Research Article

Decomposition of mangrove leaves in the estuary of Paraíba do Sul River Rio de Janeiro, Brazil

Taísa Barroso-Matos¹, Elaine Bernini¹ & Carlos Eduardo Rezende¹

¹Universidade Estadual do Norte Fluminense (UENF), Centro de Biociências e Biotecnologia (CBB) Laboratório de Ciências Ambientais (LCA), Av. Alberto Lamego 2000, Horto 28015-602 Campos dos Goytacazes, Rio de Janeiro, Brazil

ABSTRACT. The decomposition rate of senescent leaves of *Avicennia germinans, Laguncularia racemosa* and *Rhizophora mangle* in their respective areas of dominance were analyzed in the estuary mangrove of the Paraíba do Sul River, Rio de Janeiro, by the method of litter bags. Results indicated that the rate of decomposition of leaves of *L. racemosa* (3.2×10^{-3}) did not differ significantly from *A. germinans* and *R. mangle* (P > 0.05), but that *A. germinans* (5.1×10^{-3}) exhibits a higher decomposition rate than *R. mangle* (2.7×10^{-3}) (P < 0.05). These differences may be explained by different leaf traits among species (*e.g.* water content, concentrations of tannin, and nitrogen). The half-life calculated was 138, 216 and 257 days for *A. germinans*, *L. racemosa* and *R. mangle*, respectively. Considering that *A. germinans* has the greatest abundance in relation to *R. mangle*, and its kinetics of decomposition was faster, we suggest that the former species represents a major source of organic matter originated in mangroves of the estuary of Paraíba do Sul River.

Keywords: Avicennia, Laguncularia, Rhizophora, litter bags, mangroves, Rio de Janeiro, Brazil.

Descomposición de hojas de mangle en el estuario del Río Paraíba do Sul Rio de Janeiro, Brasil

RESUMEN. La tasa de descomposición de las hojas senescentes de *Avicennia germinans, Laguncularia* racemosa y *Rhizophora mangle* en sus respectivas áreas de dominio se analizaron en los manglares del estuario del río Paraíba do Sul, Rio de Janeiro, por el método de bolsas de resíduos. Los resultados indicaron que la tasa de descomposición de las hojas de *L. racemosa* $(3,2 \times 10^{-3})$ no difirió significativamente de *A. germinans* y *R. mangle* (P > 0,05), pero *A. germinans* $(5,1 \times 10^{-3})$ presentó una mayor tasa de descomposición que *R. mangle* $(2,7 \times 10^{-3})$ (P < 0,05). Según la literatura, estas diferencias se deben a las distintas características foliares de las especies (por ejemplo, el contenido de agua, ó la concentración de taninos y nitrógeno). La vida media calculada fue 138 días, 216 y 257 de *A. germinans, L. racemosa* y *R. mangle*, respectivamente. Considerando que *A. germinans* tiene la mayor prevalencia y abundancia en relación con *R. mangle*, y su cinética de descomposición fue más rápida, se sugiere que esta especie representa la principal fuente de materia orgánica originada en los manglares del estuario del río Paraíba do Sul, así como a las cadenas alimentarias en la región.

Palabras clave: Avicennia, Laguncularia, Rhizophora, bolsas de residuos, Rio de Janeiro, Brasil.

INTRODUCTION

Mangroves are critical ecosystems due to their ecological roles, as well as to their economic and social importance (Field, 1995). They grow in tropical and subtropical coastal regions, mainly in sheltered areas such as estuaries, bays and lagoons, and are

among the most productive ecosystems in the world (Alongi, 2009; Kathiresan & Bingham, 2001).

Quantification of litter production has been widely used to assess productivity of the mangroves, for its logistics and economic viability. The litter may represent up to one third of mangroves' primary production (Robertson *et al.*, 1992). It may be re-

Corresponding author: Carlos Eduardo Rezende (crezende@uenf.br)

mineralized along the decomposition process, thus accumulating on the sediment and/or exported to adjacent areas (Pool *et al.*, 1975). Exportation of dissolved organic matter and nutrients is a key process for productivity of coastal waters, with clear effects on the food chain, this theme being the focus of several studies over the last three decades (Odum & Heald, 1975; Alongi, 1990; Dittmar *et al.*, 2006; Rezende *et al.*, 2007).

Decomposition is one of the most important stages in the cycling of nutrients and it is ruled, mainly by three groups of variables: the nature of the community in decomposition (diversity and abundance of macro and micro organisms), the characteristics of the organic material that determine its degradability (the substrate quality), and the physical-chemical conditions of the environment, which are controlled by the climate and by sediment characteristics of the site (Correia & Andrade, 1999; Chapin III *et al.*, 2002).

Among the biotic factors, the diversity and abundance of bacteria and fungi have shown a high importance in the decomposition, especially for leaf tissues that have compounds that inhibit the action of predators and decomposers (Chapin III *et al.*, 2002). These compounds include tannins among other secondary metabolic compounds, demonstrating the importance of the substrate's quality. *Rhizophora mangle* has leaves with higher tannin content rendering them more resistant to degradation compared to *Laguncularia racemosa* (Lacerda *et al.*, 1986). Aquatic invertebrates, such as crustaceans, also play an important role, especially in the removal and reduction of leaf litter size, thus facilitating the decomposition process (Meentmeyer, 1978).

In general, climatic conditions, particularly temperature, are among the main abiotic factors explaining variations in rates of decomposition, with low temperatures directly affecting metabolism of decomposing organisms, and thus reducing their activity and the intensity of mass decay (Meentmeyer, 1978; Gholz *et al.*, 2000). Other important abiotic factors that influence rates of decomposition in mangroves as well are tides and salinity (Chale, 1993; Aké-Castillo *et al.*, 2006; Alvarez & Bécares, 2006). Periods of periodic flooding, which induce cycles of anoxia with subsequent inhibition of decomposition, promote the accumulation of organic matter in the sediment (Pool *et al.*, 1975).

In Brazil, studies on decomposition of mangrove leaves are scarce and most of them are still in the form of dissertations and theses (Adaime, 1985; Panitz, 1986; Sessegolo & Lana, 1991; Menezes & Schaeffer-Novelli, 2000; Mendonça, 2006). Quantifying decomposition rates of the leaf tissues of mangrove species is important to understand the biogeochemistry of coastal environments, particularly considering the importance of this process for regional dynamics through the input of organic matter (Alongi, 1990; Dittmar et al., 2006). Considering that the mangrove species exhibit differences in the physical and chemicals characteristics of their leaves (e.g. tannin and nitrogen contents; Lacerda et al., 1986; Bernini et al., 2006) it is expected that rates of decomposition differ between species. Thus, this study aims to: (1) compare mass loss from leaves of Avicennia germinans, Laguncularia racemosa and Rhizophora mangle in their respective areas of dominance in the estuarine mangrove of the Paraíba do Sul River, and (2) discuss on some experimental issues that may help in conducting future research on organic matter dynamics in mangroves.

MATERIALS AND METHODS

The estuary mangrove of the Paraíba do Sul River is the largest in the Northern Fluminense region, with approximately 800 ha. It presents two outlets, the Main Estuary and the Secondary Estuary (Fig. 1), constituted by communities of *Avicennia germinans* (L.) Stearn., *Laguncularia racemosa* (L.) Gaertn.f. and *Rhizophora mangle* L. (Bernini & Rezende, 2004). The estuary is under a microtidal regime with semidiurnal tides. Based on data from the Ponta do Ubu Terminal in Espírito Santo (20°44'S, 40°32'W), between 2005 and 2006 (study period), the average tide was 0.8 m, with a >0.2 and <1.2 m (DHN, 2006).

This study was conducted in the mangrove of Gargaú, located in the Secondary Estuary of the river, in the São Francisco do Itabapoana municipality (21°36'00''S, 41°03'00''W) (Fig. 1). Three sites were selected in areas with little human interference, i.e., absence of garbage, organic and inorganic sewage discharge, and landfills. Site 1, 2 and 3 were established in locations dominated by L. racemosa (100% relative density (number of trunks) and dominance (basal area)), R. mangle (75%) of dominance and 97% relative density) and A. germinans (99% of dominance and 98% relative density), respectively (Bernini & Rezende, 2011) (Fig. 1). Sampling sites have similar physical characteristics of the sediments (sandy silt) and distances from the coast (between 2.0 and 2.5 km). These characteristics create a very similar physical-chemical environment in the three sites, where the salinity of interstitial waters is around two during the rainy season (Table 1), and the salinity of river waters around seven during dry season (F. Brito, unpublished data). the



Figure 1. Study sites analyzed in the estuary mangrove of the Paraíba do Sul River, Rio de Janeiro, Brazil. Site 1: dominance of *Laguncularia racemosa*, Site 2: dominance of *Rhizophora mangle*, Site 3: dominance of *Avicennia germinans*.

Figura 1. Sitios de estudio analizados en los manglares del estuario del Río Paraíba do Sul, Rio de Janeiro, Brasil. Sitio 1: dominancia de *Laguncularia racemosa*, Sitio 2: dominancia de *Rhizophora mangle*, Sitio 3: el dominancia de *Avicennia germinans*.

Table 1. Characterization of depositional microenvironments of sites studied in the mangrove of the Paraíba do Sul River estuary (Source: Bernini, 2008).

Tabla 1. Caracterización de los microambientes deposicionales de los sitios estudiados en el manglar del estuario del Río

 Paraíba do Sul, Rio de Janeiro (Fuente: Bernini, 2011).

Variable	Site 1 n = 3	Site 2 n = 3	Site 3 n = 3
Coarse sand (%)	< 0.5	< 0.5	2 ± 4
Medium sand (%)	8 ± 5	5 ± 6	12 ± 9
Fine sand (%)	21 ± 1	27 ± 7	31 ± 3
Silt (%)	65 ± 7	62 ± 12	51 ± 13
Clay (%)	6 ± 3	5 ± 1	4 ± 2
Textural classification	Sandy silt	Sandy silt	Sandy silt
Interstitial water salinity	2.3 ± 0.3	2.7 ± 0.3	2.0 ± 0.1
Distance from coast (km)	2.0	2.0	2.5

Such homogeneity allowed the comparison of decomposition rates of the mangrove tree species while controlling for environmental factors. The only exception was for microtopography, with sites dominated by *L. racemosa* and *R. mangle* showing higher complexity than the site dominated by *A. germinans*. This latter site was selected, as no other

appropriate area dominated by A. germinans was found.

Decomposition rates were estimated from substrate mass loss using the litter bags technique (Villela & Proctor, 2002). In March 2006, yellowish senescent leaves of *R. mangle, L. racemosa* and *A. germinans* were collected from 15 trees for each species. Trees

were located within 10 x 10 m plots 5 m from the river. The same sites were sampled for vegetation structure by Bernini & Rezende, 2011.

In the laboratory, leaves were washed and weighed (wet weight) in portions of about 30 g, and then placed in nylon bags of 30 x 35 cm and mesh 1.0 mm in diameter (big enough to allow the entry of water and small organisms and for preventing the entry of large consumers, such as crabs, which usually eat leaves). After packaging, litter bags were wrapped in a nylon rope spaced at 30 cm, in a total of 33 bags for each species. The litter bags were returned to the field, where they were put in contact with sediment within the plots of original collection. In each plot, three litter bags were collected at predefined time intervals: 1, 2, 3, 4, 7, 15, 30, 60, 90, 120 and 183 days. Sampling began in March 2006. As they were being collected, the bags were taken to the laboratory where the leaves were carefully washed with distilled water to remove mud. After washing, a new wet weight was measured and the leaves placed in individual paper envelopes and dried in an oven (80°C / ~72 h) until constant weight. After drying, the material was weighed. The same procedure was done with a sample of 100 g of leaves from each site, and this material used to control the percentage of water which afterwards is necessary to calculate the dry weight of leaves of each species.

The initial dry weight of leaves was estimated using a conversion factor calculated for each species. To calculate this factor, samples of leaves of each species were weighed (wet weight), dried at 80°C for about three days, and then re-weighed in order to obtain the dry weight. Dry weight of each sample was divided by its wet weight, resulting in an index. The initial dry weight estimate of leaves was obtained by, multiplying the weight of wet sheets placed in each litter bags by the conversion factor corresponding to the species.

The decomposition constant (k) was calculated from the exponential function previously tested and used in other studies (Panitz, 1986; Chale, 1993; Aké-Castillo *et al.*, 2006). From the k value the half-life of leaves was calculated. As suggested by Olson (1963), the time required for 50% mass loss was calculated by using the following equation: $t50 = \ln 2 k^{-1}$, where $\ln 2$ = 0.693. Thus: $t50 = 0.693 k^{-1}$, where k is the decomposition constant and t50 is the time necessary for 50% of leaf material to be decomposed. The heterogeneity and homogeneity of variances were tested. The k and half-life values were subjected to a one-way ANOVA and Tukey *post-hoc* test for evaluating differences in decomposition rates between the three species. The values of mass loss among species and periods were compared using two-way ANOVA and Tukey *post-hoc* test.

RESULTS

The one-way ANOVA and Tukey test showed that the decomposition rate of leaves of *L. racemosa* (3.2 x 10^{-3}) did not differ significantly from *A. germinans* and *R. mangle* (P > 0.05), but *A. germinans* (5.1 x 10^{-3}) exhibited a higher decomposition rate than *R. mangle* (2.7×10^{-3}) (P > 0.05). The half-life differed among species ($P \le 0.05$) and was estimated at 138, 216 and 257 days for *A. germinans, L. racemosa* and *R. mangle*, respectively.

There were significant differences in the values of mass loss among periods (P < 0.05). The mass loss was rapid during the first 15 days of decomposition for the three species, followed by a slower loss in the remainder of the period (Fig. 2). A. germinans (Fig. 2a) had higher mass reduction in the first period $(\sim 40\%)$, followed by L. racemosa (30%) (Fig. 2b) and R. mangle ($\sim 25\%$) (Fig. 2c). The three species exhibited similar behavior in relation to mass loss over time (P > 0.05), with the exception of A. germinans (Fig. 2a), which on the 30th day showed a mass gain, as did *R. mangle* on the 90th and the 183rd days (Fig. 2c). Laguncularia racemosa showed no increase in mass during the experiment (Figure 2b). The coefficients of variation for the mean and ranges were 10% and 2 to 24% for A. germinans, 4% and 1 to 15% for L. racemosa, and 11% and 5 to 28% for R. mangle.

DISCUSSION

The pattern of decomposition observed in the estuarine mangrove of the Paraíba do Sul River is similar to those observed in other studies, such as mangroves in Cananéia (SP), Florianópolis (SC), Tanzania and the Gulf of Mexico (Adaime, 1985; Panitz, 1986; Chale, 1993; Aké-Castillo et al., 2006; Fernando & Banner, 2009). The rapid weight loss observed for the three studied species in the first 15 days of decomposition is consistent with results from other studies as well (Chale, 1993; Ake-Castillo et al., 2006). It is probably related to the leaching of soluble organic compounds, which in turn explains why the most abundant form of organic carbon exported from mangroves is in dissolved fraction (Dittmar et al., 2006; Rezende et al., 2007). After 15 days, the decomposition of leaves of the three species occurred more slowly. In the second phase particles are populated by microorganisms and/or mechanical fragmentation is caused by tides, rain and crabs,



Figure 2. Mean and standard deviation (n = 3) of the mass of leaf material remaining in the experiments of decomposition for three species in the estuary mangrove of the Paraíba do Sul River, Rio de Janeiro.

Figura 2. Media y desviación estándar (n = 3) de la masa de material de las hojas que quedan en los experimentos de descomposición de tres especies en el manglar del estuario del Río Paraíba do Sul, Rio de Janeiro.

leading to greater surface exposure to microorganisms and solubility of molecules with higher molecular weight. At this stage, molecules which are more resistant to bacterial activities may form humic substances with complex chemical structure (Chapin III *et al.*, 2002).

In this study, the species differed with respect to the decay rate (k) and half-life with A. germinans exhibiting a greater value of k over R. mangle, whereas L. racemosa did not differ in relation to the other two species. The process of decomposition of leaves is dependent on the species composition of each forest and environmental factors such as humidity, temperature and the soil factors that regulate the kinetics. Moreover, the structure of leaves, their chemical components, and water content have a significant role in this process (Dutta & Agrawal, 2001; Chapin III et al., 2002; Romero et al., 2005). Avicennia germinans exhibits higher concentrations of nitrogen in relation to the other two species considered in this study (Bernini et al., 2006; Medina & Francisco, 1997) and this feature, together with the fact that the substrate remained flooded for relatively long periods, could explain the greater rates of decomposition of leaves of this species. Rhizophora mangle, in turn, displays greater succulence and higher tannin content (Lacerda et al., 1986), which makes the decomposition of its leaves slower. Similar results were reported for the species Avicennia marina and Rhizophora mucronata (Fernando & Banner, 2009). In the estuarine mangrove of the Paraíba do Sul River, the values of dominance and relative density of species are respectively 53 and 35% for A. germinans, 28 and 57% for L. racemosa and 19 and 9% for R. mangle (Bernini & Rezende, 2011). Considering that A. germinans has higher prevalence and abundance in relation to R. mangle, and their kinetics of decomposition was faster, we suggest that this species represents the main source of organic matter from the mangrove to the estuary of the Paraíba do Sul River, as well as for the regional food chains.

The variation coefficients indicate that there was high heterogeneity for quantification of mass loss. This heterogeneity can be attributed to the difficulty of handling and cleaning the collected material. After 90 days of decomposition, the leaf materials (mainly *A. germinans*) were difficult to clean because the residues were incorporated to the sediment within the litter bags. The presence of sediment associated with the debris of leaves in later stages of decomposition leads to an increase in the percentage of remaining material, making the consideration of all values together difficult. This explains mass increases after reaching the half-life period (Fig. 2). Similar observations were reported by Castanho & Oliveira (2008) and Tam *et al.* (1998).

The percentage of remaining material of *R. mangle* and *L. racemosa* at the end of the experiment was higher than the value found by Adaime (1985), Ake-Castillo *et al.* (2006), Menezes & Schaeffer-Novelli (2000) and Panitz (1986). When comparing the percentage of remaining material of *R. mangle* with the decomposition studies carried out by Aké-Castillo *et al.* (2006), in Mexico, it is noted that over a period of 90 days, approximately 50% of the mass of *Rhizophora* had already decomposed, whereas in this study only 30% had decomposed. This result is attributed to the different environments in which the

f mangrove vicennia hizophora	Location Cananeia (Brazil) Florianopolis (Brazil) Kunduchi (Tanzania) Rio de Janeiro (Brazil) Cananeia (Brazil) Florianopolis (Brazil) Gulf of Mexico Cananeia (Brazil) Rio de Janeiro (Brazil) Cananeia (Brazil)	k 1.2 x 10^{-2} 1.1 x 10^{-3} 4.5 x 10^{-3} 5.1 x 10^{-3} 8.8 x 10^{-3} 6.4 x 10^{-3} 8.4 x 10^{-3} 8.4 x 10^{-3} 3.0 x 10^{-3} 2.7 x 10^{-3}	$\begin{array}{c} r^2 \\ 1,00 \\ 0,94 \\ 0,95 \\ 0,75 \\ 0,75 \\ 0,76 \\ 0,84 \\ 0,84 \\ 0,56 \\ 0,98 \\ 0,98 \\ 0,98 \\ \end{array}$	Half-life (days) 58 58 30 154 154 138 79 90 70 189 189 257	Reference Adaime (1985) Panitz (1986) Chale (1993) Present study Adaime (1985) Panitz (1986) Aké-Castillo <i>et al.</i> (2006) Menezes & Schaeffer-Novelli (2000) Present study Adaime (1985)	Experimental conditions Sediment Water Water Sediment Sediment Sediment Sediment Sediment Sediment
cularia	Florianopolis (Brazil) Cananeia (Brazil) Rio de Janeiro (Brazil)	8.4 x 10 ⁻³ 5.0 x 10 ⁻³ 3.2 x 10 ⁻³	0,95 - 0,73	216	Panitz (1986) Menezes & Schaeffer-Novelli (2000) Present study	Water Sediment Sediment

Tabla 2. Las tasas de descomposición y vida media de las hojas senescentes de manglares diferentes. Table 2. Decomposition rates and half-life of senescent leaves of different mangroves.

I abla 3. Comparacion	de la metodologia uti	lizada en algunos e	studios sobi	re la desco	mposicion de hojas senescentes de r	manglares.		
Author and species	Location of experiment	Size of mesh	Size of bag	Mass	Procedure while processing samples	Time scale (days)	Sampling interval	Final weight (mass loss)
Chale (1993) A. marina	Laboratory leaves incubated in estuarine water	Leaves incubated in Erlenmeyer flasks	Not informed	~1,0 g	Incubation of 1 g of senescent leaves (previously dried) in 100 ml of filte- red estuarine water (0.45 µm filters). After incubation the sheets were washed several times with distilled water.	86	Not informed	~40%
Aké-Castillo <i>et al.</i> (2006) <i>R. mangle</i>	Field Stuck to tree roots	1 x 1mm 3 x 7mm	20 x 20 cm	مع 10 هو	Senescent leaves dried for 20 days. Bags tied around their roots in three lines 50 cm apart from each other. 1 bag of each line was collected per month. Material collected was was- hed with distilled water using sieves of 5, 2, 0.5 and 0.25 mm to separate material and organisms. Leaves dried at 60°C.	150	30, 60. 120, 150 days	Fine mesh 40%, Coarse mesh 70%
Panitz (1986) A. schaueriana R.mangle L. racemosa	Field In water	2 x 2 mm	Not informed	~20 g	Senescent leaves previously dried. Leaves collected were washed out. Material placed in an oven 85°C.	330	30 days	As ~97% Lg~92 % Rh~89%
Adaime (1985) A. schaueriana R. mangle L. racemosa	Field In water	2 x 2mm	Not informed	Rh ~20 g Lg~20 g As~10 g	Senescent leaves previously dried. Leaves collected were washed out. Material placed in an oven 85°C.	Winter Lg-237 Rh-146 As-55 Summer Lg-298 Rh-298 As-116	30 days	Winter Lg \sim 77% Rh \sim 69% As \sim 54% Summer Lg \sim 70% Rh \sim 82% As \sim 80%
Present Study A. germinans R. mangle L. racemosa	Field Stuck to tree roots	l x l mm	30 x 30 cm	~30 g	Senescent leaves collected. Stuck near the roots of trees in contact with sediment. Collection, washing, drying and <i>weighing</i> the leaves.	183 days	1, 2, 3, 4, 7, 15, 30, 60, 90, 120 and 183 days	Ag ~63% Rh ~36% Lg ~42%

-**Table 3.** Comparison of the methodology used in some studies on decomposition of senescent leaves of mangroves. **Table 3.** Commerciation de la metodologic attitized an element actualise solve to decomposition de bailes conscentes f 404

experiments were carried out, since in the study by Ake-Castillo *et al.* (2006) the litter bags were water submerged during the entire period of study, while in this study there were alternating periods of flooding.

Table 2 shows the coefficients of decomposition and half-life of the litter leaf fraction from different mangroves. For Avicennia, the k value found here was higher than that found for the genus, while the half life is within the range observed in other mangroves (Adaime, 1985; Panitz, 1986; Chale, 1993). For R. mangle and L. racemosa k values were higher and half life values lower when compared to other studies (Adaime, 1985; Panitz, 1986; Menezes & Schaeffer-Novelli, 2000; Aké-Castillo et al., 2006). Differences in decomposition rate among different studies can be attributed to the type of vegetation, the quality of the material, the sediment pH, aeration, microbial activity present in the sediment and/or the environmental conditions, especially temperature and humidity (Chapin III et al., 2002), since these are the most important factors controlling rates of decomposition.

Decomposition experiments carried out simultaneously along gradients of latitude and longitude for different types of ecosystems have shown that climatic conditions (precipitation and temperature) and the quality of litter have a major influence on decomposition. However, specific conditions of the ecosystems or study sites (*e.g.* sediment fertility, composition and abundance of fauna) may complicate the interpretation of results (Gholz *et al.*, 2000; Cusack *et al.*, 2009; Powers *et al.*, 2009). Furthermore, it is important to note that comparisons between studies conducted in different areas are a difficult task, due to a lack of methodological and technical standardization.

Table 3 shows a comparison of methodologies used in some studies of decomposition in mangroves. This type of experiment can be carried out in laboratory or under natural conditions (water or sediment). The size of the mesh, the decomposition bag and the mass used vary widely between studies, and in some cases they are not reported. The mesh size is important, as it controls the access of the fauna that influence the decomposition (micro, meso or macrofauna) (Chapin III et al., 2002). The timescale and the collection interval also differ between studies. Such differences contribute to the mass losses, which in turn directly affect the final results of the experiments, as well as the ability of researchers to identify operating processes. Thus, it is highlighted here, after conducting a literature survey for this study, we must emphasize the need for studies comparing methodologies of experiments about decomposition in mangroves. Normalization in the minimum time scale of the experiment, intervals between collections, size and porosity of the bag of decomposition, mass and type of leaves used (*e.g.* preferably senescent and still on the tree), and analytical procedure in treatment of samples in the field and laboratory are key issues to be addressed.

CONCLUSIONS

Results indicate that while the kinetics of decomposition is similar to the studied species, *A. germinans* showed a more accelerated mass loss when compared with *R. mangle*, which, according descriptions in the literature, is related to the concentration of tannin and nitrogen. Although microenvironments are physical-chemically similar, differences in flooding regimes may have also contributed to this differentiation between species. The results of mass release obtained here are close to those described in the literature. The need for experimental standardization to enable better comparisons of results obtained in field experimental studies from different regions, is stressed.

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