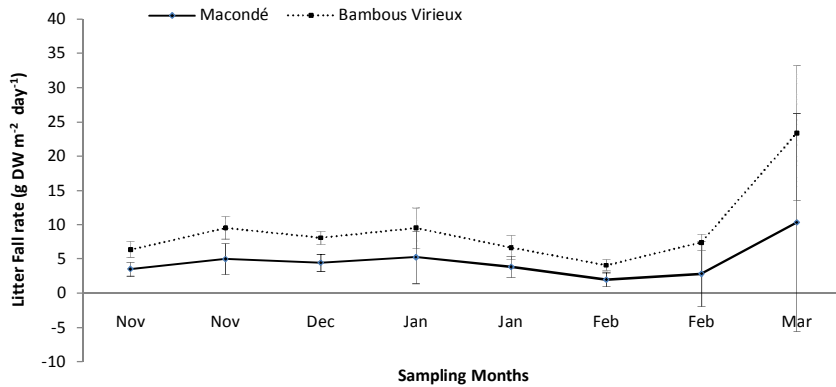


Fig. 1. Variation in mean bimonthly litter fall rates. The graph shows the highest litter fall rates occurring in the month of March at both study sites.

Mangrove litter consisted of leaves, stipules, wood, flowers, fruits and other debris that had been blown into the traps. At both sites, leaves were the most important contributors to the total litter fall, accounting for 54.2% and 47.2% of the total litter fall at Macondé and Bambous Virieux respectively.

Regression analysis showed that the parameter which can best explain the variability in litter fall production at the two sites is wind speed. Figures 2(a) and 2(b) shows the relationship between mean bimonthly litter fall rates and mean bimonthly wind speeds at Macondé and Bambous Virieux respectively. The other

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parameters (rainfall, air temperature, water temperature, salinity, pH, DO and conductivity) were excluded as they did not significantly reflect the variations in litter fall rates.

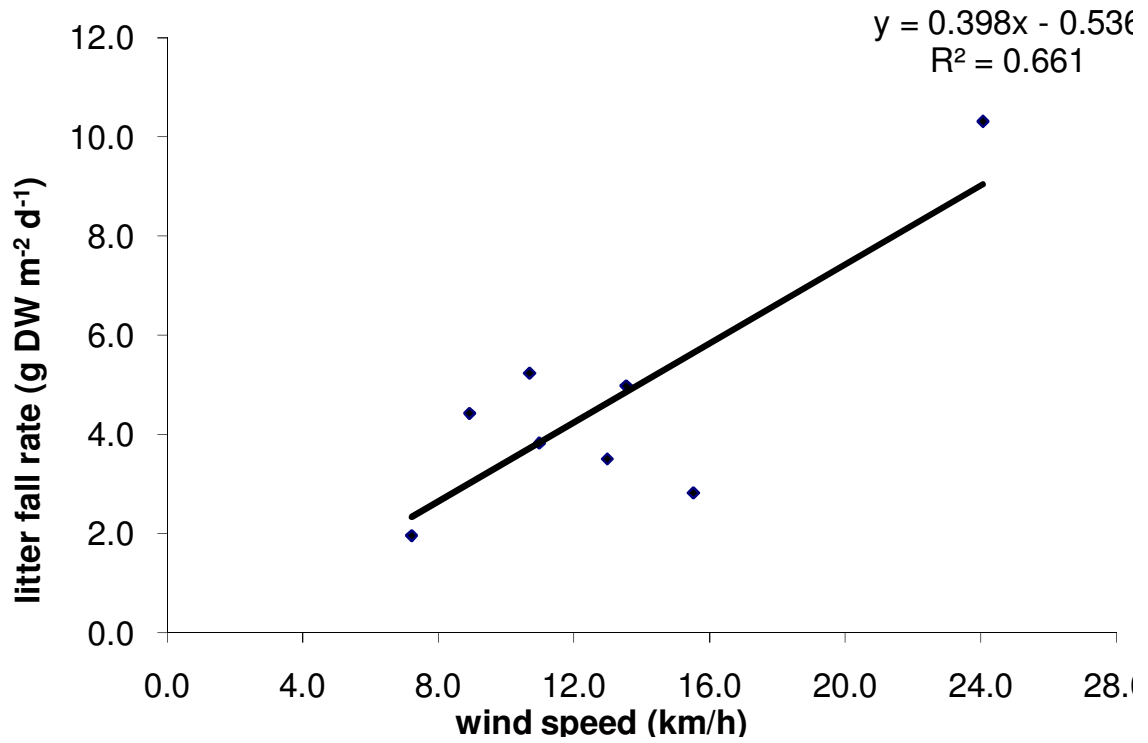


Figure 2 (a) Regression of wind speed on litter fall rate at Macondé. Wind speed is the best parameter to explain the variation in litter fall rates at the two sites.

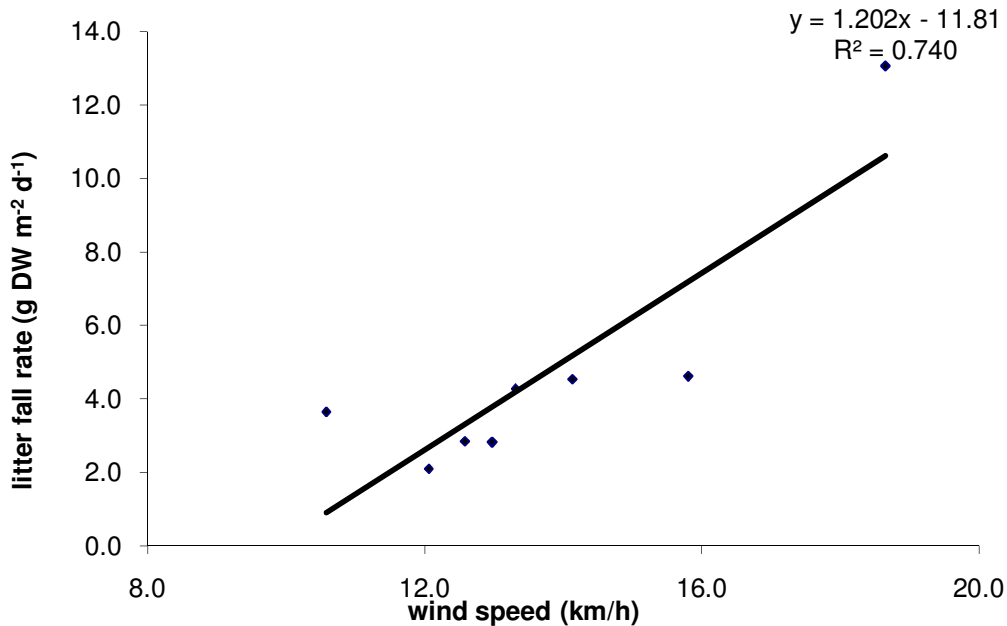


Figure 2 (b) Regression of wind speed on litter fall rate at Bambous Virieux

The equations for the regressions lines can be used to predict the litter fall rate y when wind speed x is known. For Macondé, mean daily litter fall rate was positively related to daily average wind speed according to the following equation: $y = 0.398x - 0.536$. The r^2 value for this site is 0.6613, which means that about 66% of the variation in litter fall rate is accounted for by variation in wind speed. At Bambous Virieux, mean daily litter fall rate was also positively related to average wind speed according to the following equation: $y = 1.203x - 11.811$. Wind speed is accountable for 74% of the variation in litter fall rate at Bambous Virieux.

Litter Accumulation

At Macondé, the bimonthly amount of accumulated litter ranged from 425.3 to 1275.3 g m⁻², with a mean of 780.5 ± 298.6 g m⁻². High amounts of litter accumulated on the ground in the month of December and March. The lowest amount of accumulated litter (425.3 g m⁻²) was reported during the first sampling in the month of November. At Macondé, the accumulated litter consisted mainly of mangrove leaves (36.9%).

At Bambous Virieux, the bimonthly amount of accumulated litter ranged from

177.71 to 1062.01 g m⁻², with a mean of 649.0 ± 305.1 g m⁻². The highest amount of litter accumulation (996.9 g m⁻²) occurred at the beginning of the month of January. The lowest amount of accumulated litter (425.3 g m⁻²) was reported during the first sampling in the month of November. Figure 3 shows the patterns for the mean bimonthly amounts of litter accumulating on the mangrove forest floor at the two study sites. Similarly to Macondé, the most important contributors (37.4%) to the accumulated litter at Bambous Virieux were mangrove leaves.

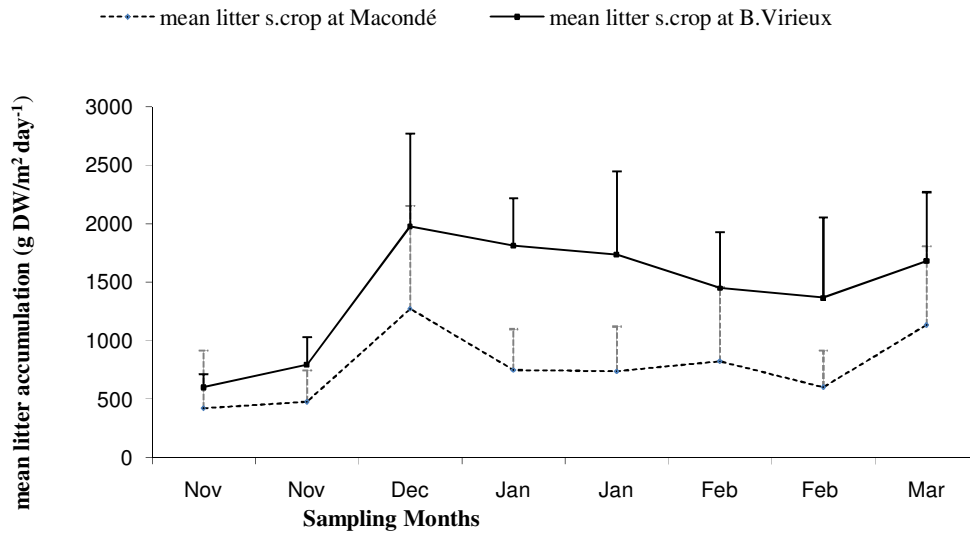


Figure 3. Variation in accumulated litter at Macondé and Bambous Virieux. There was no significant difference in the amounts of litter accumulation between the study sites ($p > 0.05$).

Two-factor ANOVA showed that there was no significant difference in the amounts of accumulated litter between the sites ($p = 0.191$, $F = 1.1$, $df = 1$) and among the samplings ($p = 0.322$, $F = 2.0$, $df = 7$). From the equation developed by Olson (1963), the turnover rates of leaf litter were 0.12 g DW m⁻² day⁻¹ and 0.14 g DW m⁻² day⁻¹ at Macondé and Bambous Virieux respectively.

Litter Associated Invertebrate Fauna

Overall, three Phyla of invertebrates were found among the litter namely Arthropoda, Mollusca and Annelida (Table 2). Most of the organisms were identified to Family level, except for arachnids and annelids. At both sites, the litter-associated invertebrates were best represented by the Phylum Arthropoda, which represented 73.0% and 52.6% of the species at Macondé and Bambous Virieux respectively. The organisms from this Phylum consisted of amphipods,

isopods, Brachyuran crabs, spiders and different families of insects. The phylum Mollusca consisted of gastropods and the annelids were characterised by polychaete and oligochaete worms. The number of species found at Macondé was 37, while 19 species were present in the litter at Bambous Virieux. There are 12 species which are common to both Macondé and Bambous Virieux.

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PHYLUM	CLASS	ORDER	FAMILY	ASSIGNED NAME	Macondé	B. Virieux
Arthropoda	Subphylum Crustacea: Class Malacostraca	Amphipoda	Talitridae	TAL1	+	+
		Isopoda	Ligidae	LIG1	+	+
			Sphaeromatidae	SPH1	+	+
		Decapoda	Grapsidae	GRA1	-	+
				GRA2	+	+
				GRA3	+	-
		Arachnida	Araneae	RTU1	+	-
				RTU2	+	+
				RTU3	+	-
	RTU4			+	-	
	RTU5			+	-	
	RTU6			+	-	
	RTU7			-	+	
	RTU8	+	-			
	Diplopoda			RTU9	+	-
	Insecta	Dermaptera	Chelisochidae	CHE1	-	+
			Forficulidae	FORf1	-	+
		Hymenoptera	Formicidae	RTU10	+	-
				FORm1	+	-
		Coleoptera	Staphylinidae	STA1	+	-
			Curculionidae	CUR1	+	-
		Hemiptera	Nabidae	RTU11	+	-
				NAB1	+	-
		Isoptera		RTU12	+	-
		Diptera	Agromyzidae	AGR1	+	-
		Dictyopera	Blattidae	BLA1	+	+
				BLA2	+	-
BLA3				+	-	
Collembola		RTU13	+	-		
Mollusca	Gastropoda	Archaeopulmonata	Ellobiidae	ELO1	+	+
				ELO2	-	+
				ELO3	+	+
				ELO4	+	-
				ELO5	+	+
				ELO6	+	+
				ELO7	-	+
		Neritopsina	Neritidae	NER1	+	-
				NER2	+	-
				NER3	+	-
Neotaenioglossa	Assimineidae	ASS1	+	+		

Annelida	Polychaeta			RTU14	-	+
	Oligochaeta			RTU15	+	+

Table 2. Checklist of litter associated organisms identified at different taxonomic levels

Worldwide, mangroves are important producers of litter and the major process by which the nutrient pool of a mangrove ecosystem becomes enriched is the export of decomposable organic matter, mostly in the form of plant litter (Hegazy, 1998). The influence of this organic matter provided by the mangrove litter extends beyond the coastal line, reaching the coral reef areas (Fleming *et al.*, 1990). Litter production is subjected to continuous temporal and spatial variations. These variations have been discussed below in the context of the present study of the mangrove ecosystem in Mauritius.

Forest Structure

Comparison of the heights of the *Rhizophora* stands in Mauritius (Table 1) shows that our forests are dwarf. For example, in a study conducted by Cole *et al.* (1999) in Micronesia, natural stands of *Rhizophora mucronata* plantations ranged in heights from 14 to 21 m. Structure of the forest in Mauritius appear to be similar to mangrove stands at Gazi bay in Kenya (Bosire *et al.*, 2008a, 2008b) whose heights range from 3 to 11 m with stem diameter in the range of 2.5 to 12.4 cm. Observations on basal area of *Rhizophora* in Mauritius reveals basal areas of 30.8 at Macondé and 17.6 at Bambous Virieux. Basal areas in natural mangrove forests of mean height of 7.5 m have been reported to be 34 m² per hectare in Gazi Bay, Kenya (Bosire *et al.*, 2003). Low basal areas like that reported for Bambous Virieux have been observed in *Rhizophora* stands of similar heights in Indonesia (Sukardjo and Yamada, 1992). Stand density appears to be fairly high in Mauritius, however it is difficult to explain this observation as not much data is available on the geomorphology of the site. One of the reasons evoked for larger number of trees per hectare in some islands compared to others are large-scale disturbances in the past such as hurricanes and typhoons (Cole *et al.*, 1999). Mauritius is known to be affected by cyclones, however the effects of these events on the density of plants remain to be investigated.

Litter Fall Rate

This is the first study in Mauritius to report on litter fall rates and provide baseline information on relative productivity of the mangroves in the area. Comparative studies on mangrove productivity in the Western Indian Ocean region have been carried out in Kenya (e.g. Gwada and Kairo, 2001) as well as in South Africa (Steinke and Ward (1990). In the present study the litter fall rates were 4.6 g DW m⁻² day⁻¹ and 4.7 g DW m⁻² day⁻¹ at Macondé and Bambous Virieux respectively. This is similar to litter fall rate of 4.36 g m⁻² day⁻¹ for Mida Creek that was reported by (Gwada and Kairo, 2001); but higher than litter fall production of 2.51 ± 1.15 DW gm⁻² day⁻¹ reported by Slim *et al* (1996) for Gazi mangroves. Similarly in Ecuador, Twilley *et al.* (1997) reported a litter fall of 1.5 g m⁻² day⁻¹ in a mangrove stand dominated by *Rhizophora mangle*. These results indicate great variability in litter fall rates across the world; mostly influenced by climate, species, management regimes and seasons.

According to Steinke and Ward (1990), greater litter production is directly related to peak rainfall and very strong winds. This may account for the general trend observed in litter production at the two mangrove sites, with the lowest litter fall rate occurring during February. Litter production in mangroves is known to respond to seasonality in rainfall, river flow, soil salinity, air temperature, irradiation, winds (Day *et al.*, 1996) and to storm conditions (Woodroffe, 1982). In the present study, however, no significant correlations were found between litter fall rates and rainfall, air temperature as well as the physical parameters. A significant correlation between mean bimonthly litter fall rates and mean bimonthly wind speed was reported at both study sites. The lowest litter fall rates at both sites corresponded to low wind speeds. For Macondé, the lowest mean litter fall rate (1.96 g DW m⁻² day⁻¹) corresponded to a wind speed of 7.21 km/h, while at Bambous Virieux, the lowest litter fall rate (2.10 g DW m⁻² day⁻¹) corresponded to a wind speed of 12.06 km/h. The highest litter fall rates at both Macondé and Bambous Virieux occurred in the beginning of the month of March, which was also characterised by a cyclone, named “Diwa” which hit the island on the 3rd March 2006. Data from the Mauritius Meteorological Services showed that during the cyclonic period, the mean amount of rainfall in Mauritius was 229 mm which represented 95% of the mean amount of rainfall normally occurring in the month of March. Gusts of more than 100 km/h were reported during the cyclone. The last sampling was performed approximately one week after the cyclone. This led to the conclusion that wind speed, especially during the cyclone, had the strongest effect on litter fall. A sharp increase in litter fall rates were observed during the cyclonic period: Macondé recorded a litter fall rate of 10.31 g DW m⁻² day⁻¹ and at Bambous Virieux, the litter fall rate was 13.06 g DW m⁻² day⁻¹. Thus, the cyclone had influenced the litter fall rates in a significant way, creating a disproportionate peak in the pattern of litter fall throughout the sampling period. According to Woodroffe (1982), storms may merely precipitate the fall of litter which would have fallen naturally in the following weeks and hence, this peak in the litter rates during the last sampling would not have been recorded. High standard errors at the last sampling could be due to the increased randomness of the falling of the debris into the different litter traps as a result of the violent gusts of more than 100 km/h during the cyclone. The high standard error bars recorded during the last sampling in March may be accounted for by the random fall of the mangrove debris in the traps, which are influenced by the directions of the wind and wind speeds. The violent gusts during the cyclonic period had further contributed to the random fall of the debris. These gusts have also precipitated the abscission and fall of mangrove structures. Unfortunately, no previous studies have been made on the mangrove litter production during cyclonic periods. Therefore, no comparison can be made with previous cyclonic periods with respect to the litterfall rates. It is important to note here that the short period for which the present study lasted might bring some bias to the correlation of litter production and other seasonal and biochemical fluctuations. The amount of data obtained might not be sufficient to allow such correlations.

In most litter production studies on mangroves (e.g. Twilley *et al.*, 1986; May, 1999; Gwada and Kairo, 2001; Mfilinge *et al.*, 2005), leaf fall is found to be the

dominant contributor to total litter yield. At Macondé and Bambous Virieux sites of this study, leaves contributed the most to the total litter. In fact, the high productivity of mangroves is also expressed in terms of leaf litter production (Snedaker & Snedaker, 1984). According to May (1999), two factors are likely to precipitate leaf senescence and abscission. First, the actively growing fruits and new leaves may successfully compete with older leaves for photosynthates (May, 1999). The subsequent diversion of resources into fruit and new leaves leads to the elimination of old inefficient leaves by the mangrove tree. Secondly, the seasonal increases in substrate salinity which precedes the reduction in photosynthetic capacity will hasten the abscission of aging leaves. In a study by Slim *et al.* (1996) on the litter fall of *Rhizophora mucronata* in a mangrove forest in Kenya, a mean leaf litter fall rate of $2.51 \pm 1.15 \text{ g DW m}^{-2} \text{ day}^{-1}$ was recorded. At Macondé and Bambous Virieux, higher leaf fall rates were recorded: $2.9 \pm 1.0 \text{ g DW m}^{-2} \text{ day}^{-1}$ and $3.2 \pm 1.0 \text{ g DW m}^{-2} \text{ day}^{-1}$ respectively.

Litter Accumulation

At both sites, there was high variability in the amount of litter accumulating on the forest floor during the whole sampling period. In a study by Conacher *et al.* (1996), it was suggested that tidal inundation and rainfall were the main means by which mangrove litter is removed from the mangrove forest floor. In this same study, it was found that when rainfall was higher and the tides were more frequent and inundated the forest for a longer period of time, less litter accumulated on the ground as it was washed directly into the sea. Temporal variation in all these factors may have influenced the amount of accumulated litter at the mangrove forests under study. There was no significant difference in the amount of litter accumulating on the forest floor between the sites or among the samplings. This may be due to the fact that both sites are influenced by tides the same amount of time per day, that is, they are both submitted to diurnal tides and they are also subjected to nearly the same amount of rainfall. The amount of litter accumulating on the floor also depends on its rate of decomposition, which is in turn controlled by temperature, humidity, soil pH, aeration and the nature of plant material, microbial populations and soil fauna (Lugo & Snedaker, 1974). However, in the present study no experiments have been performed on the decomposition rates of mangrove litter. In this respect, the leaf litter turnover rates can reflect the decomposition rates of mangrove litter (Twilley *et al.*, 1997) such that higher turnover and lower residence time can be related to higher decomposition by mangrove fauna, the main decomposers being crabs. Leaf litter turnover rates between the two sites are not significantly different: it is approximately $0.12 \text{ g DW m}^{-2} \text{ day}^{-1}$ at Macondé and $0.14 \text{ g DW m}^{-2} \text{ day}^{-1}$ at Bambous Virieux. Hence, there was no major site effect on the amount of litter accumulating on the ground as the sites underwent nearly the same climatic and biophysical influence.

Litter-Associated Invertebrate Fauna

Since leaf breakdown plays a key role in ecosystem function, species richness of leaf litter may be important in determining the nature of relationships between biodiversity and ecosystem properties. Litter-associated organisms are fundamental in the recycling of organic matter in the mangrove ecosystem; in the absence of the faunal component, decomposition would not proceed beyond a certain point (Alfaro, 2006). To show the importance of mangrove associated fauna

in litter decomposition, Slim *et al.* (1997) studied the leaf litter removal by the snail *Terebalia palustris*, which revealed that buried *R. mucronata* leaves were 100% removed by benthic species, therefore resulting in unavailability of litter for tidal transport.

A diversity of organisms was found to be associated with the mangrove litter. These were composed of organisms from the phyla Arthropoda, Mollusca and Annelida. The mangrove litter acted both as a source of food and as habitats for these organisms. In fact, according to Ferraris *et al.* (1999), the most successful benthic species in the mangal are those that can adapt to the salinity and temperature stresses that characterise these environments. In the present study, the litter-associated invertebrates were mainly represented by arthropods.

The study showed that at Macondé, the litter was richer in terms of diversity of species than at Bambous Virieux. A reduction in diversity of species has also often been cited as a response to anthropogenic disturbance (Alfaro, 2006). At Bambous Virieux, an agricultural area of land is found adjacent to the mangrove forest. Thus, there may be leakage of fertilisers into the mangrove area and hence, only the tolerant species are able to thrive in the mangrove ecosystem at Bambous Virieux. However, this remains only a hypothesis which needs to be proved and there may be other reasons to account for the difference in species richness between the sites, for example, in a study by Morrisey *et al.* (2003), the different nature of the sediment was suggested to be the cause for the differences in benthic faunal diversity between two study sites in New Zealand. As suggested by Skilleter and Warren (2000), there is a great potential for experimental artifacts in soft-sediment systems such as mangrove forests because virtually all activities lead to some disruption of the substratum, with subsequent effects on the biota. This means that these artifacts could lead to an underestimate of the species richness in the mangrove litter.

Among the crustaceans found in the mangrove litter were the grapsid crabs. According to Lee (1999), grapsid crabs consume large proportions of mangrove leaf litter and consequently large amounts of processed material in the form of crab faeces can enrich a coprophagous food chain as well as provide an alternative form of export from the mangrove forests. Faeces of the animals living in the mangrove habitat are an important constituent of the surface layers of the soil and are an important source of nitrate, phosphate and other substances for the photosynthetic micro-organisms of the soil (Macnae, 1968).

Isopods from the families Sphaeromatidae and Ligidae and amphipods, namely *Platorchestia platensis*, were also present in the litter. Litter is a source of food for these infaunal communities, thereby increasing organic matter in the sediment (Chapman & Tolhurst, 2004). The isopods do not only benefit the mangrove ecosystem by recycling detritus, but some may also cause damage to this ecosystem. Isopods from the Sphaeromatidae family, namely *Sphaeroma terebrans* are known as wood borers (Brooks & Susan, 2002) that caused damage to mangrove roots. However, initiation of lateral root growth by the mangrove in response to isopod has been one of the most commonly cited examples to support

the concept of beneficial herbivory by the isopods (Brooks & Bells, 2002). As for the insects present in the litter, they form a complex food web as they may act as predators on other insects and snails (Doyen, 1976) and they may themselves act as prey to other faunal groups such as spiders. This may be the reason why a number of different species of arachnids were found in the mangrove litter. Most insects such as species of *Collembola* (Maynard, 1951), Coleoptera, particularly staphylinids (Doyen, 1976) and members of the class Hymenoptera (Speight *et al.*, 1999) that have been found in the litter, feed on dead plant materials. However, a few species of *Collembola* subsist on dead animals such as mollusc, crustaceans, worms and fishes (Maynard, 1951). As for the members of the Formicidae family, namely the ants, they are the dominant burrowers in many ecosystems (Schowalher, 1996). In fact, many of the mangrove fauna which thrives in the litter, such as crabs and amphipods are known as good burrowers which help to aerate the substrate, thus ameliorating anoxic conditions (Nybakken, 1988). Ants also prey on arthropod, namely on insects (Holldobler & Wilson, 1990) and hence, they regulate the insect population in the mangrove litter.

In many studies (Lee, 1999), annelids were found to be present among the mangrove litter. These, especially the polychaetes act as burrowing scavengers and deposit feeders in the mangrove forests and they are the main prey component in many food webs: they are the principle diet of many gastropods and fish (Gladstone & Shreider, 2003). The presence of this diversity of organisms in the mangrove litter is certainly an evidence of how rich the mangrove ecosystem in Mauritius is.

The present study has contributed in providing information about forest structure, litter production and faunal composition of the mangrove ecosystem in Mauritius. This study may act as a reference to the future and more in-depth studies that will be made on the Mauritian mangrove forest.

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