

Leaf-litter decomposition of the mangrove species *Avicennia schaueriana*, *Laguncularia racemosa* and *Rhizophora mangle*

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This study evaluated the decomposition process of leaf litter from the main Brazilian mangrove species Avicennia schaueriana, Laguncularia racemosa and Rhizophora mangle. Senescent leaves were collected, dried and placed in nylon bags with different mesh sizes (fine: 2 × 2 mm and coarse: 8 × 8 mm). The bags were distributed over the sediment, and replicates of each species and mesh size were collected periodically over 4 months. In the laboratory, the dry weight of the samples was measured, and the decomposition coefficient (k) for each species and mesh size was obtained over time. All species showed a rapid decomposition rate at the beginning of the experiment, followed by a slower but steady rate of decomposition over time. The rate of leaf litter decomposition was highest in A. schaueriana, intermediate in L. racemosa and lowest in R. mangle. The difference was mainly linked to the activity and abundance of detritivores, together with the different litter quality of the species, which determined their palatability and probably influenced the decomposition process.

Keywords: litter mesh bag, mangrove, Brazil

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INTRODUCTION

Mangroves are highly productive ecosystems which can be potential sources of organic matter and nutrients, mainly through detritus, as particulate organic matter (POM) and dissolved organic matter (DOM) exported to estuarine and adjacent coastal areas, especially in the more oligotrophic regions (Robertson *et al.*, 1992; Jennerjahn & Ittekkot, 2002; Dittmar *et al.*, 2006). Litterfall, which is composed primarily of leaves (Robertson *et al.*, 1992; Aké-Castillo *et al.*, 2006), provides a large input of organic material (Jennerjahn & Ittekkot, 2002; Mfilinge *et al.*, 2005), and leaf detritus is an important food source for decomposer food webs, which can be recycled within the mangrove forest or exported (Jennerjahn & Ittekkot, 2002; Kristensen *et al.*, 2008).

The process of leaf-litter decomposition on the sediment has an important role in the availability of organic matter and nutrient cycling in mangroves and adjacent areas (Kathiresan & Bingham, 2001; Barroso-Matos *et al.*, 2012). This process can be divided into two stages: (1) a rapid weight loss, mainly due to leaching and degradation of soluble compounds such as certain sugars and tannins (Davis *et al.*, 2003; Kristensen *et al.*, 2008); (2) slower decomposition resulting from the deterioration of structural

and refractory materials such as lignin (Melillo *et al.*, 1982; Ananda *et al.*, 2008).

Decomposition depends on the degree and frequency of tidal inundation, climatic factors such as temperature, humidity and rainfall, substrate conditions and the presence of leaf detritus-consuming fauna (Twilley *et al.*, 1986; Tam *et al.*, 1990; Mackey & Smail, 1996; Alongi, 2009; Galeano *et al.*, 2010). The detritivores affect decomposition by shredding, ingesting and assimilating litter, which facilitates leaf decomposition and can increase microbial colonization (Imgraben & Dittmann, 2008; Alongi, 2009). Crustaceans, molluscs and annelids are the main macrofauna groups that process leaf litter into smaller particles (Alongi, 1998; Oliveira *et al.*, 2012).

Bacteria and fungi participate significantly in decomposition, especially in its early stage (Cundell *et al.*, 1979; Kathiresan & Bingham, 2001), through the enrichment of leaves by mineralization or immobilization of some nutrients, making the leaves more attractive for detritivores. Alongi *et al.* (1992) noted that organic materials that are rich in nitrogen (low C:N ratio) favour mineralization, whereas nitrogen-poor material (high C:N ratio) favours the immobilization of this nutrient. The dynamics of nitrogen are important because the litter quality of the leaf is given by the C:N ratio, in which low values of the ratio indicate high concentrations of nitrogen and higher litter quality (Wafar *et al.*, 1997; Ashton *et al.*, 1999).

The leaf decomposition rate varies among plant species and depends mainly on the structure and chemical composition of the leaf, especially the lignin and nutrient concentrations

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(Tam *et al.*, 1998). Decomposition is also influenced by the amount of polyphenols, usually in the form of tannins, which are astringent secondary metabolites and act as a defence mechanism against herbivores (Kandil *et al.*, 2004).

Mangroves occur along 92% of the Brazilian coastline (6786 km), and show wide variability in their structural and spatial attributes, related to their geographical distribution (Schaeffer-Novelli *et al.*, 1990, 2000). *Avicennia schaueriana* Stapf & Leechman, *Laguncularia racemosa* C.F. Gaertn and *Rhizophora mangle* L. are the three main species found in Brazilian subtropical mangrove forests (Schaeffer-Novelli *et al.*, 1990; Colpo *et al.*, 2011). They have different chemical constituents, especially the concentrations of nutrients and secondary metabolites (Godoy *et al.*, 1997; Bernini *et al.*, 2006). These differences in chemical composition may affect the degradation and subsequent decomposition of their leaves.

The nylon-mesh bag technique is most frequently used to study leaf litter decomposition. Despite its limitations, the litterbag technique is useful because it does reflect trends and can provide comparisons between treatments (Tam *et al.*, 1990; Bosire *et al.*, 2005). Studies commonly test the effect of the exclusion of specific faunal groups through the deployment of bags with different mesh sizes, in order to determine the effects of these animals on the decomposition process (Bradford *et al.*, 2002). A fine mesh allows small invertebrate consumers to enter, in conjunction with the microbial decomposition activity, but excludes large invertebrate consumers (i.e. large Decapoda and Gastropoda) and prevents much of the particulate organic matter from being flushed from the bag (Robertson, 1988; Silva *et al.*, 2007; Imgraben & Dittmann, 2008). A coarse mesh enables observation of a nearly natural decomposition process, by allowing entry of macroinvertebrates and facilitating physical fragmentation (Nanda *et al.*, 2009).

As noted by Kristensen *et al.* (2008), understanding nutrient cycling and the factors controlling nutrient pathways is essential to reveal ecosystem capacity; and decomposition, as one of its factors, can have important trophic implications (Alongi, 2009). The few investigations of leaf-litter decomposition dynamics in Brazilian mangrove forests include those of Sessegolo & Lana (1991), Moura (1997) and Barroso-Matos *et al.* (2012). In order to better understand the leaf-litter decomposition process and its potential implications in biogeochemical cycling and trophic webs in subtropical mangroves, this study analysed and compared the rates of leaf decomposition of Brazilian mangrove species (*A. schaueriana*, *L. racemosa* and *R. mangle*) in nylon-mesh bags (fine: 2 × 2 mm and coarse: 8 × 8 mm) over time.

MATERIALS AND METHODS

The study was conducted in a subtropical mangrove located along the banks of the Itapanhaú River in the municipality of Bertioga (23°50'11"S 46°09'10"W) on the southern coast of São Paulo, Brazil. The mangrove sediments are fine (Queiróz-Neto & Küpper, 1965), and tides are semidiurnal and range around 1.5 m. The annual rainfall ranges from 1500 to 4000 mm; the mean annual temperature is 22°C, with a minimum of 10°C and a maximum of 35°C; and the relative humidity oscillates around 80% (Afonso, 2006).

The experiment was conducted over four months during autumn and early winter (March–July 2011). Senescent

leaves of each species (*Avicennia schaueriana*, *Laguncularia racemosa* and *Rhizophora mangle*), which were yellow and close to abscission, easily detached from the twigs (Ashton *et al.*, 1999), were collected in the mangrove. In the laboratory, the leaves were air-dried at room temperature for 48 h to remove part of the moisture (Imgraben & Dittmann, 2008). Dried leaves (5 g) of each species were placed in nylon litter bags of two kinds, fine mesh (2 × 2 mm) and coarse mesh (8 × 8 mm), measuring 18 × 13.5 cm. The litter bags with fine and coarse mesh were randomly arranged on the sediment inside the mangrove forest. The bags were tied to tree trunks or roots at 15 m from the river bank, to ensure the same tidal conditions. Also, three extra bags containing 5 g of air-dried but undecomposed leaves of each species were dried at 60°C for 96 h to determine the initial dry weight (DW_0) (Aké-Castillo *et al.*, 2006).

Three litter bags of each species and type of mesh were collected randomly from the study site 7, 12, 19, 27, 41, 57, 70, 84, 97 and 112 d after the beginning of the experiment and taken to the laboratory. Initially the bags were collected weekly, since changes occur more rapidly in the early stages of decomposition (Moura, 1997). In the laboratory, the leaves from the collected bags were gently rubbed and washed under tap water on a sieve with mesh size of 0.25 mm, to remove the sediment and retain the leaf debris. Then, each sample was dried at 60°C for 96 h to obtain the dry weight (Silva *et al.*, 2007). In order to determine the decomposition rate we used a mathematical model described by Olson (1963), by adjusting the curves for dry-weight loss to the exponential model:

$$DW/DW_0 = e^{-kt}$$

in which DW_0 is the initial dry weight, DW is the final dry weight, k is the coefficient of decomposition and t is the time elapsed. The decomposition coefficient (k) of each sample indicates its decomposition rate.

To compare the decomposition rates of the three mangrove species, as influenced by the different meshes, over time, the data were subjected to a repeated measures ANOVA (between-subjects factors: species (three levels: *A. schaueriana*, *L. racemosa* and *R. mangle*), mesh (two levels: fine and coarse) and within-subjects factor: time (10 levels: 7, 12, 19, 27, 41, 57, 70, 84, 97 and 112 d)) (Zar, 1999). The homogeneity of variances was determined through the Cochran test, and when necessary the data were transformed using $\ln(x)$. The Student–Newman–Keuls (SNK) test was used *a posteriori* to detect significant differences (Underwood, 1997).

The invertebrates associated with the leaves and found during washing were separated and preserved in 70% ethanol. Later, the specimens were identified and counted under a stereomicroscope.

RESULTS

The repeated-measures ANOVA showed that the decomposition coefficient of all species was highest on the first sampling day (day 7), and decreased significantly by the second sampling day (day 12). Subsequently the coefficient gradually decreased until the 112th day (Table 1; Figure 1). After the 12th day the decomposition entered a slower phase.

Table 1. Summary of repeated measures ANOVA, showing the effects of species, mesh and time on the decomposition process, for the decomposition coefficient (k).

	Decomposition coefficient (k)			
	C = 0.1004 (ns)			
	DF	MS	F	P
Species	2	10.34	55.34	<0.001
Mesh	1	6.46	34.59	<0.001
Species × mesh	2	1.06	5.66	0.019
Error	12	0.187		
Time	9	3.97	28.06	<0.001
Time × species	18	0.13	0.94	0.532
Time × mesh	9	0.17	1.20	0.301
Time × species × mesh	18	0.16	1.15	0.319
Error time	108	0.14		

C, Cochran's C-test; ns, not significant.

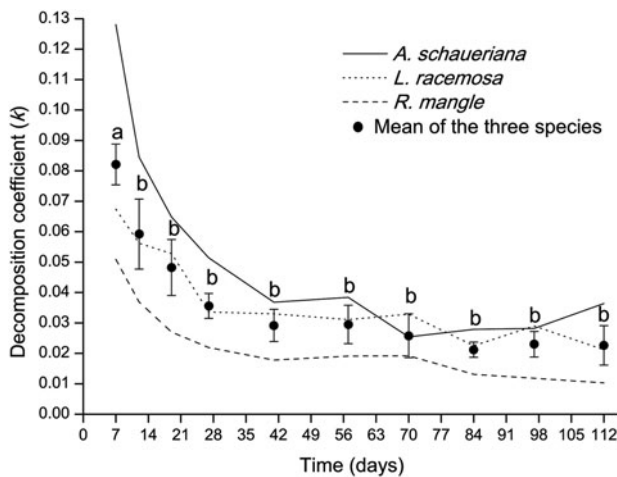


Fig. 1. Decomposition coefficient (k) of leaves from each mangrove species over time. Dots indicate the overall mean and SE of k for the three species. Different letters indicate a statistical difference ($P < 0.01$).

The decomposition coefficient of *Avicennia schaueriana* leaves was similar in the bags of different meshes, while for *Laguncularia racemosa* and *Rhizophora mangle* the decomposition coefficients were higher in the coarse mesh than the fine mesh (Table 1; Figure 2). Leaves of *L. racemosa* in coarse-mesh bags decomposed 100% faster than in fine-mesh bags, and in *R. mangle* this difference was 47% faster. Comparison of coefficients between each species and mesh indicated that *A. schaueriana* in both meshes (fine mesh = 0.049 ± 0.006 , mean \pm SE; coarse mesh = 0.054 ± 0.006) and *L. racemosa* in coarse mesh (0.051 ± 0.007) decomposed at a similarly rapid rate. Similar intermediate coefficients were recorded for the fine mesh of *L. racemosa* (0.025 ± 0.002) and coarse mesh of *R. mangle* (0.027 ± 0.003). The fine mesh of *R. mangle* showed the slowest decomposition rate recorded (0.018 ± 0.002) (Figure 2).

Arthropods and annelids were found in the decomposition bags (coarse and fine mesh). Crustaceans were the most diverse group, with representatives from Peracarida (orders Isopoda, Tanaidacea and Amphipoda) and Decapoda (juveniles of the families Sesamidae, Ocypodidae and Xanthidae). Chironomid larvae (Diptera) were also recorded. Among

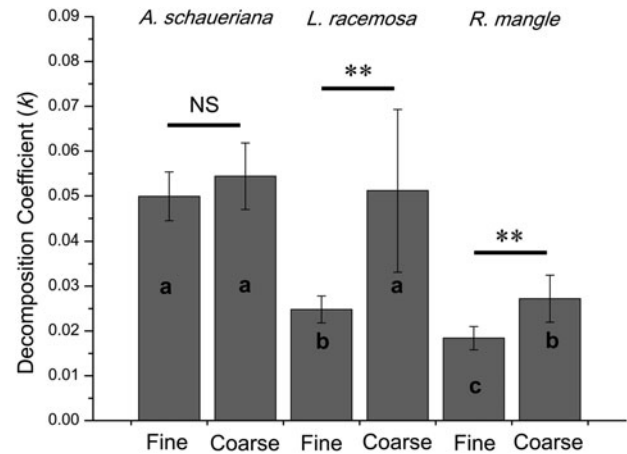


Fig. 2. Mean decomposition coefficient (k) of *Avicennia schaueriana*, *Laguncularia racemosa* and *Rhizophora mangle* in fine- and coarse-mesh bags (mean and SE). Different letters indicate a statistical difference ($P < 0.05$). **, $P < 0.01$; NS, $P > 0.05$.

Annelida, polychaetes of the order Phyllodocta (families Nereididae, Nephtyidae and Goniadidae) and subclass Oligochaeta were found. Invertebrate abundance in the decomposition bags reached its maximum on the 19th day for *R. mangle* and on the 27th day for *A. schaueriana* and *L. racemosa* (Figure 3). Juveniles of Decapoda predominated

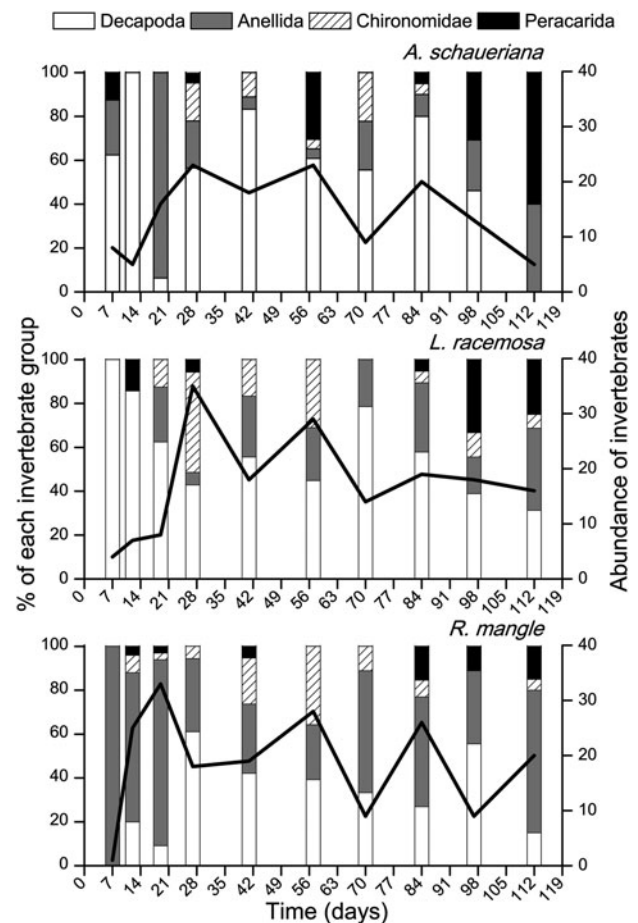


Fig. 3. Relative and total abundance of main macrofauna groups on mangrove leaves in mesh bags during the decomposition process.

throughout the survey in *A. schaueriana* and *L. racemosa*, and comprised 54.1% and 54.6%, respectively, of the total of invertebrates in the bags. However, in *R. mangle*, annelids predominated on six of the ten sampling days and comprised 55.9% of the invertebrate abundance in the bags of leaves of this species (Figure 3).

DISCUSSION

All species showed a high decomposition rate in the first week of the decomposition process, with a pronounced decrease of the coefficient in the following weeks, as reported in several other litter-decomposition studies; the period of decrease can vary from days to weeks (Robertson *et al.*, 1988; Dick & Osunkoya, 2000; Davis *et al.*, 2003; Aké-Castillo *et al.*, 2006; Barroso-Matos *et al.*, 2012). This rapid weight loss, which results from the high decomposition rate in the beginning of the experiment, is usually attributed to leaching of soluble compounds such as sugars, organic acids, proteins and phenols (Mfilinge *et al.*, 2002; Davis *et al.*, 2003, 2007; Kristensen *et al.*, 2008). After the first week a slower phase began, with a constant and decreasing decomposition rate. This phase is normally marked by a more gradual decomposition (Ananda *et al.*, 2008; Galeano *et al.*, 2010) and is well recognized in the literature as a period of intense microbial action, when the N content increases (Robertson *et al.*, 1988, 1992; Wafar *et al.*, 1997; Davis *et al.*, 2007).

Leaves placed in coarse-mesh bags usually have higher decomposition rates than leaves in fine-mesh bags, since they are more exposed to leaching, physical abrasion and loss of particles (Bradford *et al.*, 2002; Aké-Castillo *et al.*, 2006). In the present study, leaves of *Laguncularia racemosa* in coarse-mesh bags decomposed 100% faster than in fine-mesh bags, while in *Rhizophora mangle* this difference was 47% faster. Meyer *et al.* (2011), in a study in a Hawaiian rain forest, observed 17% faster decomposition in treatments that did not exclude large invertebrates (larger than 2 mm). Middleton & McKee (2001) found that the participation of these invertebrates is indispensable, and with macroinvertebrates present the decomposition rate was three times faster than with microorganisms alone. However, in this study, *Avicennia schaueriana* showed a similar decomposition rate in bags of both mesh sizes. This similarity could have resulted from the high litter quality of its leaves, as represented by the low C:N ratio previously reported for this genus (Wafar *et al.*, 1997; Bernini *et al.*, 2006; Sánchez-Andrés *et al.*, 2010). Leaves with a low C:N ratio are normally preferred by detritivores (Poovachiranon *et al.*, 1986; Nordhaus *et al.*, 2011), which in turn might have led to the high weight loss and decomposition rates in both meshes observed here.

According to the classification of Ananda *et al.* (2008), all three species had rapid decomposition rates ($k > 0.01$). In general, setting aside the effect of mesh size, the decomposition rate for *A. schaueriana* was higher during most of the decomposition process, followed closely by *L. racemosa* with intermediate coefficients, and last by *R. mangle*. Similar differences between members of these genera have been found previously in other studies worldwide, as shown by an overview of the k range in Table 2; and usually follow the same pattern, in which k of *Avicennia* $>$ k of *Laguncularia* $>$ k of *Rhizophora*. However, comparisons among studies scattered

around the world have their limitations, mainly because of the lack of methodological standardization.

The initial chemical composition of the leaves, especially the concentrations of N, tannins and lignin, which determine litter quality, is regarded as a regulator of the decomposition rate (Melillo *et al.*, 1982; Wafar *et al.*, 1997; Mfilinge *et al.*, 2002), in addition to leaf morphology (Steinke *et al.*, 1990; Ashton *et al.*, 1999), and has been invoked as the main explanation for the differences in decomposition rate among these genera (Fernando & Bandeira, 2009; Galeano *et al.*, 2010; Sánchez-Andrés *et al.*, 2010; Barroso-Matos *et al.*, 2012). Twilley *et al.* (1986) suggested that a higher concentration of N in *Avicennia germinans* L. induced degradation at twice the rate observed for *R. mangle*. According to Middleton & McKee (2001), in addition to the high concentration of N, low tannin amounts contributed to the faster weight loss of leaves of *A. germinans* compared to *R. mangle* and *L. racemosa*. Also for the same genus, *Avicennia officinalis* L. showed a decomposition coefficient four to five times higher than those of *Rhizophora apiculata* Blume, *Rhizophora mucronata* Lam. and *Sonneratia alba* J. Smith, probably as a consequence of its thinner leaves, which fragment easily and accelerate decomposition (Wafar *et al.*, 1997). *Avicennia* leaves tend to decompose faster than other species because they are thinner and have a high N content and low concentrations of lignin and tannin (Godoy *et al.*, 1997; Wafar *et al.*, 1997; Kathiresan & Bingham, 2001; Bernini *et al.*, 2006). Comparing the two remaining species, Moura (1997) found that the lower decomposition rate of *R. mangle* compared with *L. racemosa* is probably because of the thick waxy cuticle and epidermis, which impede shredders (Cundell *et al.*, 1979), besides the higher lignin content (Godoy *et al.*, 1997). Since the leaves in this experiment were under the same environmental conditions, it is likely that the observed differences among species were influenced mainly by the litter quality.

The predominance of crabs in bags with *A. schaueriana* and *L. racemosa* leaves may be a consequence of their food preferences, and of the litter quality of these plant species. Nordhaus *et al.* (2011) suggested that plants with larger amounts of nitrogenous compounds were the preferred food for mangrove crabs. The low N content and the thick cuticle of *R. mangle* may repel the crabs, but also these features may attract the annelids that were the predominant invertebrate group in this mangrove species. Most annelid species in estuarine areas are surface deposit-feeders, with discrete motility and opportunistic behaviours (Magalhães & Barros, 2011; Oliveira *et al.*, 2012). They feed on microorganisms, sediments and organic matter that settle on the leaf surface (Oliveira *et al.*, 2012). The leaves of *R. mangle*, which showed the lowest decomposition rate, may be a more stable substrate than *A. schaueriana* and *L. racemosa* for the establishment of annelids and their food source. The different abundances of decapods and annelids on the three mangrove species and their respective decomposition rates may also suggest that annelids are less efficient shredders than decapods, although Camilleri (1992) and Oliveira *et al.* (2012) noted the important role of polychaetes in processing leaves in tropical mangroves.

The different meshes of litter bags used in this study did not prove significant for mediating macrofauna access when the litter quality was taken into account, as in the case of *A. schaueriana*, but may have had some influence on leaching

Table 2. Overview of decomposition rates, represented by the worldwide range of the coefficient (*k*).

Species	Location	Litter-bag mesh size (mm)	Coefficient (<i>k</i>)	Leaves	Reference
<i>Avicennia schaueriana</i> Stapf & Leechman	São Paulo (Brazil)	2 × 2; 8 × 8	0.049; 0.054	Yellowish senescent	Present study
<i>A. schaueriana</i>	Paraná (Brazil)	2 × 2	0.013–0.043	Yellowish senescent	Sessegolo & Lana (1991)
<i>Avicennia germinans</i> (L.) Stearn	Rio de Janeiro (Brazil)	1 × 1	0.0051	Yellowish senescent	Barroso-Matos <i>et al.</i> (2012)
<i>A. germinans</i>	Archipelago of San Andrés, Providencia and Santa Catalina (Colombia)	4 × 4	0.012–0.024	Yellowish senescent	Galeano <i>et al.</i> (2010)
<i>A. germinans</i>	Sonora (Mexico)	1.5 × 1.5	0.032	Freshly fallen	Sánchez-Andrés <i>et al.</i> (2010)
<i>A. germinans</i>	Florida (USA)	1 × 1	0.0037–0.027	Yellowish senescent	Proffitt & Devlin (2005)
<i>Avicennia marina</i> (Forsk.) Vierh.	Maputo (Mozambique)	1 × 1	0.004–0.014	Yellowish senescent and freshly fallen	Fernando & Bandeira (2009)
<i>A. marina</i>	Hong Kong (China)	5 × 5	0.0126	Dried fresh green	Tam <i>et al.</i> (1990)
<i>A. marina</i>	New South Wales (Australia)	1 × 1	0.0005–0.0116	Dried fresh green	Dick & Osunkoya (2000)
<i>A. marina</i>	Queensland (Australia)	2 × 1	0.0071–0.0158	Freshly fallen	Mackey & Smail (1996)
<i>Laguncularia racemosa</i> C.F. Gaertn	São Paulo (Brazil)	2 × 2; 8 × 8	0.025; 0.051	Yellowish senescent	Present Study
<i>L. racemosa</i>	Paraná (Brazil)	2 × 2	0.008–0.016	Yellowish senescent	Sessegolo & Lana (1991)
<i>L. racemosa</i>	Rio de Janeiro (Brazil)	1 × 1	0.0032	Yellowish senescent	Barroso-Matos <i>et al.</i> (2012)
<i>L. racemosa</i>	Bahia (Brazil)	2 × 2	0.022–0.031	Yellowish senescent	Oliveira <i>et al.</i> (2013)
<i>L. racemosa</i>	Archipelago of San Andrés, Providencia and Santa Catalina (Colombia)	4 × 4	0.014–0.023	Yellowish senescent	Galeano <i>et al.</i> (2010)
<i>L. racemosa</i>	Sinaloa (Mexico)	2.25 × 2.25	0.052	Dried fresh fallen	Flores-Verdugo <i>et al.</i> (1987)
<i>Rhizophora mangle</i> L.	São Paulo (Brazil)	2 × 2; 8 × 8	0.018; 0.027	Yellowish senescent	Present study
<i>R. mangle</i>	Paraná (Brazil)	2 × 2	0.003–0.015	Yellowish senescent	Sessegolo & Lana (1991)
<i>R. mangle</i>	Rio de Janeiro (Brazil)	1 × 1	0.0027	Yellowish senescent	Barroso-Matos <i>et al.</i> (2012)
<i>R. mangle</i>	Bahia (Brazil)	2 × 2	0.016–0.022	Yellowish senescent	Oliveira <i>et al.</i> (2013)
<i>R. mangle</i>	Archipelago of San Andrés, Providencia and Santa Catalina (Colombia)	4 × 4	0.012–0.016	Yellowish senescent	Galeano <i>et al.</i> (2010)
<i>R. mangle</i>	Florida (USA)	1 × 1	0.0026–0.0061	Yellowish senescent	Proffitt & Devlin (2005)
<i>Rhizophora mucronata</i> Lamk.	Coast (Kenya)	1 × 1	0.01–0.41	Yellowish senescent	Bosire <i>et al.</i> (2005)
<i>R. mucronata</i>	Maputo (Mozambique)	1 × 1	0.002–0.028	Yellowish senescent and freshly fallen	Fernando & Bandeira (2009)
<i>R. mucronata</i>	Karnataka (India)	1 × 1	0.004–0.160	Freshly fallen	Ananda <i>et al.</i> (2008)
<i>R. mucronata</i>	Perak (Malaysia)	1 × 1	0.0057–0.0204	Yellowish senescent and freshly fallen	Ashton <i>et al.</i> (1999)
<i>Rhizophora apiculata</i> Blume	Goa (India)	12 × 5	0.0024	Yellowish senescent	Wafar <i>et al.</i> (1997)
<i>R. apiculata</i>	Perak (Malaysia)	1 × 1	0.0091–0.0163	Yellowish senescent and freshly fallen	Ashton <i>et al.</i> (1999)

and fragmentation, leading to the differences found for *L. racemosa* and *R. mangle*. Therefore, we conclude that the differences in litter quality among the species, which determine their palatability, together with the abundance and activity of the detritivorous fauna (mediated in this study by the mesh sizes) were the main factors that regulated the decomposition rate of leaf litter, and may control the decomposition dynamics as estimated in this Brazilian subtropical mangrove forest.

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