

# Breakdown of leaf litter under different environmental conditions in a tropical mangrove

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Abstract: This study evaluated the decomposition process of leaf litter of Avicennia schaueriana Stapf & Leechm. ex Moldenke, Laguncularia racemosa (L.) C.F. Gaertn and Rhizophora mangle L. in the mangrove forest of the Mamanguape River estuary, Brazil. Senescent leaves were placed in litterbags and submitted to three experimental conditions: supratidal, not subjected to tidal inundation (SUP), intertidal 1, on the forest floor and subjected to inundation (INT1) and intertidal 2, on the bottom of a tidal creek (INT2). The leaf material showed rapid loss of mass in the first 30 days, followed by slower decay until the end of the experiment. The treatment effect was greater than the differences among species. Leaf litter subjected to flooding exhibited higher decomposition rates and lower half-life ( $t_{50\%}$ ) and 95% lifespan ( $t_{95\%}$ ) values compared to leaves exposed to air. In the SUP treatment,  $t_{50\%}$  and  $t_{95\%}$ values indicated that mass loss was significantly slower in *R. mangle*, intermediate in *L*. racemosa, and more accelerated in A. schaueuriana. Under conditions of higher tidal inundation frequency (INT2), decomposition rates were faster for R. mangle leaves, intermediate for A. schaueriana, and slower for L. racemosa. The results found in the present study suggest that environmental factors may have more influence on decomposition rates than species characteristics.

**Key words:** leaf decomposition, *Avicennia schaueriana*, *Laguncularia racemosa*, *Rhizophora mangle*.

Decomposição de folhas de serapilheira sob diferentes condições ambientais em um manguezal tropical. Resumo: Este estudo avaliou o processo de decomposição de folhas da serapilheira de Avicennia schaueriana Stapf & Leechm. ex Moldenke, Laguncularia racemosa (L.) C.F. Gaertn e *Rhizophora mangle* L. no manguezal do estuário do Rio Mamanguape, Brasil. Folhas senescentes foram colocadas em sacos de decomposição (*litterbaqs*) e submetidas a três condições experimentais: supratidal, não submetido à inundação pelas marés (SUP), intertidal 1, no chão da floresta e submetido à inundação (INT1) e intertidal 2, no fundo de um canal de maré (INT2). O material foliar apresentou rápida perda de massa nos primeiros 30 dias, seguido por uma decomposição mais lenta até o final do experimento. O efeito do tratamento foi maior do que as diferenças entre espécies. As folhas de serapilheira submetidas à inundação exibiram maiores taxas de decomposição e menores valores de meia vida ( $t_{50\%}$ ) e vida útil de 95% ( $t_{95\%}$ ) em relação às folhas expostas ao ar. No tratamento SUP, os valores de  $t_{50\%}$  e  $t_{95\%}$  indicaram que a perda de massa foi significativamente mais lenta em R. mangle, intermediária em L. racemosa e mais acelerada em A. schaueuriana. Sob condições de maior frequência de inundação pelas marés (INT2), as taxas de decomposição foram mais rápidas para folhas de R. mangle, intermediárias para A. schaueriana e mais lentas para L. racemosa. Os resultados encontrados no presente estudo sugerem que os fatores ambientais podem exercer maior influência nas taxas de decomposição do que as características das espécies.

**Palavras-chave:** decomposição foliar, *Avicennia schaueriana*, *Laguncularia racemosa*, *Rhizophora mangle*.

# Introduction

Mangrove forests are very productive ecosystems (Donato *et al.* 2011) which store blue carbon disproportionately to their small area (Alongi 2022). The high carbon sequestration and storage capacity of mangrove forests represent relevant natural mechanisms for climate change mitigation (Alongi 2020, Adame *et al.* 2021, Zhu & Yan 2022).

An important component of the primary productivity of mangroves is leaf litter. Tons of leaves fall from each hectare of mangrove forest every year and undergo a series of physical and chemical transformations resulting in the breakdown of whole leaves into smaller particles. These leaf litter fractions (i.e. particulated and dissolved organic matter) are exported to adjacent coastal waters and exert significant effects on coastal and marine food chains (Golley *et al.* 1962, Odum & Heald 1975, Jennerjahn & Ittekkot 2002, Dittmar *et al.* 2006). Leaf litter decomposition is therefore a key process that regulates nutrient cycling and energy conversion in mangrove forests (Wafar *et al.* 1997, Kathiresan & Bingham 2001).

The rate of leaf decomposition can be affected by environmental factors such as temperature, humidity, salinity, oxygen concentrations, electrical conductivity, pH, inundation, frequency/duration, macrofauna performance, and activity of the decomposer community (Robertson 1988, Tam et al. 1998, Middleton & McKee 2001, Chapin et al. 2002, Romero et al. 2005, Bouillon et al. 2008, Imgraben & Dittmann 2008, Alongi 2009, Rezende et al. 2013, Márquez et al. 2016). Interspecific differences are also know to influence leaf decomposition. For example, leaves of mangrove species that have lower tannin and lignin contents, low C:N ratio and higher nitrogen concentrations tend to decompose faster because they are more easily degraded by fungi and bacteria (Lacerda et al. 1986, Sherman et al. 1998, Tam et al. 1998, Mfilinge et al. 2002, Bosire et al. 2005, Galeano et al. 2010, Muliawan et al. 2020, Vinh et al. 2020).

After detachment from trees, mangrove leaves can experience distinct conditions (Ananda *et al.* 2008): (1) they can be trapped in the canopy and decompose without being exposed to brackish or salt water; (2) they can fall during high tide and be carried to deep water with the ebb tide; (3) they can fall during low tide and be trapped in the sediment, or even be covered, and experience alternating

Pan-American Journal of Aquatic Sciences (2023), 18(1): 1-10

exposure to air and salt water. These conditions determine the course of decomposition of leaf material and influence nutrient cycling and carbon storage in mangrove forests. Continuously submerged leaves degrade more rapidly than those not exposed to inundation, with an intermediate decomposition rate for leaves subjected to periodic tidal inundation (Sessegolo & Lana 1991, Mendonça 2006, Galeano *et al.* 2010; Oliveira *et al.* 2013).

In Brazil there are few studies that have investigated the dynamics of leaf decomposition in mangrove forests (e.g. Sessegolo & Lana 1991, Barroso-Matos et al. 2012, Oliveira et al. 2013, Rezende et al. 2013, Lima & Colpo 2014). Estimating mangrove leaf decomposition rates under different environmental conditions is essential to understanding the biogeochemistry of coastal particularly environments, considering the importance of the mangrove ecosystem in carbon sequestration and storage and its role in mitigating climate change (Alongi 2020, Adame et al. 2021). Thus, the objective of this study was to evaluate the decomposition process of leaf litter of Avicennia schaueriana Stapf & Leechm. ex Moldenke, Laguncularia racemosa (L.) C.F. Gaertn and Rhizophora mangle L. exposed to air and tidal inundation in the mangrove forest of the Mamanguape River estuary. We expect differences in decomposition rates to occur because mangrove leaves show high rates of mass decay when exposed to flooding (Sessegolo & Lana 1991, Twilley et al. 1997) and due to interspecific differences in their chemical composition (Lacerda et al. 1986, Bernini et al., 2006, Muliawan et al. 2020, Vinh et al. 2020).

#### **Material and Methods**

Study area: The mangrove forest of the Mamanguape River estuary is located in the State of Paraíba, northeastern Brazil and is inserted in the Mamanguape River Mouth Environmental Protection which overlaps Area, with the Mamanguape River Mouth Area of Relevant Ecological Interest. The region's climate is tropical and rainy (Am, in the Köeppen classification), with mean annual temperature ranging between 24° and 27°C (Marcelino et al. 2012), annual precipitation between 1,600 and 1,900 mm and the rainy season concentrated between February and August (Alvares et al. 2013).

The mangrove forest presents an area of approximately 4,620 hectares (Freires 2022) and is composed of *Avicennia germinans* (L.) L., *Avicennia schaueriana* Stapf & Leechm. *ex* Moldenke, *Laguncularia racemosa* (L.) C.F. Gaertn and *Rhizophora mangle* L. Along the estuary, the mangrove forest presents average heights from 5.1 to 11.8 m, average diameters at breast height from 6.3 to 16.0 cm, basal area from 4.8 to 30.2 m<sup>2</sup>/ha and density from 1,333 to 3,000 trunks/ha (Vasconcelos 2021). The present study was developed in the lower Mamanguape River estuary, where *A. schaueriana*, *L. racemosa* and *R. mangle* occur (06° 55' 80" S; 34° 55' 88" W).

# Methodology

Decomposition rates of mangrove leaves were estimated using litterbags (Ashton *et al.* 1999) for *A. schaueriana, L. racemosa* and *R. mangle*. The experiment was conducted from May to October 2014. Senescent leaves without signs of damage and about to fall were collected from 10 randomly selected trees of each species. The collected material was placed in plastic bags and cooled to inhibit bacterial activity during transport to the laboratory. Thirty grams of fresh leaves of each species were selected and then dried (60°C) to estimate the initial dry mass. This procedure is necessary to determine the conversion factor in order to estimate the initial dry weight of the leaves placed in the decomposition bags.

For the decomposition experiment, the leaves were weighed (wet weight) in portions of 10 g, and then placed in nylon bags (litterbags) of  $20 \times 20$  cm with 1.0-mm diameter mesh (big enough to allow the entry of water and small organisms while preventing the entry of large consumers). Subsequently, the litterbags were taken to the field and subjected to three conditions: supratidal, not subjected to flooding and below the mangrove forest canopy (treatment SUP), intertidal 1, on the forest floor and subjected to flooding (treatment INT1, 3 m away from the tidal creek) and intertidal 2, at the bottom of a tidal creek (treatment INT2). The litterbags in treatment INT2 remained flooded longer (semidiurnal tidal, twice daily immersed) than the litterbags in treatment INT1 (twice daily immersed).

The experiment consisted of 162 decomposition bags (54 per species), with three replicates per treatment × three treatments × three species × six collection intervals. Three bags from each treatment and each species were removed after

zero, nine, 28, 61, 92 and 131 days after installation. Material from litterbags was rinsed with fresh water, then oven-dried (at 60 °C) until a constant weight was achieved and weighed using an analytical scale (0.0001 g).

Decay constants (*k*) were calculated using the exponential decay model of Olson (1963):

$$M_t = M_0 e^{-\kappa t} \tag{1}$$

where  $M_t$  = percentage of the initial material (100%),  $M_0$  = remaining after time *t* (days) and *k* = decay constant.

Half-life ( $t_{50\%}$ ) and 95% lifespan ( $t_{95\%}$ ) were estimated from k values using the following equations (Olson 1963):

$$t_{50\%} = \frac{t_n(0.5)}{(k)} = \frac{0.693}{(k)}$$
(2)

$$t_{95\%} = \frac{t_n(0.05)}{(k)} = \frac{3}{(k)}$$
(3)

The data for decomposition constant, half-life and 95% lifespan were subjected to two-way ANOVA and Tukey's test to investigate the effects of species and treatment. The analyses were performed in R Software (R Development Core Team 2021).

### Results

The leaf material of each species showed rapid mass loss during the first week, followed by a slower reduction after this period in treatments INT1 and INT2 (Fig. 1). In the first nine days of the decomposition process, the senescent leaves showed losses of approximately 29% and 25% of their dry weight in treatments INT1 and INT2, respectively. In the SUP treatment, the leaves lost only 3% of their weight during the first week, with a rapid decrease until 28 days and a slower reduction in mass loss after this period (Fig. 1).

Overall, the results indicated that the treatment effect was greater than the differences among species (Table I). There were higher decomposition rates in the treatments subjected to flooding for all species, resulting in shorter periods to decompose 50% and 95% of the leaf material compared to the SUP treatment (Table II; Fig. 1). The half-life ranged from 43 to 70 days and the 95% lifespan from 181 to 301 days in the INT1 and INT2 treatments, showing significantly lower values compared to those recorded for the SUP treatment (half-life from 177 to 369 days and 95% lifespan from 768 to 1,595 days; Table II).



**Figure 1.** Remaining dry mass of leaf litter of *Avicennia schaueriana* (A), *Laguncularia racemosa* (B) and *Rhizophora mangle* (C) analyzed in the Mamanguape River mangrove. SUP: supratidal; INT1: intertidal 1; INT2: intertidal 2.

**Table I.** Summary of two-way ANOVA for decay constant (*k*), half-life ( $t_{50\%}$ ) and 95% lifespan ( $t_{95\%}$ ). \*\* = p < 0.01; \* = p < 0.05; ns = not significant.

Source of variance	k	<b>t</b> 50%	<b>t</b> 95%
Species (S)	**	ns	ns
Treatment (T)	**	**	**
$S \times T$	ns	*	*

In the INT2 treatment, higher *k* values were recorded for *R*. *mangle* in relation to *L*. *racemosa*, with intermediate values for *A*. *schaueriana* (Table

II). The species also showed significant differences for half-life and 95% lifespan in the SUP treatment, with a higher value for *R. mangle* and lower for *A. schaueriana* (Table II).

# Discussion

The species three showed similar decomposition kinetics in the different treatments over time, with high leaf mass loss in the first 30 days, followed by a more gradual decomposition by the end of the experiment. These findings are consistent with those reported in other studies (Robertson 1988, Twilley et al. 1997, Ashton et al. 1999, Ake-Castillo et al. 2006, Galeano et al. 2010, Sánchez-Andrés et al. 2010, Barroso-Matos et al. 2012, Loría-Naranjo et al. 2019, Vinh et al. 2020). The onset of decomposition is characterized by leaching of more labile components, such as sugars, proteins, phenols, and organic acids, which results in accelerated loss of leaf mass (Benner & Hodson 1985, Middleton & McKee 2001, Mfilinge et al. 2002). After the first 30 days, mass losses depend on the action of communities of bacteria and fungi that develop rapidly in mangrove leaves (Benner et al. 1988). At this stage, degradation is slower because the organic matter becomes more refractory due to increased relative concentrations of recalcitrant compounds (e.g. cellulose and lignin) or the high C/N ratio of the remaining material (Tam *et al.* 1998, Chapin et al. 2002).

Although the stages of the decomposition process were similar, the treatments subjected to flooding showed more accelerated leaf mass loss compared to the SUP treatment. According to the classification of Ananda *et al.* (2008), leaf litter showed a slow rate of decomposition in the SUP treatment (k < 0.005) and a fast rate of degradation in the INT1 and INT2 treatments (k > 0.01). The similar rate of decomposition recorded for treatments INT1 and INT2 is possibly due to the small difference in tidal inundation frequency at the sites where the experiment was conducted.

The decomposition rate of leaves subjected to inundation was 3 to 8 times faster than that of leaf material exposed only to air. Consequently, the halflife and 95% lifespan of the SUP treatment were notably longer. Similar results have been reported by Sessegolo & Lana (1991), Ashton *et al.* (1999) and Mendonça (2006) (Table III) and can be explained by the fact that exposure of leaf litter to air promotes temperature and humidity conditions that hinder the activity of decomposer organisms. The frequent

**Table II.** Values of decay constant (*k*), regression coefficient ( $\mathbb{R}^2$ ), half-life ( $t_{50\%}$ ) and 95% lifespan ( $t_{95\%}$ ). *k*: decay constant. Lower-case letters compare the values of each species among treatments and upper-case letters compare the values among species within each treatment. Distinct letters indicate significant differences (p <0.05). SUP: supratidal; INT1: intertidal 1; INT2: intertidal 2.

Species	Treatment	Decay equation	$\mathbf{R}^2$	k	<i>t</i> <sub>50%</sub>	<b>t</b> <sub>95%</sub>
Auiconnia	SUP	$Y = 94.11052e^{-0.00391X}$	0.86	0.00392 bA	177 aB	768 aB
Avicennia	INT1	$Y = 66.81970e^{-0.01150X}$	0.73	0.01194 aA	60 aA	258 aA
schuuertunu	INT2	$Y = 79.72061e^{-0.01528X}$	0.93	0.01452 aAB	48 aA	207 aA
Laguncularia racemosa	SUP INT1 INT2	$\begin{split} \mathbf{Y} &= 91.26471 e^{-0.00308X} \\ \mathbf{Y} &= 73.16774 e^{-0.01017X} \\ \mathbf{Y} &= 79.17230 e^{-0.0112X} \end{split}$	0.48 0.87 0.90	0.00260 bA 0.01042 aA 0.01026 aB	268 aAB 70 bA 69 bA	1,155 aAB 301 bA 295 bA
Rhizophora mangle	SUP INT1 INT2	$\begin{split} Y &= 97.54449 e^{-0.00207X} \\ Y &= 81.90399 e^{-0.0143X} \\ Y &= 89.20018 e^{-0.01561X} \end{split}$	0.86 0.93 0.98	0.00212 bA 0.01435 aA 0.01636 aA	369 aA 49 bA 43 bA	1.595 aA 211 bA 185 bA

**Table III.** Comparison of decay constants (k) and half-life (t50%) of leaf litter of some mangrove species under different experimental conditions.

Species	Location	Experimental	k	t <sub>50%</sub>	References
-		conditions		(days)	
Avicennia	Paraíba (Brazil)	Supratidal	0.0040	177	This study
schaueriana		Intertidal	0.0120	60	-
		Intertidal	0.0145	48	
	Paraná (Brazil)	Supratidal	0.0130	55	Sessegolo & Lana (1991)
		Intertidal	0.0190	15	<b>G ( )</b>
		Subtidal	0.0430	11	
	Santa Catarina (Brazil)	Intertidal (summer)	0.0095	-	Rezende <i>et al.</i> (2013)
		Intertidal (winter)	0.0055	-	
	Santa Catarina (Brazil)	Subtidal	0.0011	30	Panitz (1986)
	São Paulo (Brazil)	Intertidal	0.0490	-	Lima & Colpo (2014)
Laguncularia	Bahia (Brazil)	Intertidal	0.0220	43	Oliveira <i>et al.</i> (2013)
racemosa		Intertidal	0.0230	45	
		Intertidal	0.0270	40	
		Subtidal	0.0310	31	
	Colombia	Intertidal	0.0185	-	Galeano <i>et al</i> . (2010)
		Subtidal	0.0300	-	
	Mexico	Intertidal	0.052	-	Flores-Verdugo <i>et al</i> . (1987)
	Pará (Brazil)	Supratidal	0.0056	123	Mendonça (2006)
		Intertidal	0.0131	53	
		Subtidal	0.0293	24	
	Paraíba (Brazil)	Supratidal	0.0026	268	This study
		Intertidal	0.0104	70	
		Intertidal	0.0103	69	
	Paraná (Brazil)	Supratidal	0.0080	102	Sessegolo & Lana (1991)
		Intertidal	0.0120	71	
		Subtidal	0.0160	26	
	Rio de Janeiro (Brazil)	Intertidal	0.0032	216	Barroso-Matos et al. (2012)
	São Paulo (Brazil)	Intertidal	0.025	-	Lima & Colpo (2014)
Rhizophora	Bahia (Brazil)	Intertidal	0.0160	32	Oliveira <i>et al</i> . (2013)
mangle		Intertidal	0.0200	30	
		Intertidal	0.0170	26	
		Subtidal	0.0220	23	
	Colombia	Intertidal	0.0136	-	Galeano <i>et al</i> . (2010)
		Subtidal	0.0280	-	
	Mexico	Intertidal	0.0084	70	Aké-Castillo et al. (2006)
	Pará (Brazil)	Supratidal	0.0067	104	Mendonça (2006)
		Intertidal	0.0069	100	
		Subtidal	0.0222	31	
	Paraíba (Brazil)	Supratidal	0.0021	369	This study
		Intertidal	0.0144	49	
		Intertidal	0.0164	43	

Species	Location	Experimental conditions	k	t <sub>50%</sub> (days)	References
	Paraná (Brazil)	Supratidal	0.0030	249	Sessegolo & Lana (1991)
		Intertidal	0.0060	119	
		Subtidal	0.0150	36	
	Rio de Janeiro (Brazil)	Intertidal	0.0027	257	Barroso-Matos et al. (2012)
	Santa Catarina (Brazil	Intertidal (summer)	0.0140	-	Rezende <i>et al.</i> (2013)
		Intertidal (winter)	0.0060	-	
	Santa Catarina (Brazil)	Subtidal	0.0064	90	Panitz (1986)
	São Paulo (Brazil)	Intertidal	0.0180	-	Lima & Colpo (2014)

flooding accelerates leaching and maintains humidity and temperature levels favorable for saprophytic decomposition (Tam *et al.*, 1990, Middleton & McKee 2001).

The results indicated that leaf litter can take approximately 9 months to lose 50% of its mass while it takes 2 to 4 years for 95% of the leaf litter to decompose in the SUP treatment. In this case, in situ decomposition may play an essential role in nutrient recycling, because the leaf litter tends to remain in place when it is not subject to tidal inundation (Twilley 1985, Twilley et al. 1986). On the other hand, senescent leaves subjected to flooding took only 2 months to lose 50% of their mass, with rapid recycling of nutrients that can be incorporated into the sediment or exported to adjacent waters. However, the decomposition experiment using litterbags may underestimate actual decomposition, since the confined leaves are subjected to a different microclimate compared to the natural environment (Tam et al. 1990) and the mesh size prevents the entrv of macrofauna that could accelerate fragmentation (Oliveira et al. 2013). In addition, the speed of decomposition may also be reduced due to an eventual increase in the percentage of material throughout the experiment due to the incorporation of sediment into the leaf material inside the litterbags (Tam et al. 1998), as observed in the present study. However, this method reflects trends and allows comparison among treatments and species (Wieder & Lang 1982).

Leaf litter exposed to air showed lower decomposition rates and higher half-life values compared to other studies conducted with the same species (Mendonça 2006, Sessegolo & Lana 1991, Table III). As for the intertidal zone, the values of k and  $t_{50\%}$  are within the range reported for tropical and subtropical mangroves (Table III). Such studies demonstrate that decay and half-life rates exhibit wide variation even for a single species, because the decomposition process is influenced by several factors, such as latitude, season and tidal inundation frequency/duration and methodology (Lee 1989, Mackey & Smail 1996, Tam *et al.* 1998, Mfilinge *et* 

*al.* 2002, Bosire *et al.* 2005, Barroso-Matos *et al.* 2012, Rezende *et al.* 2013, Loría-Naranjo 2019).

In the mangrove forest of the Mamanguape River, differences in leaf mass loss were also found among species when subjected to the same environmental conditions. Although the decay constants did not show significant interspecific differences in the SUP treatment, the half-life and 95% lifetime results indicated that mass loss was significantly slower in *R. mangle*, intermediate in *L. racemosa*, and faster in *A. schaueuriana*.

The differences in decomposition rate are attributed to species characteristics. Rhizophora leaves exhibit thicker cuticle than Avicennia and Laguncularia leaves (Tam et al. 1998, Lima et al. 2013) and this may restrict the leaching of labile substances, resulting in reduced leaf mass loss over time (Galeano et al. 2010). In addition, leaves of Rhizophora spp. decompose more slowly because they exhibit characteristics that are less attractive to microbial activity, such as lower nitrogen concentration, higher C:N ratio, and high tannin concentration compared to leaves of Avicennia spp. (Lacerda et al. 1986, Wafar et al. 1997, Middleton & McKee 2001, Bernini et al. 2006, Muliawan et al. 2020).

Our results showed higher *k* values for *R*. mangle relative to L. racemosa, with intermediate values for A. schaueriana in the INT2 treatment. Rezende et al. (2013) observed higher decay rate for *R. mangle* relative to *A. schaueriana* in a subtropical mangrove in Brazil (Table III). However, most studies have shown that leaf mass loss is faster for Avicennia leaves when compared to Laguncularia and Rhizophora leaves, regardless of environmental conditions (Robertson 1988, Wafar et al. 1997, Middleton & McKee 2001, Nordhaus et al. 2017, Muliawan et al. 2020, Table III). The results found in the present study suggest that environmental factors may exert a greater influence on decomposition rates than species characteristics.

The mangrove forest of the Mamanguape River exhibits a high abundance of *R. mangle* because of the wide distribution of tidal channels in

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the lower and middle estuaries (Freires 2022). Presumably, this species accounts for the major input of plant material to the estuary and plays a key role in the food chain and nutrient dynamics of adjacent coastal waters.

Mangroves are sensitive to changes in the duration/frequency of flooding, so sea level rise associated with global climate change is one of the main threats to this ecosystem (Ellison 2012; Che et al. 2022). Mangroves may be lost when the rate of sea level rise exceeds the rate of sediment accumulation (Godoy & Lacerda 2015). Increases in flooding duration can promote changes in species composition (Gilman et al. 2008), because they lead to the death of plants on mangrove margins (He et al. 2007). In the case of the Mamanguape River estuary, R. manale would be more affected by the fact that it occurs in areas with greater frequency/duration of flooding. Changes in the plant community due to sea level rise could result in changes in primary productivity and in the decomposition of organic matter, with impacts on nutrient cycling in the mangrove and adjacent coastal ecosystems (Ellison, 2012, Dhaou et al. 2022).

# Acknowledgments

The authors wish to thank the Federal University of Paraíba (Campus IV) for the infrastructure and transportation support with field activities and the Environmental Protection Area of Barra do Rio Mamanguape, which authorized this research. The second author is grateful for a Scientific Initiation fellowship from CNPq.

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Received: August 2022 Accepted: December 2022 Published: April 2023