



Litterfall in a mangrove in Southeast Brazil

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Abstract. Litter production in forests dominated by *Avicennia germinans*, *Laguncularia racemosa* and *Rhizophora mangle* was measured over a two year period (2005-2006) in the mangrove estuary of the Paraíba do Sul River (PSR), located in Southeastern Brazil. Total litter production was higher in the *R. mangle* forest ($4.26 \pm 2.84 \text{ g.m}^{-2}.\text{day}^{-1}$), followed by *A. germinans* ($3.59 \pm 3.18 \text{ g.m}^{-2}.\text{day}^{-1}$) and *L. racemosa* ($3.58 \pm 2.91 \text{ g.m}^{-2}.\text{day}^{-1}$) and did not vary between years. For the three species, the leaf fraction was the main component of the litter, followed by fruit, wood, flowers and miscellaneous. Litter production was seasonal, with higher values in the rainy season. There was no relation between litter production and vegetation structure. The environmental variables, rainfall, mean air temperature and wind speed explained little of the seasonal litter variability. This study showed the mangrove estuary of the PSR has high production values of litter to be an environment dominated by river.

Key words: Estuary of the Paraíba do Sul River, leaf litter, primary production

Resumo. Produção de serapilheira em uma floresta de mangue do Sudeste do Brasil. A produção de serapilheira em florestas dominadas por *Avicennia germinans*, *Laguncularia racemosa* e *Rhizophora mangle* foram quantificadas por um período de dois anos (2005-2006) no manguezal do estuário do Rio Paraíba do Sul (RPS), localizado no Sudeste do Brasil. A produção total de serapilheira foi maior para a floresta de *R. mangle* ($4,26 \pm 2,84 \text{ g.m}^{-2}.\text{day}^{-1}$), seguida por *A. germinans* ($3,59 \pm 3,18 \text{ g.m}^{-2}.\text{day}^{-1}$) e *L. racemosa* ($3,58 \pm 2,91 \text{ g.m}^{-2}.\text{day}^{-1}$) e não exibiu variação entre os anos analisados. A fração folhas foi o principal componente da serapilheira para as três espécies, seguido por frutos, madeira (galhos), flores e miscelânea. A produção de serapilheira foi sazonal, com maiores valores no período chuvoso. Não houve relação entre a produção de serapilheira e a estrutura da vegetação. As variáveis ambientais pluviosidade, temperatura média do ar e velocidade dos ventos explicaram pouco a variabilidade sazonal da produção de serapilheira. Este estudo mostrou que o estuário do RPS apresenta altos valores de produção de serapilheira por ser um ambiente dominado por rio.

Palavras chave: Estuário do Rio Paraíba do Sul, folhas de serapilheira, produção primária

Introduction

The mangrove is an ecosystem influenced by tides and is found in tropical and subtropical regions (Lugo and Snedaker 1974). This ecosystem occurs mainly in sheltered areas such as estuaries, bays and lagoons and is considered an open system due to its significant material exchanges with terrestrial, ocean, estuarine and atmospheric environment (Lugo 2002). In tropical coastal

regions, the mangrove occupies the second position in terms of gross productivity, only being exceeded by coral reefs (Qasim & Wafar 1990, Duarte & Cebrián 1996). Because it is logistically and economically viable, litter production has been widely used to evaluate the productivity of mangroves (Putz & Chan 1986, Hegazy 1998, Silva *et al.* 1998, Aké-Castilho *et al.* 2006, Nascimento *et al.* 2006, Ramos e Silva *et al.* 2006, Fernandes *et al.*

2007), although there is no evidence of correlation between this compartment and the primary production of the ecosystem (Clough 1992). Besides being used as an indicator of productivity, litter can also provide indirect evidence about plants phenology (Proctor 1983).

Litter can represent up to one third of mangrove primary production (Robertson *et al.* 1992), and may be remineralized by decomposition, accumulated in the sediment and/or exported to adjacent areas (Pool *et al.* 1975). The export level of dissolved and particulate materials from the litter depends on geomorphology and tidal amplitude, and tends to be larger in mangroves located in coastal areas dominated by tides or under strong river influence (Woodroffe 1992, Twilley *et al.* 1997, Twilley & Day 1999). However, import of organic material in this ecosystem is possible as described by Rezende *et al.* (1990) and Dittmar & Lara (2001).

In general, leaves are the main components of litter accounting with more than 50% of the total production. Although there are regional differences in its fall and variations in exchange with the ocean, the annual global production rate of this component is estimated at 92×10^{12} g C, of which 25% accumulates in the sediment, 25% is recycled within the ecosystem and 50% is exported to the coastal zone (Robertson & Daniel 1989). The export of organic matter and dissolved nutrients is important for the productivity of coastal waters, since it has a recognizable effect on food chains (Odum & Heald 1975, Jennerjahn & Ittekkot 2001, Dittmar *et al.* 2006). According to Dittmar *et al.* (2006), approximately 10% of dissolved organic carbon transported from the mainland to the ocean is from mangroves, although this ecosystem occupies less than 0.1% of the continents' surface.

Litter production of mangrove forests usually presents seasonal variation because it is influenced by several factors mainly related to the chemical and physical environment (for example: air temperature, solar radiation, rainfall, type of substrate, nutrient concentration, freshwater availability) (Clough 1992, Twilley & Day 1999). On a global scale, litter production varies between 1.0 and 20.3 $\text{ton} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$, and in spite of regional and local variations, the values tend to decline with increase in latitude (Saenger & Snedaker, 1993, Mehlig 2001). Riverine forests are the most productive, followed by fringe and basin forests (Twilley & Day 1999).

In Brazil, where mangroves cover about 1.4 million hectares (Spalding *et al.* 1997), studies on litterfall are numerous, but there are

no report data on forests subjected to a strong river influence, as the mangrove of the estuary of the Paraíba do Sul River, located in southeastern Brazil. Thus, the purpose of this study is: (1) quantify and compare litter production in riverine forests of *Avicennia germinans* (L.) Stearn., *Laguncularia racemosa* (L.) Gaertn. f. and *Rhizophora mangle* L. and (2) evaluate the influence of environmental factors on the productivity of the mangrove in this estuary.

Material and methods

The study was conducted in the mangrove of the estuary of the Paraíba do Sul River, located in São Francisco de Itabapoana, State of Rio Janeiro, in Southeastern Brazil ($21^{\circ}36'00''$ S, $41^{\circ}03'00''$ W) (Figure 1). The mangrove area covers approximately 7.2 km^2 (Bernini *et al. in press*) and is composed of *Avicennia germinans*, *Laguncularia racemosa* and *Rhizophora mangle* (Bernini & Rezende 2004). Based on data from the Terminal da Ponta do Ubu, State of Espírito Santo ($20^{\circ}44'S$, $40^{\circ}32'W$) from 2005 and 2006, the average tidal amplitude was 0.8 m (DHN 2006). The estuary is located in a region where the predominant climate is type Aw (hot and humid with rain in the summer).

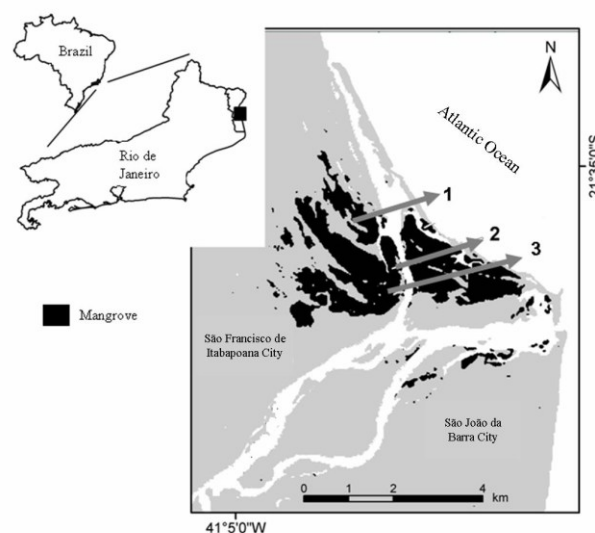


Figure 1. Location of the study sites in the mangrove estuary of the Paraíba do Sul River, Rio de Janeiro State, Brazil. 1. Forest dominated by *Laguncularia racemosa*; 2. Forest dominated by *Rhizophora mangle*; 3. Forest dominated by *Avicennia germinans*.

To estimate the litter production three types of coastal forests were selected, with dominance of *Avicennia germinans*, *Laguncularia racemosa* and *Rhizophora mangle* (Figure 1). The vegetation

structure and the environmental variables of the forests sediment were analyzed by Bernini (2008) and are presented in table I.

In each forest, a 70x40 m plot was established approximately 5 m away from the shore of the channel, where 7 baskets of 70x70 cm were randomly installed. The baskets were made with an aluminum structure and 2 mm nylon mesh, 50 cm deep and were suspended in the trees about 1.3 m above the substrate. Collection was carried out from January 2005 to December 2006 scheduled at fortnightly intervals over two annual cycles, totaling 48 samples. The material collected was oven dried until constant weight (80°C/72 h) and then sorted and weighed, into the following fractions: leaves, wood (twigs), flowers, fruit and miscellaneous (all plant material < 2 mm and occasional structures of other species).

Litter production is the result obtained as the average of the values found for the seven collectors each forest in each sample, converted to m², according to day interval between collections and it is expressed as g.m⁻².day⁻¹. The production data were also transformed for ton. ha⁻¹. year⁻¹. The

nonparametric test of Friedman was used to assess differences in litterfall between collection intervals (48 samples) over the two years analyzed. Variations in annual rates (2005 and 2006) of litter production were analyzed with the non-parametric Mann-Whitney. Variations among species (*A. germinans*, *L. racemosa* and *R. mangle*) were analyzed with the non-parametric Kruskal-Wallis and Dunn tests (Zar 1996).

The climatic data were obtained from the evapotranspirometric station of the Agricultural Science and Technology Center of the Universidade Federal do Norte Fluminense (UENF), located 30 km from the estuary of the Paraíba do Sul River. River discharge data were provided by the Environmental Sciences Laboratory, of the UENF. Multiple linear regression analysis was used to relate the mean fortnightly values of the litter production, mean rainfall, wind speed, river flow, and mean, minimum and maximum air temperature. This analysis was performed for all variables. However, we present the results only for variables that showed statistical significance.

Table I. Vegetation structure and abiotic factors of the sediment in the mangrove forests analyzed in the estuary of the Paraíba do Sul River (Bernini, 2008). * Mean and standard deviation. DBH: diameter at breast height.

Variable	Forest		
	<i>A. germinans</i>	<i>L. racemosa</i>	<i>R. mangle</i>
Vegetation structure			
Average height (m)	10.4	5.5	8.8
Average DBH (cm)	16.6	5.7	12.7
Dominance (%)	99.0	100.0	75.0
Relative density (%)	97.0	100.0	97.0
Abiotic factors of the sediment			
Textural classification	Sandy silt	Sandy silt	Sandy silt
Organic matter (%)*	17.57 ± 0.13	8.23 ± 1,01	13.86 ± 3.40
Salinity of porewater*	2.7 ± 0,3	2.3 ± 0.3	2.0 ± 0.0

Results

Environmental variables

The mean air temperature was 22.3°C in 2005 and 23°C in 2006 with higher values from January to March (25.2-27.3°C) and the lower values between June and August (19.6-21.4°C). Total rainfall was higher in 2005 (1,385 mm) compared to 2006 (874 mm) (Figure 2). In general, most rainfall occurred between the months of September and February. The prevailing wind direction was northeast and the mean intensity during the period 2005-2006 was 2.0 m.s⁻¹. In the Lower Paraíba River region, the river flow was higher in 2005 compared

to 2006, as well as the particulate material in suspension (Figure 3).

Litter production

Table II presents the values of daily litter production of different fractions of litter for the studied period. The mean production of total litter for the forests in the years 2005 and 2006 was significantly higher for the *R. mangle* forest, followed by *A. germinans* and *L. racemosa*, which did not differ between them. The values of the standard deviation showed a wide variation among collection dates, indicating seasonality in litter fall, which was statistically significant (Friedman, $p \leq$

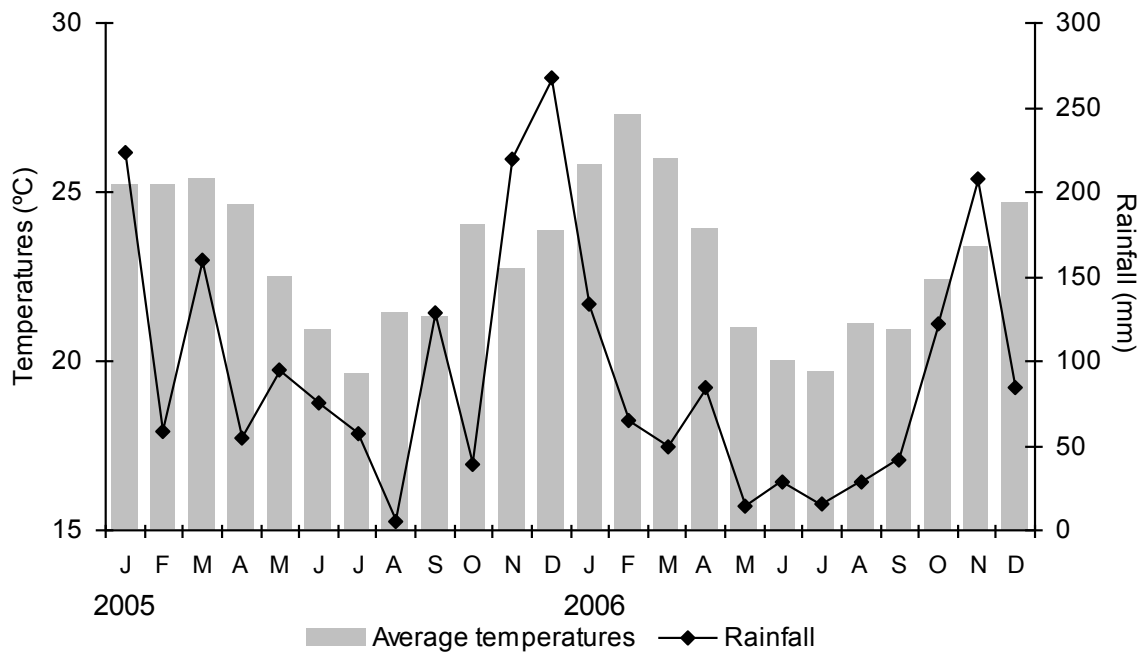


Figure 2. Monthly average temperatures and monthly total rainfall from January 2005 to December 2006 for the city of Campos dos Goytacazes, Rio de Janeiro State, located approximately 30 km away from the estuary of the Paraíba do Sul River (Data source: the Evapotranspirometric station of the Agricultural Science and Technology Center, North Fluminense State University, PESAGRO-RIO).

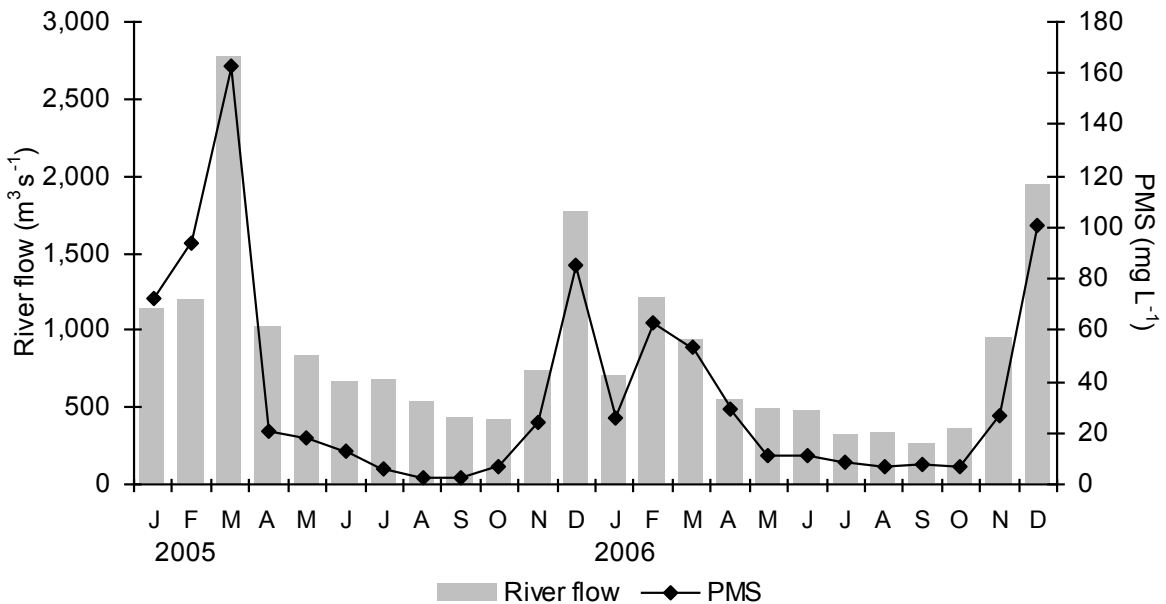


Figure 3. The river flow and suspended particulate matter (SPM) in the Lower Paraíba do Sul River region in the period of January 2005 to December 2006 (Source: Environmental Sciences Laboratory, University of North Fluminense).

0.05). The daily production ranged from 0.81 to 27.73 g.m⁻² for *A. germinans*, from 0.16 to 18.32 g.m⁻² for *L. racemosa* and from 0.88 to 26.71 g.m⁻² for *R. mangle*.

The components of litterfall differed significantly (Kruskal-Wallis and Dunn test, $p \leq 0.05$) between forests and followed the order: *R. mangle* > *L. racemosa* > *A. germinans*, for the leaves; *A. germinans* = *R. mangle* > *L. racemosa*, for the

wood; *A. germinans* = *R. mangle* > *L. racemosa*, for the flowers; *R. mangle* > *A. germinans* > *L. racemosa*, for the fruits and miscellaneous; and *R. mangle* > *A. germinans* = *L. racemosa*, for total litterfall (Table II). There was no significant difference in total production and different litter components between the years 2005 and 2006 (Mann-Whitney, $p > 0.05$; Table III), except for leaves in *L. racemosa*, which was higher in 2005.

Table II. Production of the different litter fractions (g.m⁻².day⁻¹) of the three mangrove forests studied in the estuary of the Paraíba do Sul River, for the period from January 2005 to December 2006. Different lowercase letters indicate significant differences between different species within each fraction ($p < 0.05$). SD = standard deviation.

Forest	Leaves	Wood	Flowers	Fruits	Miscellaneous	Total
<i>Avicennia germinans</i>						
Mean ± SD	1.82±0.73 c	0.53±1.33 a	0.24±0.29 a	0.95±2.53 b	0.05±0.03 b	3.59±3.18 b
Median	1.73	0.11	0.12	0.02	0.04	2.64
Minimum and Maximum	0.40-4.08	0-11.43	0-1.32	0-24.83	0-0.30	0.81-27.73
<i>Laguncularia racemosa</i>						
Mean ± SD	2.20±1.39 b	0.34±1.17 b	0.05±0.07 b	0.96±2.22 c	0.04±0.03 c	3.58±2.91 b
Median	2.03	0.04	0.02	0	0.03	2.99
Minimum and Maximum	0.12-8.42	0-13.20	0-0.39	0-13.51	0-0.20	0.16-18.32
<i>Rhizophora mangle</i>						
Mean ± SD	2.74±1.26 a	0.52±1.73 a	0.24±0.25 a	0.59±1.05 a	0.16±0.33 a	4.26±2.84 a
Median	2.65	0.01	0.16	0.15	0.06	3.60
Minimum and Maximum	0.61-7.61	0-18.44	0-1.54	0-9.26	0-3.73	0.88-26.71

Overall, the three species had a similar temporal pattern, with greater total litter production during the rainy season (September-February) (Figure 4). Specifically, the leaf fraction was present every month, showing significantly higher values in the rainy season for *L. racemosa* and *R. mangle* and no seasonal pattern in the *A. germinans* forest. Wood (twigs) fall was almost continuous; however, it was higher in the rainy season for the three forests (Figure 4).

In general, the forests exhibited the largest flower production in the rainy season. A higher production of fruits was registered in the rainy season in the *A. germinans* and *R. mangle* forests, although *R. mangle* produced fruits practically throughout the year. The *L. racemosa* forest showed higher values between the end of the rainy season and the beginning of the dry season (Figure 4).

Multiple regression analysis indicated that rainfall, mean air temperature and wind speed were the independent variables that best fit the model, but in general, explained a small percentage of the change in the litter during the studied period. There have been several cases of lack of correlation and negative interactions between litterfall and rainfall (Table IV).

Discussion

The annual litter production estimated for the mangrove forests of the estuary of the Paraíba do Sul River is within the range documented for tropical and subtropical mangroves (Table V). However, the estimates for *A. germinans*, *L. racemosa* and *R. mangle* forests are higher when compared to forests of the same species in other regions, including other areas in low latitudes (Silva *et al.* 1998, Fernandes 2003, Arreola-Lizárraga *et al.* 2004, Aké-Castilho *et al.* 2006).

Saenger & Snedaker (1993) showed that the annual litter production was negatively correlated with latitude, in response to abiotic factors, such as solar radiation. However, regional and local variations occur due to the influence of different environmental variables (tides, river flow, and winds) associated with the geomorphologic types (Twilley 1995). A high litter production rate (as observed in this study) indicates optimal habitats for the mangrove, allowing the primary net productivity of mangrove forests to be favorably compared with tropical forests (Clough 1992, Saenger & Snedaker 1993, Table VI).

Considering the different physiographic types, the litter production ranged from 320 to 1,700

$\text{g.m}^{-2}.\text{year}^{-1}$ for riverine forests, from 430 to 1,082 $\text{g.m}^{-2}.\text{year}^{-1}$ for fringe forests and 250 to 970 $\text{g.m}^{-2}.\text{year}^{-1}$ for bay forests (Lugo *et al.* 1988). According to Pool *et al.* (1975), the production rate of mangrove litter is closely related to fresh water supply, which is higher in riverine forests (Lugo & Snedaker 1974). The three forests examined in the estuary of the Paraíba do Sul River are riverine type and present values (1,289 to 1,534 $\text{g.m}^{-2}.\text{year}^{-1}$) that fit in the range observed for this physiographic type. The high productivity recorded reflects the low salinity of the interstitial water (2.0 to 2.7), available adequate nutrients and good weather (temperature and rainfall) in the region.

The *A. germinans* forests showed better structural development (higher values of average height, diameter at breast height and basal area) when compared to *L. racemosa*. Despite this variation, there was no significant difference between the two forests for annual litter production. However, these forests showed significantly lower values in relation to *R. mangle* forests, where intermediate structural characteristics were shown. These results suggest no relationship between the vegetation structure and the litter production, corroborating observations made in other mangrove forests (Lopez-Portilho & Ezcurra 1985, Mackey & Smail 1995, Twilley & Day 1999, Fernandes 2003).

Table III. Production of the different litter fractions ($\text{g.m}^{-2}.\text{day}^{-1}$) of the three mangrove forests studied in the estuary of the Paraíba do Sul River, during the years 2005 and 2006. Different lowercase letters indicate significant differences between years within each species ($p \leq 0.05$). SD = standard deviation.

Forest	Leaves	Wood	Flowers	Fruits	Miscellaneous	Total
<i>Avicennia germinans</i>						
2005						
Mean \pm SD	1.81 \pm 0.75 a	0.53 \pm 1.40 a	0.26 \pm 0.32 a	0.81 \pm 1.68 a	0.05 \pm 0.03 a	3.46 \pm 2.27 a
Median	1.69	0.13	0.14	0.02	0.04	2.74
Minimum and Maximum	0.61-4.06	0-11.43	0-1.32	0-8.72	0-0.13	0.81-13.38
2006						
Mean \pm SD	1.83 \pm 0.70 a	0.53 \pm 1.27 a	0.22 \pm 0.26 a	1.08 \pm 3.16 a	0.06 \pm 0.04 a	3.71 \pm 3.88 a
Median	1.83	0.09	0.09	0.01	0.05	2.59
Minimum and Maximum	0.40-3.89	0-8.72	0-1.27	0-24.83	0-0.30	0.95-27.73
<i>Laguncularia racemosa</i>						
2005						
Mean \pm SD	2.37 \pm 1.45 a	0.32 \pm 1.34 a	0.06 \pm 0.08 a	1.09 \pm 2.54 a	0.04 \pm 0.03 a	3.89 \pm 3.21 a
Median	2.18	0.06	0.01	0	0.03	3.03
Minimum and Maximum	0.12-8.42	0-13.20	0-0.39	0-13.51	0-0.16	0.16-18.32
2006						
Mean \pm SD	2.01 \pm 1.30 b	0.35 \pm 0.96 a	0.05 \pm 0.06 a	0.82 \pm 1.79 a	0.05 \pm 0.03 a	3.27 \pm 2.52 a
Median	1.81	0.03	0.01	0	0.04	2.88
Minimum and Maximum	0.14-5.65	0-6.09	0-0.35	0-9.36	0-0.20	0.16-15.00
<i>Rhizophora. mangle</i>						
2005						
Mean \pm SD	2.75 \pm 1.09 a	0.45 \pm 1.39 a	0.24 \pm 0.25 a	0.59 \pm 1.16 a	0.12 \pm 0.13 a	4.15 \pm 2.55 a
Median	2.79	0.03	0.17	0.11	0.06	3.57
Minimum and Maximum	0.61-5.98	0-14.27	0-1.54	0-9.26	0.01-0.71	0.99-22.76
2006						
Mean \pm SD	2.73 \pm 1.41 a	0.60 \pm 2.03 a	0.24 \pm 0.25 a	0.60 \pm 0.92 a	0.20 \pm 0.46 a	4.38 \pm 3.12 a
Median	2.39	0.01	0.15	0.22	0.07	3.62
Minimum and Maximum	0.64-7.61	0-18.44	0-1.12	0-6.47	0-3.73	0.88-26.71

Due to sudden weather changes and differentiated production of plant material over the years, it is recommended that assessment of litter production is done for a period exceeding one year (Proctor 1983), although most studies considered only an annual cycle. In this study, the total litter fall rate and of the

different fractions did not vary between years. The factors which control the structure and productivity of mangrove forests vary in time and space. Inter-annual variability in mangrove productivity is affected by long-term variation in such factors as air temperature, river flow, total precipitation and

porewater salinity (Williams et al. 1981). Extremes of the various factors may be more important than means (Day et al. 1996). The similar pattern of litter production between 2005 and 2006 described in this study is an indication that the variation in environmental conditions between years (eg precipitation 63% higher in 2005 compared to 2006) caused no changes in litter production. This may be due to the constant frequency of flooding of forests and values low of porewater salinity.

The sequence of the components of litterfall found in this study (leaves> fruits> wood> flowers> miscellaneous) is consistent with data obtained in other mangroves (Mackey & Smail 1995, Parkinson et al. 1999, Ochieng & Erfemeijer 2002, Sherman et al. 2003). The production of leaves usually represented the largest fraction (> 50%), as observed in this study, but in some cases can exceed 80%, regardless of latitude, weather conditions or type of forest (Day et al. 1996, Mehlig 2001).

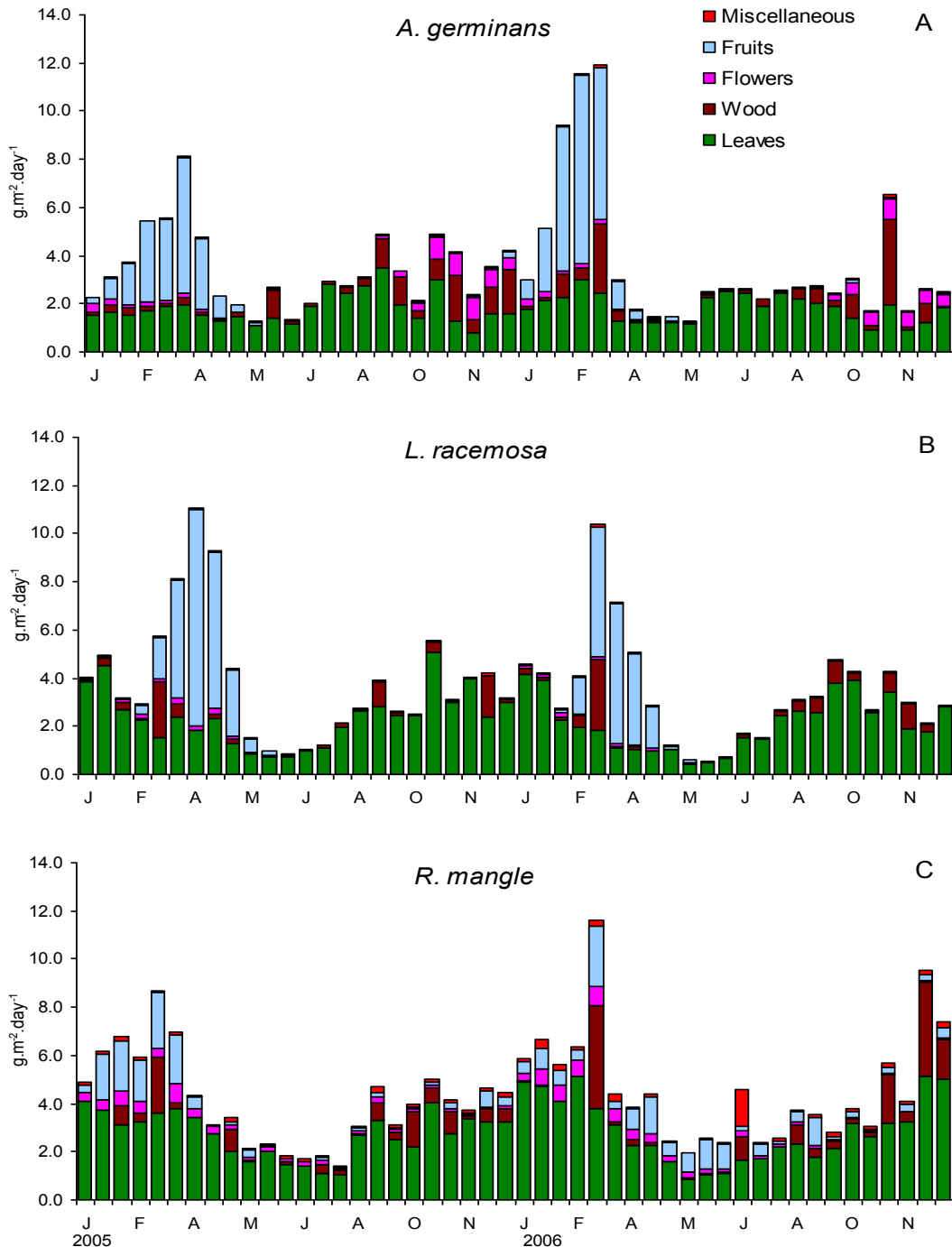


Figure 4. Litter production of the three mangrove forests examined in the estuary of the Paraíba do Sul River, over the intervals sampled in 2005 and 2006. A: *Avicennia germinans*; B: *Laguncularia racemosa*; C: *Rhizophora mangle*.

Table IV. Results of multiple linear regression performed for the data of litter production from the three species examined in the mangrove of the estuary of the Paraíba do Sul River X_1 : rainfall. X_2 : mean air temperature and X_3 : wind speed. *Values statistically significant to $p < 0.05$.

	Equation	R ²	F	p
<i>A. germinans</i>				
Leaves	$Y = 3.25 - 0.31^*(X_1) - 0.29(X_2) + 0.24(X_3)$	0.19	4.24	0.010875*
Wood	$Y = -0.86 + 0.17(X_1) - 0.01(X_2) + 0.77^*(X_3)$	0.20	4.47	0.008622*
Flowers	$Y = -0.99 + 0.26^*(X_1) + 0.17(X_2) + 0.51^*(X_3)$	0.49	10.80	0.000010*
Fruits	$Y = -6.19 - 0.11(X_1) + 0.63^*(X_2) - 0.29^*(X_3)$	0.37	9.26	0.000094*
Miscellaneous	$Y = -0.08 + 0.03(X_1) + 0.24(X_2) + 0.61^*(X_3)$	0.44	11.9	0.000011*
Total	$Y = -5.12 - 0.06(X_1) + 0.43^*(X_2) + 0.15(X_3)$	0.15	3.57	0.022529*
<i>L. racemosa</i>				
Leaves	$Y = -3.51 + 0.08(X_1) + 0.19(X_2) + 0.66^*(X_3)$	0.51	15.30	0.000001*
Wood	$Y = -1.36 + 0.04(X_1) + 0.19(X_2) + 0.32^*(X_3)$	0.10	2.61	0.065042
Flowers	$Y = -0.38 - 0.19^*(X_1) + 0.82^*(X_2) - 0.42^*(X_3)$	0.69	32.06	0.000000*
Fruits	$Y = -11.06 - 0.31^*(X_1) + 0.67^*(X_2) - 0.33^*(X_3)$	0.46	13.19	0.000004*
Miscellaneous	$Y = -0.09 - 0.16(X_1) + 0.57^*(X_2) + 0.33^*(X_3)$	0.40	10.26	0.000410*
Total	$Y = -16.84 - 0.22(X_1) + 0.77^*(X_2) + 0.07(X_3)$	0.52	15.94	0.000001*
<i>R. mangle</i>				
Leaves	$Y = -6.78 - 0.08(X_1) + 0.68^*(X_2) + 0.33^*(X_3)$	0.65	27.50	0.000000*
Wood	$Y = -1.81 + 0.12(X_1) + 0.18(X_2) + 0.23(X_3)$	0.06	1.93	0.140693
Flowers	$Y = -0.85 - 0.14(X_1) + 0.67^*(X_2) - 0.33^*(X_3)$	0.43	11.72	0.000013*
Fruits	$Y = -1.77 + 0.07(X_1) + 0.40^*(X_2) - 0.21^*(X_3)$	0.14	3.21	0.033274*
Miscellaneous	$Y = 0.30 - 0.06(X_1) - 0.10(X_2) + 0.13(X_3)$	-0.05	0.38	0.482700
Total	$Y = -11.53 + 0.11(X_1) + 0.64^*(X_2) + 0.14(X_3)$	0.48	14.11	0.000002*

The temporal pattern of litter production was seasonal with higher production in the rainy season, corroborating the results found in several other mangroves (Pool *et al.* 1975, López-Portilho & Ezcurra 1985, Twilley *et al.* 1997, Sherman *et al.* 2003, Arreola-Lizárraga *et al.* 2004, Aké-Castillo *et al.* 2006). These studies suggest that high temperatures, increased day length, higher rainfall rates and fresh water flow are probably the factors responsible for the largest litter fall during the rainy season.

In this study, *L. racemosa* and *R. mangle* forests showed peak of leaf production in the rainy season (September-February), in contrast with that of *A. germinans* that did not exhibit a seasonal pattern. Sherman *et al.* (2003) reported a seasonal pattern of increase of leaf litter during the rainy months for mixed *A. germinans*, *L. racemosa* and *R. mangle* forests in the Dominican Republic, similar to the result obtained by Arreola-Lizárraga *et al.* (2004) who studied an *A. germinans* forest in the Gulf of California, Mexico. Larger leaf fall has been associated with the rainy season for other species of *Rhizophora* (*R. apiculata*, *R. lamarckii* and *R. stylosa*) (Williams *et al.* 1981), as well as other species of *Avicennia* (Hegazy 1998). However, Day *et al.* (1996), studying *A. germinans* and *R. mangle* forests, in Mexico and Clough *et al.* (2000),

examining a mangrove area with *R. apiculata* in Vietnam, found no clear seasonal pattern in leaf fall, similar to the results recorded here for *A. germinans* forests.

Several studies describe the occurrence of seasonality in the production of reproductive structures of mangrove species (Day *et al.* 1996, Fernandes 2003). In the mangrove of the estuary of the Paraíba do Sul River, the highest incidence of flowers was recorded in the rainy season. Fruit production was higher between the end of the rainy season and the beginning of the dry season for *L. racemosa* and in the rainy season in the *A. germinans* and *R. mangle* forests. It is believed that the highest flower and fruit fall of mangrove plants is during the rainy season due to an adaptation to the flooded environment as it allows the dispersal of reproductive structures when the water levels are more favorable (Jimenez & Sauter 1991).

The coefficients of determination between the total production and environmental variables rainfall, mean air temperature and wind speed were low. Ramos and Silva *et al.* (2006) studying a *R. mangle* forest, in Natal, Rio Grande do Norte, Brazil, found no correlation between litterfall, variable rainfall and wind speed. Similarly, Lopez-Portilho & Ezcurra (1985) demonstrated a lack of correlation between litter production of *A. marina*

Table V. Litter production (ton.ha⁻¹.year⁻¹) in mangrove forests.

Location	Latitude	Forest	Litter production	Reference
Golfo da Califórnia, México	27°49'N	<i>A. germinans</i>	1.7	Arreola-Lizárraga <i>et al.</i> 2004
Golfo da Arábia	25°40'N	<i>A. marina</i>	17.0	Hegazy 1998
República Dominicana	19°10'N	<i>A. germinans</i> , <i>L. racemosa</i> and <i>R. mangle</i>	11.4	Sherman <i>et al.</i> 2003
Veracruz, Mexico	18°30'N	<i>R. mangle</i>	11.2	Aké-Castillo <i>et al.</i> 2006
Pulau Kecil, Malásia	04°48'N	<i>R. apiculata</i>	17.7	Putz & Chan 1986
Ilha de Maracá, Amapá, Brazil	02°10'N	<i>A. germinans</i>	7.3	Fernandes 2003
		<i>L. racemosa</i>	5.1	
		<i>R. mangle</i>	11.8	
Furo Grande, Bragança, Pará, Brazil	00°50'S	<i>A. germinans</i>	6.8	Gonçalves <i>et al.</i> 2006
		<i>R. mangle</i>	5.6	
Acarajó e Furo do Meio, Bragança, Pará, Brazil	00°52'S	<i>A. germinans</i> , <i>L. racemosa</i> and <i>R. mangle</i>	20.3	Mehlig 2001
Península de Ajuruteua, Bragança, Pará, Brazil	00°55'S	<i>A. germinans</i> , <i>L. racemosa</i> and <i>R. mangle</i>	11.8	Nascimento <i>et al.</i> 2006
Natal, Rio Grande do Norte, Brazil	05°44'S	<i>R. mangle</i>	12.3	Ramos e Silva <i>et al.</i> 2006
Estuary of the Paraíba do Sul River, Rio de Janeiro, Brazil	21°36'S	<i>A. germinans</i>	12.5	This study
		<i>L. racemosa</i>	12.3	
		<i>R. mangle</i>	14.6	
Itacuruçá, Rio de Janeiro, Brazil	23°00'S	<i>R. mangle</i>	9.6	Silva <i>et al.</i> 1998
Baía de Paranaguá, Paraná, Brazil	25°33'S	<i>R. mangle</i> , <i>L. racemosa</i> and <i>A. schaueriana</i>	4.8	Sessegolo 1997
Queensland, Australia	27°24'S	<i>A. marina</i>	8.8	Mackey & Smail 1995

Table VI. Litter production (ton.ha⁻¹.year⁻¹) in different forests of Brazil.

Forest	Local	Litter production	Reference
Mangrove forest	Estuário do rio Paraíba do Sul, Rio de Janeiro	13.1	This study
Amazon rainforest	Reserva de Curuá-Una, Pará	9.7	Smith <i>et al.</i> 1998
Amazon rainforest	Ilha de Maricá, Roraima	8.5	Villela & Proctor, 1999
Amazon rainforest	Bragança, Pará	8.7	Nascimento <i>et al.</i> , 2006
Atlantic forest	Ilha do Cardoso, São Paulo	6.3	Moraes <i>et al.</i> , 1999
Atlantic forest	Ouro Preto, Minas Gerais	5.9	Werneck <i>et al.</i> , 2001
Atlantic forest	Pinheiral, Rio de Janeiro	11.7	Toledo <i>et al.</i> , 2002
Atlantic forest	Botucatu, São Paulo	10.6	Vital <i>et al.</i> , 2004
Atlantic forest	Teresópolis, Rio de Janeiro	4.9	Gomes <i>et al.</i> 2010
Restinga forest	Maricá, RJ	6.2	Ramos & Pellens, 1994
Restinga forest	Paranaguá, RS	5.1	Pires <i>et al.</i> , 2006

and rainfall. The lack of or low coefficients of determination indicate that productivity can be influenced by other factors such as nutrient availability (Twilley 1995), located along the

gradient of flooding and geomorphologic peculiar environment where the species occurs (Lopez-Portilho & Ezcurra 1985), besides physiological characteristics of species (Twilley *et al.* 1997). Thus, the seasonal litter pattern depends on the peculiarities of each mangrove as a particular factor may be the most important for a given area and exercise less influence in another mangrove.

In summary, this study showed that the mangrove estuary of the Paraíba do Sul River has high production values of litterfall and no interannual variation, probably because it is an environment dominated by the river, which receives a high influx of nutrients and freshwater (Woodroffe 1992).

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