Litter fall and decomposition of mangrove species *Avicennia marina* and *Rhizophora mucronata* in Maputo Bay, Mozambique

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Abstract—Litter fall and decomposition of mangrove leaves were compared for different seasons, species (*Avicennia marina* and *Rhizophora mucronata*) and sites in southern Mozambique. Mangrove leaf litter fall and decomposition was estimated using small mesh collecting-baskets and litter bags respectively in 2006 and 2007 at two sites of Maputo Bay: an urban dwarf mangrove at Costa do Sol (Maputo City) and a rural well-developed mangrove at Saco (Inhaca Island). *A. marina* at Saco produced more litter (dry season 10.6 g m^{-2} and wet season 14.2 g m^{-2}) than *R. mucronata* (dry season 4.6 g m^{-2} and wet season 14.1 g m^{-2}), and leaves contributed more to total litter fall in the dry season (February/March) compared with the wet season (September/October) for both species. Decomposition by means of loss of ash free dry weight (AFDW) from leaves maintained in the subtidal was best described by double exponential models which showed loss rates of leaves along the time. Field experiments at Saco showed that submerged leaves of *A. marina* decomposed faster than *R. mucronata*. For *A. marina*, the average time required to lose half of the initial AFDW ($t_{0.5}$) was 96 days and 78 days for the dry and wet season respectively, whereas for *R. mucronata* leaves it took 151 days in the dry and 476 days in the wet season. At Costa do Sol, *A. marina* leaves took 171 and 48 days for the dry and wet seasons respectively to lose half AFDW; whereas *R. mucronata* took 98 days in the dry and 25 days in the wet season. The results showed that breakdown of leaf litter was season and species dependent. Litter decomposition in the wet season was faster than the dry season and *A. marina* had the fastest decomposition rates, appearing to act as a principle pioneer species for enrichment of the fringing mangrove habitats of sub-tropical eastern Africa.

INTRODUCTION

Mangrove forests are highly productive ecosystems (Boto *et al.*, 1984; Woodroffe, 1985; Woodroffe *et al.*, 1988; Nybakken, 1993) and this productivity is mainly attributed to the high degradation of litter fall and efficient recycling of nutrients (Bosire *et al.*, 2005; Morrisey *et al.*, 2007). Methods of directly measuring primary productivity in mangrove ecosystems are technically difficult but litter production has been widely used as a measure of productivity as this is one of the important components of productivity, especially in view of its nutrient contribution to the estuarine systems (Woodroffe *et al.*,

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1988; Mall *et al.*, 1991; Chale, 1996; Morrisey *et al.*, 2007). Thus, quantifying litter fall and decomposition becomes essential to assess the productivity of the ecosystem as a whole (Wafar *et al.*, 1997).

Litter production and fall is accepted as the main pathway to enrich the ecosystem with nutrients (Tam *et al.* 1998) but it tends to vary with geographic location (Twilley, 1985; Woodroffe *et al.* 1988) and seasons (Bosire *et al.*, 2005). In some locations litter production and fall occurs throughout the year with peak fall in summer rainy seasons as documented by Tam *et al.* (1998) in China.

The decomposition of plant material is the process in which organic substances are physically broken down and converted into simple chemical substances, resulting in the production of carbon dioxide, water and released energy (Chapman, 1986). Decomposition rate can be summarized as the time a body spends to lose mass to half of its initial value or half life (Hogarth, 1999). Decomposition of organic substances and recycling of detritus have great importance in nutrient release from ground organic substance (Raffaelli & Hawkins, 1996), enabling the substance to become available for new growth of plants (Chapman, 1986; Hogarth, 1999; Shunula & Whittick, 2001).

Mangrove leaf litter degradation depends mainly on seasonal variability and on the degree and frequency of tidal inundation (Twilley, 1985; Wafar *et al.*, 1997, Dick & Osunkoya 2000, Bosire *et al.*, 2005). The objective of this study was to document mangrove litter fall and decomposition rates in two contrasting mangrove habitats: a well-developed mangrove habitat in a rural setting and a dwarf mangrove in an urban setting.

MATERIALS AND METHDOS

Study area

This study was undertaken in two distinct mangrove habitats, a well developed mangrove in a rural setting (Inhaca Island)

and a dwarf mangrove in an urban setting (Costa do Sol). These two locations occur in Maputo Bay, southern Mozambique (Fig. 1) and there are no tidal differences between the two sites as they are exposed to the same bi-diurnal tidal regimes, with the highest spring tide amplitude reaching close to 4 m (Mundlovo, 2006)). The study was undertaken during the two main seasons: wet (September and October) and dry (February and March). Maputo Bay has an area of 960 km^2 (Afonso, 2001) and five main rivers, namely the Incomati, Maputo, Matola, Tembe and Umbeluzi which empty into Maputo Bay. The climate is subtropical, with a rainy warmer season from October to February, and a dry, cooler season from March to September (Mundlovo, 2006). According to data collected from Instituto Nacional de Meteorologia from 1998 to 2008, precipitation varies from the extremes 34.7- 211.9 mm a month in the wet season and 7.7 - 77.3 mm in the dry.

The dwarf mangrove forest at Costa do Sol is subjected to anthropogenic impacts such as land reclamation for building construction (Saket & Matusse, 1994; Barbosa *et al.*, 2001). Within this approximately 1.5 sq. km forest, *A. marina* is the dominant species and is known to tolerate high salinities (Hogarth, 1999; Yong Ye *et al.*, 2005; Beentje & Bandeira 2007). The average height of this mangrove species is 1.5 metres, and the dwarf appearance is thought to be due to high salinity, up to 45.9 ppt (see Simango, 2007). The mangroves at Saco occur in the southern bay of Inhaca Island (Fig. 1) which is protected from wind and strong waves. There is no river on the island but some fresh groundwater from inland reaches the mangroves (Kalk, 1995). These mangroves are part of the forestry reserve of Inhaca Island (Kalk, 1995) that has been protected for around 40 years and are considered fully-developed, and including a range of species including *A. marina* and *R. mucronata*.
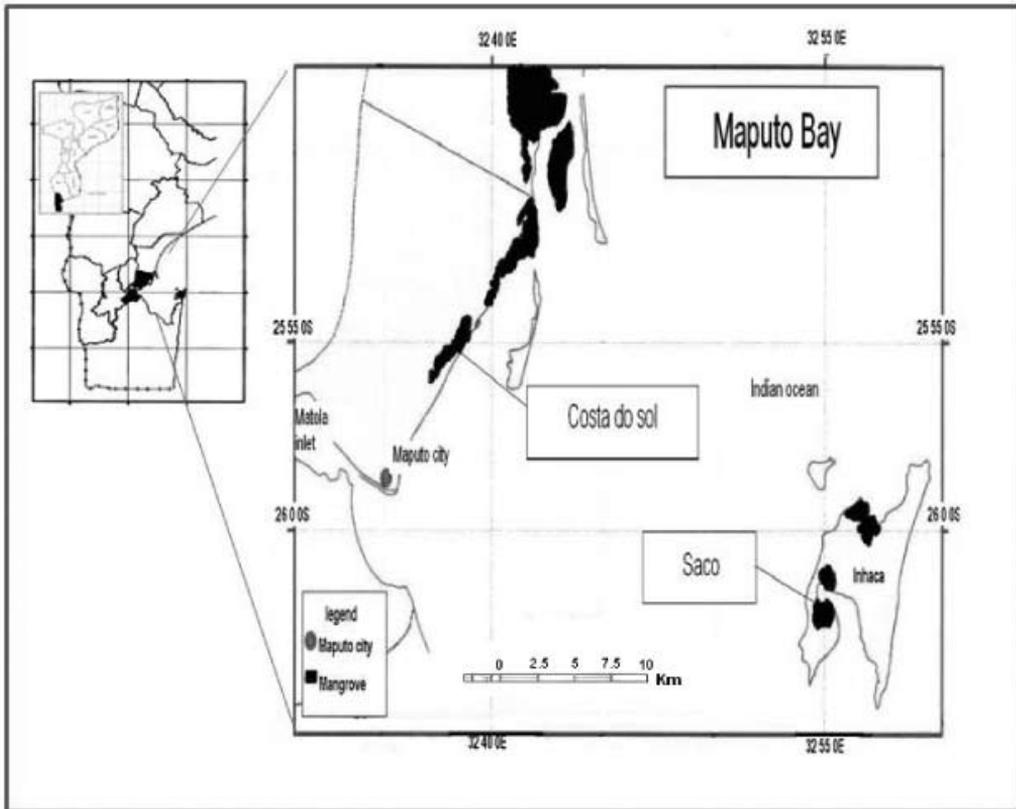
Fig. 1. Map depicting the study areas in southern Mozambique

Litter fall

For the determination of daily rates of litter fall, bags with an area of 0.25 m² and mesh of 1 mm (see Ellis & Bell, 2004) were tied to branches up to 2 m above the forest floor, in order to prevent them from getting wet during high tide (following Tam *et al.*, 1998). Bags were kept at least 10 m apart from each other. Five replicate bags were tied in the branches of the trees in the *A. marina* and *R. mucronata* zones. The samples were harvested biweekly (14, 28, 42 and 56 days period), covering two months for each season (dry and wet). The harvested litter was immediately placed in plastic bags and returned to the laboratory where it was identified and divided into leaf, branch and fruit categories (following Tam *et al.*, 1998; Ellis & Bell, 2004). The litter was dried in aluminium paper at a temperature of 100°C for 72 h and subsequently weighed as dry weight (Woodroffe, 1985; Ellis & Bell, 2004). This experiment was carried out only at Saco (normal mangrove) because at Costa do Sol (the dwarf mangrove stand) the plants were shorter than 1.5 m resulting in the leaf litter washing away during spring high tides.

Decomposition

In order to estimate the rate of mangrove breakdown, litter bags were used for both *Rhizophora mucronata* and *Avicennia marina* at both study sites. The leaves used

were senescent (yellowish in colour) either freshly fallen or easily hand picked from the trees and surrounding area (see Van Der Valk & Attwill, 1984; Ashton *et al.*, 1999). These are normally the majority of the leaves on the forest floor and they have already started their decomposition (Ashton *et al.*, 1999; Bosire *et al.* 2005). These leaves were air dried for 24 h to remove surface water, and then 28 g of each species was placed into 15 x 15 x 25 cm plastic bags with a mesh size of 1 mm^2 (Ashton *et al.*, 1999). The mesh bags were securely tied to aerial roots so that they lay flat on the sediment. Eight bags for each species were removed from each site at each of 14, 28, 42 and 56 days, covering two months per season (dry and wet). In total 64 litter bags were placed per season, at the beginning of the decomposition experiment to ensure independence of sampling (Underwood, 1997). These bags were returned to the laboratory where they were gently washed in a sieve to remove sediment. The resulting litter was oven dried to constant mass at 100ºC for 72 h and the final dry mass recorded (Ellis & Bell, 2004).

Data analyses

Differences in litter production between the dry and wet season for the two mangrove species (*A. marina* and *R. mucronata*) were tested using factorial ANOVA. The relationship between the percentage dry biomass of remaining mass in litter bags and species sampling time, at both sites, best fitted a negative single exponential model (Ref): $X_t = X_o\ e^{-Kt}$. Where X_t is the percentage of the initial material X_o remaining after time *t* (days) and K is a decay coefficient (d^{-1}). The times required for the decomposition of half the initial material (t_{50}) were determined (t = ln 2/K). The exponential curves obtained were converted to straight lines (log_{10}) and ANOVA tests were carried out for every combination of litter bags. All statistical analyses were performed using the "Statistica" program. A significance level of p = 0.05 was accepted.

RESULTS

Litter fall

Litter production and fall were observed throughout the year at Saco and there was a distinct seasonal pattern, with peak fall during summer rains and little fall in winter. Leaves were the dominant form of litter (Table 1) and contributed more to total litter in the dry season compared with the wet season for the two species. Twig fall was almost continuous representing a small percentage of the total litter fall (up to 20% of dry weight). The fall of reproductive parts (fruits and flowers) was strongly seasonal as this was higher during the wet season. Reproductive parts weighed more than the other litter components. *R. mucronata* propagules contributed 47.7% to total litter fall in the wet season. Observations and herbarium records from Inhaca Island have shown that *R. mucronata* flowering occurs in the periods of October-December and fruiting in December-May and, *A. marina* flowering occurs in September-December and fruiting in December-May. There was no significant difference in total litter production between the wet and dry season (P > 0.05) although it appeared that total litter production was greater for *A. marina* (10.64 g m^{-2} in dry season and 14.18 g m^{-2} in wet season) compared with *R. mucronata* (4.64 g m^{-2} in dry and 14.11 g m^{-2} in wet season).

Decomposition

When leaves fall on the sediment, decay initiates and rapid weight loss occurs. At Costa do Sol in the wet season, the first 28 days resulted in 50% of the initial dry weight lost in *R. mucronata* while in *A. marina* the same percentage loss occurred over 56 days (Fig. 2). At the Saco mangroves of Inhaca Island, leaves only decomposed up to a third of the initial dry weight during all field measurements (eight weeks) (Fig. 2). The decomposition rate during the dry season was much slower in these two study areas.

Table 1. Percentage contribution of plant material to litter fall at Inhaca Island (Saco) for *A. marina* (Am) and *R. mucronata* (Rm)

	Species	Season	Mean ± S.D.	%
Leaves	Am	Wet	24.91 ± 22.65	76.5
		Dry	14.99 ± 3.62	85.9
	Rm	Wet	17.22 ± 7.42	34.9
		Dry	31.24 ± 14.20	79.4
Twigs	Am	Wet	5.78 ± 4.00	12.8
		Dry	1.44 ± 1.99	13.0
	Rm	Wet	0.55 ± 0.63	1.1
		Dry	5.93 ± 11.76	20.4
Inflorescence	Am	Wet	1.92 ± 3.39	0.3
		Dry	0 ± 0	0
	Rm	Wet	3.98 ± 2.49	8.2
		Dry	0.04 ± 0.07	0
Propagules	Am	Wet	5.24 ± 9.29	10.4
		Dry	0 ± 0	0
	Rm	Wet	23.54 ± 47.08	47.7
		Dry	0 ± 0	0
Fruit	Am	Wet	0 ± 0	0
		Dry	0.04 ± 0.08	1.1
	Rm	Wet	4.10 ± 8.21	8.3
		Dry	0.03 ± 0.05	0.3
Total	Am	Wet	37.86 ± 18.49	100
		Dry	16.47 ± 3.01	100
	Rm	Wet	49.40 ± 59.00	100
		Dry	37.23 ± 4.82	100

The times required to lose half of the initial AFDW ($t_{0.5}$) of periodically submerged leaves at the Saco mangrove were 96 days (in the dry season) and 78 days (during the wet season) for *A. marina* and 151 days (dry season) and 476 days (wet season) for *R. mucronata*. While at Costa do Sol this was 171 days (dry season) and 48 days (wet season) for *A. marina* and 98 days (dry season) and 25 days (wet season) for *R. mucronata*. There was no significant difference in decomposition rates of mangrove leaves in the two study areas. Analysis of variance showed that there were significant differences in percentage dry mass remaining between sites ($P < 0.05$), season ($P < 0.05$) and species ($P < 0.05$).

DISCUSSION AND CONCLUSION

Litter fall

Litter fall could not be measured at Costa do Sol because of tidal flooding relative to height of branches, however, observations indicated that litter fall rates were lower in these dwarf or stunted mangroves compared to the fully-developed mangroves of Saco at Inhaca Island. Mangroves in New Zealand as documented by Woodroffe (1985) and Morrisey at al. (2007) recorded lower litter fall from stunted mangroves. At Costa do Sol, the dwarf plants had a small diameter, average height up to 1.5 m and low biomass (Amade, 2006), contributing to
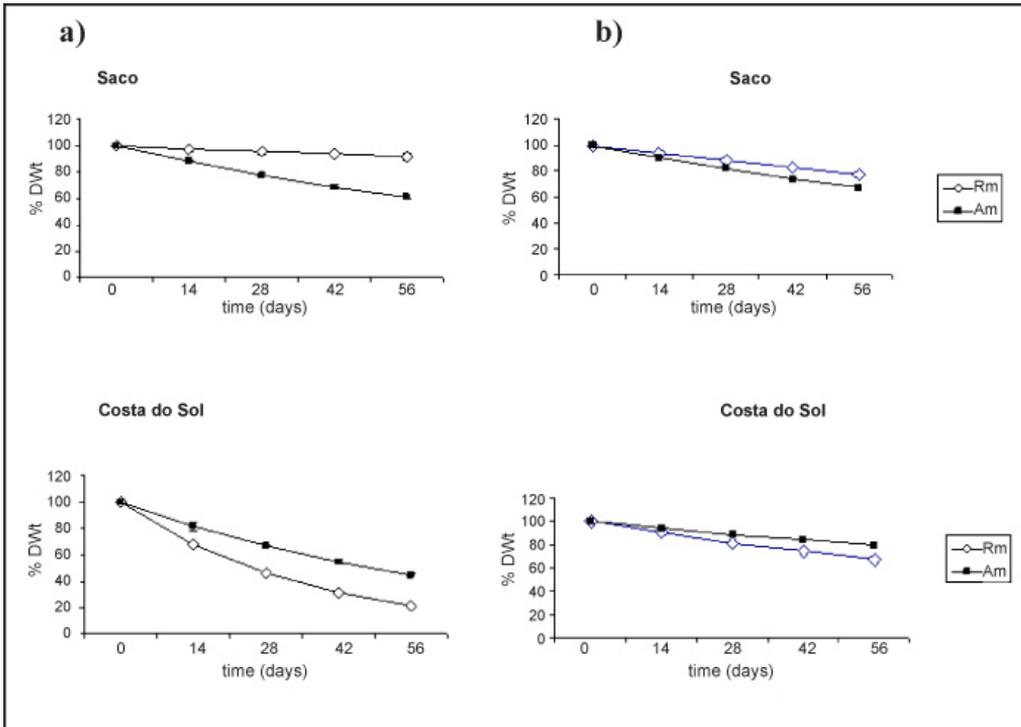
Fig. 2. Change in percentage dry weight of *A. marina* and *R. mucronata* in the wet season (a) and dry season (b)

a generally low productivity. Dwarf mangroves occur as a result of high salinities associated with desiccation due to fewer inundation periods (mainly restricted to spring tides) as observed in other stunted mangrove areas from Hong Kong (Yong Ye *et al.*, 2005). This stress reduces seed establishment, and consequently impacts on plant development (Yong Ye *et al.*, 2005).

The contribution of leaf fall to total litter was negatively related to that of the reproductive materials as the peak production of the reproductive materials occurred when leaf litter production was minimum (and vice versa). *R. mucronata* flowering occurs during January-March, June-August, October-December and fruiting in January-March, July-August, November-December (Kalk, 1995; Beentje & Bandeira, 2007).

Studies of *R. mucronata* litter fall carried out in India revealed that twig fall was almost continuous but rarely exceeded a few percent

(up to 20%) of total litter fall (Wafar *et al,* 1997). Fall of flowers and fruit was confined to the wet season, and their contribution to total litter fall was quite substantial as observed elsewhere (Wafar *et al.*, 1997; Hegazy, 1998). High temperature, longer duration of light, higher evapo-transpiration rates and more flushing by fresh water during summer months appears to be among the factors responsible for this high litter fall (Tam *et al.*, 1998).

Despite mangroves being found only in tropical areas with similar environmental conditions, patterns of litter fall per square meter vary. This study showed different results, 38.8 −51.8 tones ha^{-1} year^{-1} for *A. marina* and 16.9 −51.5 tones ha^{-1} year^{-1} for *R. mucronata*. In India litter fall was 10.2-11.8 tones ha^{-1} year^{-1} for *Avicennia* and *Rhizophora* respectively (Wafar *et al.*, 1997). This difference may be due to age and height of trees and type of forest associated with the kind of mangrove forest such as the fringing river estuary or deltaic type.

Table 2. Decay constant (Kd) and calculated half lives (t50) of R. mucronata and A. marina at Costa do Sol and Inhaca during the dry and wet season

| Site	Litter type	Season	Kd (day^{-1})	t$_{50}$
Costa do Sol	*A. marina*	Dry	0.004	171
		Wet	0.014	48
	R. mucronata	Dry	0.007	98
		Wet	0.028	25
Saco (Inhaca)	*A. marina*	Dry	0.007	96
		Wet	0.009	78
	R. mucronata	Dry	0.005	151
		Wet	0.002	476

Decomposition

Studies have shown that the decomposition rate of leaves was higher in the subtidal compared with the intertidal region and during the rainy season compared to the dry season, because water soaking causes leaching of labile materials (Robertson, 1988; Dick & Osunkoya, 2000). In addition, higher temperatures of the wet season might enhance microbial activity, increase nutrient content of litter and accelerate decomposition rates (Tam *et al.*, 1990). Similarly, Wafar *et al.* (1997) who undertook decomposition rate studies in India, found that the wet season resulted in rapid leaching. This study found the highest t$_{50}$ (half life) value for *R. mucronata* in the wet season at Saco, Inhaca, for the well-developed mangrove. *A. marina* leaves decomposed more rapidly than *R. mucronata* for both seasons at Inhaca. This was ascribed to differences in leaf morphology, texture and composition. According to Alongi *et al.* (2000) differences in leaf quality are known to affect decomposition rates as leaf tannin concentration and the nutritional value may vary. High tannin concentrations are known to be averse to detritivores and inhibit microbial activity (Van Der Valk & Attwill, 1984; Robertson, 1988; Shunula and Whittick, 2001). Differences in litter tannin content might contribute to differences in mangrove leaf decomposition rate as microbial colonization of *R. mucronata* leaf litter appeared to occur after the tannin content of decomposing leaves dropped to a lower level (Tam *et al.*, 1998; Ellison & Farnsworth, 1997). At Costa do Sol, *R. mucronata* had lower decomposition than those documented elsewhere for Rhizophoraceae mangrove species (Ashton *et al.*, 1999; Alongi, *et al.*, 2000; Bosire *et al.*, 2005). Few species of *R. mucronata* occurred at the dwarf mangrove site and the few leaves available to test decomposition might have already been leached, but further efforts are needed to measure the decomposition rates of *R. mucronata* from a stunted type of mangrove forest.

An overview of decay constant values (K$_d$) for mangrove leaf litter reported in the literature is presented in Table 3. Generally decay rates are seen to be affected by temperature, substrate characteristics and geographical regions (Woodroffe, 1985; Ellison and Farnsworth, 1997; Tam *et al.*, 1998). The comparatively higher decomposition rates encountered at Saco de Inhaca could be due to the existence of high clay content in the substrate with a higher water retention capacity and higher organic matter percentage as documented by de Boer (2000). Larger macrofauna densities at Inhaca (Guerreiro *et al.*, 1996) and the existence of a true mangrove forest compared to dwarf stands at Costa do Sol may have also prompted this difference in decomposition rate. The constants of decay observed in the study were relatively lower in relation to the studies in Kenya (Bosire

Table 3. Overview of decay constant values (K$_d$) for mangrove leaf litter reported in the literature, arranged from low to high rates of decomposition

Litter type	Remarks	K$_d$ (day^{-1})	Source
Avicennia marina	Dry season (Costa do Sol)	0.004	Present study
Avicennia marina	Dry season (Saco)	0.007	Present study
Avicennia marina	Wet season (Saco)	0.009	Present study
Avicennia marina		0.012-0.021	Tam *et al.* (1998)
Avicennia marina	Winter	0.0126	Tam *et al.* (1990)
Avicennia marina	Wet season (Costa do Sol)	0.014	Present study
Avicennia marina		0.063	Robertson (1988)
Rhizophora mucronata	Wet season (Saco)	0.002	Present study
Rhizophora mucronata	Dry season (Saco)	0.005	Present study
Rhizophora mucronata	Cleared forest (Malaysia)	0.0057	Ashton *et al.* (1999)
Rhizophora mucronata	Dry season (Costa do Sol)	0.007	Present study
Rhizophora mucronata	Dry season (bare treatment) (Kenya)	0.01	Bosire *et al.* (2005)
Rhizophora mucronata	Virgin reserve	0.0204	Ashton *et al.* (1999)
Rhizophora mucronata	Wet season (Costa do Sol)	0.028	Present study
Rhizophora mucronata	Wet season (bare treatment)	0.03	Bosire *et al.* (2005)
Rhizophora mucronata	Dry season (natural treatment)	0.18	Bosire *et al.* (2005)
Rhizophora mucronata	Wet season (natural treatment)	0.41	Bosire *et al.* (2005)
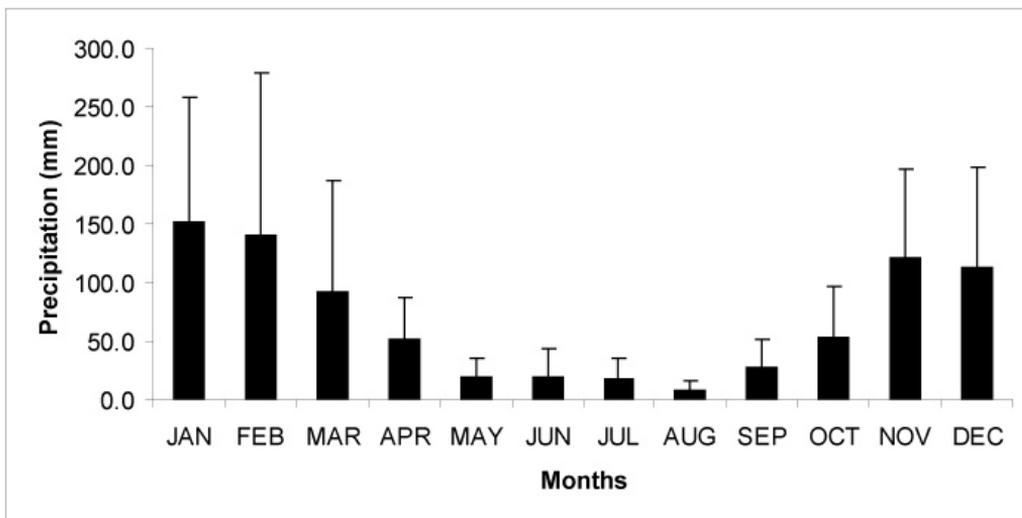
Fig. 3. Mean precipitation for a 10 year period (1998 to 2008) in Maputo Bay

et al., 2005) and Malaysia (Ashton *et al.*, 1999), possibly due to different conditions in the field. In Kenya the total annual precipitation values (1,000-1,600 mm) were very high as the rainy season extended from April to August and from October to the November months (Bosire *et al.*, 2003) contrary to Maputo Bay where the annual precipitation ranged lower (360-1,000 mm) as shown by a 10 year meteorological dataset (Fig. 3). Areas with high precipitation,

mainly along the equator (such as Kenya) have high decomposition rates compared to areas further away even though they are subjected to similar tidal regimes.

To conclude, litter fall, which is seasonally and geographically dependent, appears to be the first to establish itself or the main 'pioneer' species to enriching the mangrove habitats in southern Mozambique. In the wet season the contributions of reproductive parts were higher than in the dry season but leaves were always present in litter fall. *A. marina* decomposed more rapidly than *R. mucronata* due to morpho-physiological characteristics. Further studies are needed to understand the fate of the mangrove decomposition matter and existing connectivity with and transport into the adjacent shallow habitats such as seagrass beds and coral reefs.

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