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Leaf damage in three mangrove forests in Northeast Brazil

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Abstract: The damage types and herbivory rate in mature leaves of *Avicennia schaueriana* Stapf & Leechm ex Moldenke, *Laguncularia racemosa* (L.) Gaertn, and *Rhizophora mangle* L. were evaluated in three mangrove forests adjacent to hypersaline flats in the state of Paraíba, Northeast Brazil. Nine damage types were identified: holes, fungal spots, galls, undefined damage, margin damage, mining, necrosis, eggs, and rasping. *Laguncularia racemosa* exhibited a higher damage frequency and herbivory rate (3.17 to 7.07%) than *Rhizophora mangle* (0.77 to 1.76%) and *Avicennia schaueriana* (0.36 to 0.91%). *Laguncularia racemosa* had tougher leaves (wet weight/foliar area ratio) than the remaining species. The leaf herbivory percentages were low compared to other mangrove forests, most likely due to the high values of interstitial salinity.

Keywords: mangrove species, percent herbivory, damage types

Abstract: Danos foliares em três florestas de mangue no Nordeste do Brasil. Os tipos de danos e a taxa de herbivoria em folhas maduras de *Avicennia schaueriana* Stapf & Leechm ex Moldenke, *Laguncularia racemosa* (L.) Gaertn e and *Rhizophora mangle* L. foram avaliadas em três florestas de mangue adjacentes a planícies hipersalinas no Estado da Paraíba, Nordeste do Brasil. Nove tipos de danos foram identificados: buracos, fungos, galhas, indefinidos, danos nas margens, minas, necrose, ovos e raspagem. *Laguncularia racemosa* exibiu maior frequência de danos e taxa de herbivoria (3,17 a 7,07%) em relação à *Rhizophora mangle* (0,77 a 1,76%) e à *Avicennia schaueriana* (0,36 to 0,91%). *Laguncularia racemosa* teve maior dureza foliar (razão peso úmido/ área foliar) em relação às demais espécies. Os percentuais de herbivoria foliar foram mais baixos quando comparados a outras florestas de mangue, provavelmente devido aos altos valores de água intersticial.

Palavras-chave: espécies de mangue, percentual de herbivoria, danos foliares

Introduction

Mangrove forests are some of the most carbon-rich forests in the tropics (Donato *et al.* 2011). The increased primary production of these ecosystems supports the productivity of the adjacent coastal waters through export of particulate and dissolved organic matter (Adame & Lovelock 2011). These ecosystems also exhibit increased herbivore richness, and these animals use mangrove leaves directly as food sources or as reproductive sites (Burrows 2003, Giri *et al.* 2011). Herbivores play an important part in nutrient cycling and energy transfer between trophic levels. However, herbivory can also negatively affect plant fitness, patterns of nutrient and energy transfer through food chains, and organism diversity within communities (Coley & Barone 1996).

Herbivory percentages in mangrove forests vary between 1 and 47% of total leaf area consumed (Lacerda *et al*. 1986, Robertson & Duke 1987, Feller 1995, Saur *et al*. 1999, Erickson *et al*. 2004, Romero *et al*. 2006, Tong *et al*. 2006, Feller & Chamberlain

2007, Kihia *et al*. 2012, Santos 2014). Insects and crabs are the herbivores with the highest impact on the structure and functioning of mangrove forests (Cannicci *et al.* 2008, Feller *et al.* 2013). These organisms depend on the quantity and quality of the plants for their growth, development, and reproduction, which may have a significant impact on the ecosystem (Begon *et al*. 2007).

Most studies report moderate insect impact, which accounts for approximately 10% of canopy biomass loss (Alongi 2009), but episodes of severe defoliation have been reported (e.g., Anderson & Lee 1995, Menezes & Mehlig 2005). The percentage of the immediate decrease in foliar area caused by chewers or drillers is the type of herbivory most often studied in mangrove forests. However, other types of leaf damage, such as necrosis, rasping, galls, and fungal spots, may compromise ecosystem productivity (Lacerda *et al*. 1986) due to loss of photosynthetically active leaf area. However, few studies have recorded these types of leaf damage in mangrove forests (Romero *et al*. 2006, Menezes & Peixoto *et al*. 2009).

The effects of herbivory tend to be quantitatively small when the populations of the groups involved share an evolutionary history. Plants develop resistance against attacks by herbivores, decreasing their detrimental effects. This resistance is generally associated with the development of physical structures and production of chemical components that protect the plants more effectively, decreasing damage caused by herbivores (Aoyama & Labinas 2012). High leaf tannin and lignin concentrations have been shown to protect mangrove leafs from herbivores, whereas high levels of nitrogen and carbohydrates promote increased herbivory rates (Lacerda *et al*. 1986, Loyola & Fernandes 1993, Feller & Chamberlain 2007). High interstitial salinity increases secondary metabolite production (Petridis 2012) and sclerophylly (toughness) in plants, which decreases their palatability.

Mangrove forests adjacent to hypersaline flats may exhibit high interstitial salinity. Brazil has large areas of mangrove forests, but few studies have been conducted on their herbivory (Lacerda *et al*. 1986, Araújo 2002; Menezes & Mehlig 2005, Ignácio *et al*. 2005, Menezes & Peixoto 2009), and there are no studies of mangroves adjacent to hypersaline flats.

The objective of this study was to evaluate the damage types and quantify leaf herbivory rates in three mangrove forests in the state of Paraiba, Northeast Brazil, to determine the occurrence of interspecific variations in mangroves adjacent to hypersaline flats. Considering that the mangrove species exhibit differences in the physical and chemicals characteristics of their leaves (Lacerda et al., 1986; Bernini et al., 2006) it is expected that rates of herbivory differ among species.

Material and methods

The study was performed in three mangrove forests adjacent to hypersaline flats in three estuaries in the state of Paraiba, Northeast Brazil.

Site 1 was located at the Gramame River estuary (7°14’72” S and 34°48’43” W) in the Southern Coast of the state of Paraiba. The region of the Gramame River basin has as tropical wet climate according to the Köeppen climate classification, with a rainy season from June to August. The mean annual rainfall varies between 800 and 1800 mm (Fonseca 2008). The plant cover along the watershed is very degraded due to the mining, baking, and pottery industries as well as to real estate speculation, and only some remnants of mangrove, Atlantic forest, Cerrado (Brazilian savanna), and floodplains are left (Fonseca 2008).

Sites 2 and 3 were located at the Mamanguape River Bar Environmental Protection Area (EPA) (Área de Proteção Ambiental [APA] da Barra do rio Mamanguape) on the North Coast of the state of Paraiba. Site 2 was located at the Mamanguape River estuary (6°47’67” S and 34°55’68” W), and Site 3 was at the Miriri River estuary (6°51’31” S and 34°54’74” W). The region's climate is hot and humid, with a rainy season from June to August and 1634 mm mean annual rainfall (Silvestre *et al.* 2011). The Mamanguape River Bar EPA includes one of the largest and best preserved areas of mangrove forest in Northeast Brazil.

The selected mangrove forests are basin mangrove forests that occur in inland depressions (Lugo & Snedaker 1974) and are characterized by low structural development (mean tree height approximately 2.5 m). The interstitial salinity was 48.3±2.9 for Site 1, 47.0±2.7 for Site 2, and 45.0±0.8 for Site 3.

In February 2014, 50 mature leaves (third leaf pair) exposed to sunlight were collected from 10 trees of each studied species (*A. schaueriana*, *L. racemosa* and *R. mangle*) from each study site. The leaves were placed in a Styrofoam box containing ice, and leaf damage was later identified according to classification of Romero *et al.* (2006) and Menezes & Peixoto (2009) (Table I). Of the types of damage identified, only holes and margin damage directly resulted in total or partial loss of leaf material.

Table I: Description of the types of damage caused by herbivores. Adapted from Romero *et al*. (2006) and Menezes & Peixoto (2009).

Type of damage	Description
Holes	Predation of part of the leaf limb without damage to the leaf margins
Fungal spots	Dark spots on leaves
Galls	Blisters caused by arthropods
Leaf-margin	Predation of the leaf margins
Leaf-mining	Predation of the mesophyll, keeping the cuticle whole
Necrosis	Necrosis of leaf tissue
Eggs	Small cuts in the central vein
Rasping	Loss of surface layer (epidermis)
Undefined	Does not fully fit into any of the classes described

This type of damage was classified as structural damage. The remaining types of damage were classified as surface damage because they affected the leaf surface without causing direct and/or immediate loss of leaf area (Romero *et al*. 2006). Leaf wet weight was quantified for subsequent calculation of the wet weight/foliar area ratio, which is an indication of leaf toughness (Feller 1995).

The leaves were scanned, and the borders of leaves exhibiting damage at the margins were traced, following the original leaf shape, using the software program Paint. The total leaf area and area consumed by herbivores (considering holes and margin damage) were then estimated using the software program Image J 1.47. The percent herbivory was calculated as follows:

***%herbivory*= 100 * consumed area / total area (1)**

A chi-square test (χ^2) was performed to test the differences between damage type and plant species and between damage type in each species and the study site. Herbivory data and the leaf wet weight/foliar area ratio were compared with permutational multivariate analysis of variance (PERMANOVA) using random permutations (999), followed by Dunn's test for analysis of inter- (within each study site) and intraspecific (among study sites) differences. We used the R environment (2013) to perform the analysis. PERMANOVA was performed using the RVAideMemoire package (Hervé 2008).

Results

Nine types of leaf damage were identified. The results of the χ^2 test for the association between type of damage and plant species at each study site are presented in Table II, and the percentages of damaged leaves are presented in Figure 1.

Table II: χ^2 test results for different types of leaf damage analyzed in three mangrove forests of the state of Paraiba. Asterisks (*) indicate a significant association ($p \leq 0.05$) between leaf damage and plant species at each site.

Damage	Site 1		Site 2		Site 3	
	χ^2	*p*	χ^2	*p*	χ^2	*p*
Holes	24.917	0.000*	20.861	0.000*	29.268	0.000*
Fungal spots	3.804	0.149	15.643	0.000*	19.149	0.000*
Galls	2.013	0.365	-	-	3.596	0.166
Leaf-margin	27.380	0.000*	24.139	0.000*	60.263	0.000*
Leaf-mining	2.983	0.225	11.230	0.004*	16.432	0.000*
Necrosis	1.500	0.472	5.018	0.081	48.904	0.000*
Eggs	2.013	0.365	2.013	0.365	-	-
Rasping	27.592	0.000*	31.977	0.000*	7.955	0.019*
Undefined	4.113	0.128	4.113	0.128	3.648	0.161

Overall, *L. racemosa* exhibited a higher percentage of holes, margin damage, and rasping, and *A. schaueriana* exhibited a higher occurrence of fungal spots than the remaining species. *Rhizophora mangle* at Site 2 and *L. racemosa* at Site 3 exhibited a higher percentage of mining. At Site 3, necrosis was higher for *R. mangle* than for the remaining plant species.

The intraspecific comparison is presented in Table III and Figure 1. *Avicennia schaueriana* exhibited a higher percentage of galls, undefined damage, and rasping at Site 3 than at the remaining study sites. *L. racemosa* exhibited a higher frequency of holes and margin damage at Sites 1 and 3 and a higher percentage of mining at Sites 2 and 3. *Rhizophora mangle* exhibited a higher percentage of holes, margin damage, and mining at Site 2, fungal spots at Site 1, and necrosis at Site 3.

The mean leaf area consumed, represented by holes and margin damage (structural damage), varied between 3.17 and 7.07% in *L. racemosa*, 0.77 and 1.76% in *R. mangle*, and 0.36 and 0.91% in *A. schaueriana*. PERMANOVA results indicated interaction between site and species, ie, there were significant differences in herbivory percentage among the species depending on the site (Fig. 2 and Table IV). *Laguncularia racemosa* exhibited higher herbivory percentages at Sites 1 and 3 and *A. schaueriana* showed a lower herbivory percentage at Site 2 than the remaining species. The herbivory rate of *L. racemosa* was higher at Site 3 than at Sites 1 and 2, and the herbivory rate of *R. mangle* was highest at Site 2 and lowest at Site 1 (Fig. 2 and Table IV).

PERMANOVA results indicated interaction between site and species, ie, there were significant differences in leaf wet weight/foliar area ratio among the species depending on the site (Fig. 3 and Table V). Overall, *L. racemosa* exhibited a higher leaf wet weight/foliar area ratio than the remaining species. *Avicennia schaueriana* and *L. racemosa* exhibited lower leaf wet weight/foliar area ratios at Site 3 than at the remaining study sites, and *Rhizophora mangle* exhibited a higher ratio at Site 1 and an intermediate ratio at Site 3 (Fig. 3 and Table V).

Discussion

Laguncularia racemosa exhibited a higher percentage of leaves with holes and margin damage than the remaining studied species. Similar results were reported for mangrove forests in the state of Rio de Janeiro (Menezes & Peixoto 2009) and in the Mamanguape River estuary, state of Paraiba (Santos 2014). These types of leaf damage are mainly caused by caterpillars or adult insects but can also be caused by crabs and fungi (Araújo 2002). Caterpillars such as *Junonia evarete* (Lepidoptera: Nymphalidae) and *Hyblaea puera* (Lepidoptera: Hyblaeidae) have been responsible for severe defoliations in some mangroves (Araújo 2002; Menezes & Mehlig 2005, Menezes & Peixoto 2009). Severe defoliation events have been observed for *A. germinans* at the upper estuary of the Mamanguape River (Santos 2014). However, this phenomenon was not observed in the forest studied in the present study (lower estuary).

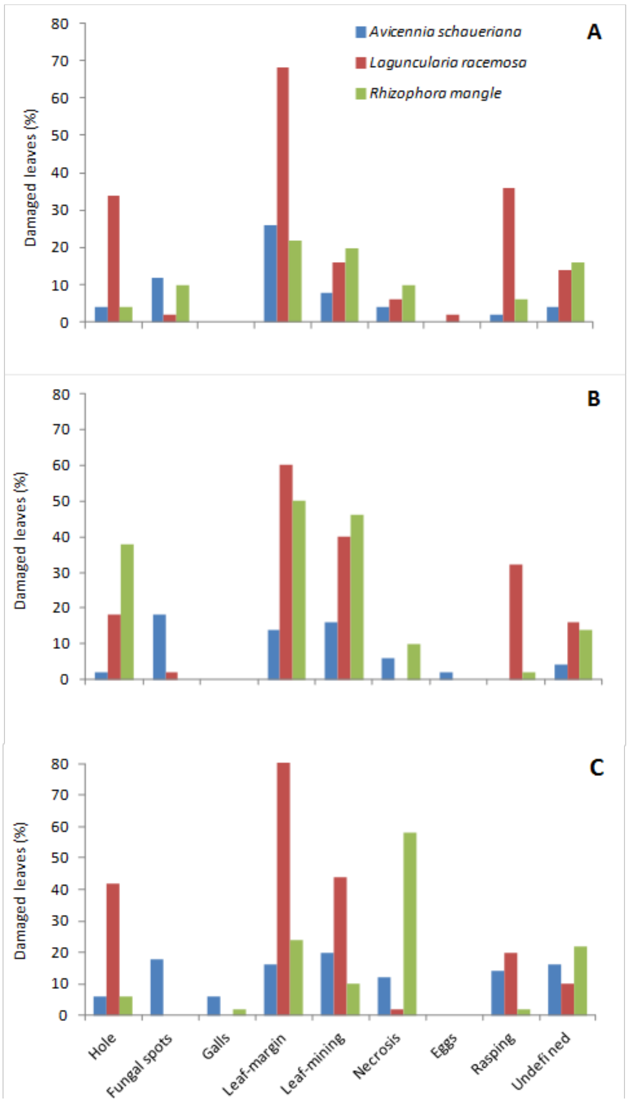

Figure 1: Frequency of leaf damage in mangrove species at Site 1 (A), Site 2 (B), and Site 3 (C) located in the state of Paraiba.

Table III: χ^2 test results for different types of leaf damage analyzed in three mangrove species in the state of Paraiba. Asterisks (*) indicate a significant association ($p \leq 0.05$) between leaf damage and the study sites for each species.

Damage	*Avicennia schaueriana*		*Laguncularia racemosa*		*Rhizophora mangle*	
	χ^2	*p*	χ^2	*p*	χ^2	*P*
Holes	1.042	0.594	6.941	0.031*	27.083	0.000*
Fungal spots	0.893	0.649	1.014	0.602	10.345	0.006*
Galls	6.122	0.047*	-	-	2.013	0.365
Leaf-margin	2.723	0.256	8.672	0.013*	11.213	0.004*
Leaf-mining	3.005	0.222	10.32	0.005*	18.257	0.000*
Necrosis	2.551	0.279	3.596	0.176	39.917	0.000*
Eggs	2.013	0.365	2.013	0.374	-	-
Rasping	11.356	0.003*	3.345	0.198	1.655	0.437
Undefined	6.522	0.038*	0.817	0.677	1.210	0.546

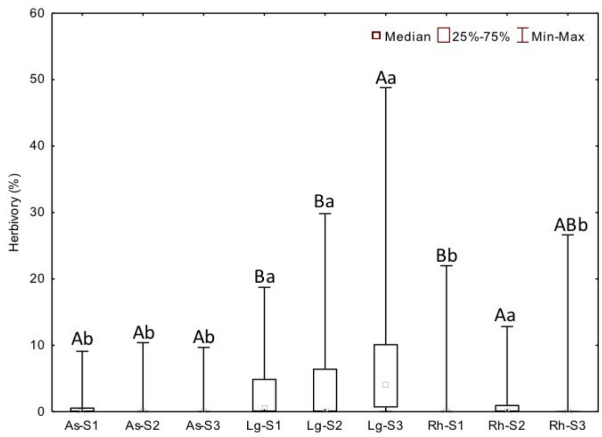

Figure 2: Leaf herbivory % of mangrove species analyzed at the three study sites in the state of Paraiba. As: *Avicennia schaueriana*; Lg: *Laguncularia racemosa*; Rh: *Rhizophora mangle*; S1: Site 1; S2: Site 2; S3: Site 3. Different upper case letters indicate significant differences for the same species among different sites, and different lower case letters indicate significant differences among different species within each site ($p \leq 0.05$).

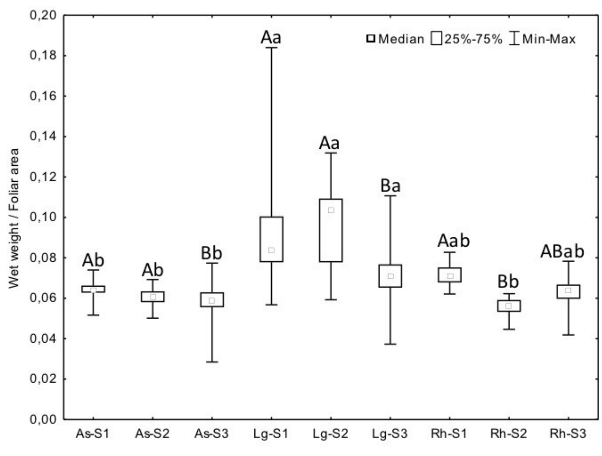

Figure 3: Leaf wet weight/foliar area ratio of mangrove species analyzed at three study sites in the state of Paraiba. As: *Avicennia schaueriana*; Lg: *Laguncularia racemosa*;

Lgend to Fig. 3 continued: Rh: *Rhizophora mangle*. S1: Site 1; S2: Site 2; S3: Site 3. Different upper case letters indicate significant differences for the same species among different sites, and different lower case letters indicate significant differences among different species within each site ($p \leq 0.05$).

Fungi were observed in the three analyzed species, with a higher percentage in *A. schaueriana*. Menezes & Peixoto (2009) studied the same three mangrove species and observed fungal damage only in *L. racemosa*, caused by *Septoria* sp., which most likely infests the plant following insect attacks. In contrast, Romero *et al*. (2006) observed fungal spots in *A. germinans* and *Rhizophora* sp. but not in *L. racemosa*.

The variations may be related to the use of different quantification methods or to temporal changes in the environmental conditions that influence herbivory rates (Menezes & Peixoto 2009). The observed differences in damage frequency and percentage of consumed leaf area may be attributed to physical and chemical characteristics of the different mangrove species (Lacerda *et al*. 1986, Feller 1995, Saur *et al*. 1999, Erickson *et al*. 2004, Tong *et al*. 2006).

Laguncularia racemosa exhibited a higher percentage of consumed leaf area, followed by *R. mangle* and *A. schaueriana*. Similar results were reported for other mangrove forests in Brazil (Ignácio *et al*. 2005, Menezes & Peixoto 2009, Santos 2014). However, Lacerda *et al*. (1986) observed a higher herbivory rate in *R. mangle* and Romero *et al*. (2006) observed a higher rate in *A. germinans* than in the remaining studied species (Table VI). Studies performed in other mangrove forests worldwide have also shown variable leaf consumption rates (Table VI).

Gall-forming insects induce formation of meristematic tissues in host plants to supply food with better nutritional quality that is free of defense compounds to their caterpillars.
These insects have been used as bioindicators for environmental quality in mangrove forests and other ecosystems (e.g., Atlantic Forest) due to characteristics such as high sensitivity to changes in the host plants and the environment and being highly affected by leaf salinity and toughness (Fernandes & Santos 2014).

In the present study, the interstitial salinity was lower at Site 3, which could explain the occurrence of galls in leaves of *A. schaueriana* and *R. mangle* observed at this study site.

In general, leaf mining is performed by insects of the family Agromyzidae, which cause linear shaped damage, with or without a defined pattern on the leaf blade (Romero *et al*. 2006). In the present study, a larger percentage of this damage was present in *L. racemosa* and *R. mangle.* Santos (2014) and Romero *et al*. (2006) also observed a higher frequency of leaf mining in *L. racemosa*.

Rhizophora mangle exhibited a higher percentage of necrosis than the remaining species. Similar results were reported by Menezes & Peixoto (2009). These authors observed that leaf necrosis at a mangrove forest in the state of Rio de Janeiro was caused by Reduviidae (Hemiptera). The rasping of leaf epidermis observed at the Mamanguape River Bar EPA has been reported to be caused by the fungus *Colletotrichum gloeosporioides* (Penz.) (Araújo 2002) but may also be caused by insects of the order Thysanoptera (Family: Phlaeothripidae), gastropods of the family Littorinidae, and the crab *Aratus pisonii* (Family: Grapsidae) (Romero *et al.* 2006). The higher occurrence of rasping in *L. racemosa* observed in the present study was also observed by Santos (2014) at the Mamanguape River Bar EPA.

Increased leaf toughness (wet weight/foliar area) may decrease leaf consumption by herbivores (Coley 1987). However, *L. racemosa* exhibited higher leaf toughness and an increased herbivory rate compared to the remaining species, indicating that other factors may be more important for defense against herbivores. *Rhizophora mangle* leaves have a high C:N ratio and soluble tannin concentration (Robertson & Duke 1987, Lacerda *et al.* 1986), which confer resistance to herbivore attacks. The lower herbivory rate in the genus *Avicennia* may be related to the presence of salt crystals originating from glands at the leaf epidermis that decrease its palatability (Newbery 1980).

A higher leaf nitrogen concentration results in higher herbivory rates (Onuf *et al*. 1977, Coley 1983). Leaves of *A. schaueriana* have been reported to have high nitrogen concentrations (Bernini *et al.* 2006, Cuzzuol & Rocha 2012). However, the quality of the available nitrogen is more important for herbivores than its quantity. Not all nitrogen found in leaves is available for herbivores because a portion is located in the vacuoles as electrolytes or in the cytoplasm as compatible solutes (Lacerda et al. 1986, Medina & Francisco 1997).

The studied mangrove forests are adjacent to hypersaline flats and have high interstitial salinity. Biosynthesis of phenolic compounds instead of growth may occur in plants under conditions of environmental stress, e.g., high salinity (Petridis, 2012). High salinity causes oxidative stress and the formation of reactive oxygen species (ROS), which causes cell damage and inhibits photosynthesis (Jithesh *et al*. 2006). ROS are unstable and extremely reactive molecules, capable of transforming other molecules with which they interact. Plants therefore produce large amounts of antioxidant compounds to eliminate or detoxify ROS. Phenolic compounds act as antioxidants, protecting plants against damage caused by the increase in the levels of ROS due to salt stress, which also protects plants against herbivory (Jithesh *et al*. 2006, Petridis *et al*. 2012). The high interstitial salinity could therefore explain the intraspecific differences and low herbivory rates observed in the present study. However, monitoring of interstitial salinity is needed to better understand the relationship between salinity and herbivory levels.

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Table IV: PERMANOVA results for leaf herbivory of mangrove species analyzed at the three study sites in the state of Paraiba. Asterisks (*) indicate a significant p value ($p \leq 0.05$).

	Sum Sq	Df	Mean Sq	F value	Pr (>F)
Site	185.7	2	92.84	4.00059	0.008*
Species	1487.0	2	743.51	32.0811	0.001*
Site:Species	281.0	4	70.25	3.0313	0.0019*
Residuals	10220.6	891	23.18		

Table V: PERMANOVA results for leaf wet weight/foliar area ratio of mangrove species analyzed at three study sites in the state of Paraiba. Asterisks (*) indicate a significant p value ($p \leq 0.05$).

	Sum Sq	Df	Mean Sq	F value	Pr (>F)
Site	0.015430	2	0.0077148	41.601	0.001*
Species	0.054124	2	0.0270618	145.928	0.001*
Site:Species	0.01860	4	0.0046699	25.182	0.001*
Residuals	0.165232	891	0.0001854		

Table VI: Leaf herbivory percentages in mangrove forests worldwide and in Brazil.

Site	**Species**	**Herbivory (%)**	**Reference**
North Queensland, Australia	*Rhizophora, Brughiera* and *Ceriops*	1.8 - 7.6	Robertson & Duke (1987)
North Queensland, Australia	*Avicennia marina*	8.8 - 12.0	Robertson & Duke (1987)
Belize, Central America	*Rhizophora mangle*	1.0 - 5.2	Feller (1995)
French Antilles	*Avicennia germinans* *Rhizophora mangle*	0.9 - 4.9 0.2	Saur *et al*. (1999)
Northern Queensland	*Avicennia marina* *Rhizophora stylosa*	6.8 - 8.5 3.8 - 4.2	Burrows (2003)
Tampa Bay, Florida	*Rhizophora mangle*	0 – 47	Erickson *et al*. (2004)
Colombian Pacific Coast	*Avicennia germinans* *Laguncularia racemosa* *Pelliciera rhizophorae*	4.9 4.7 2.1	Romero *et al*. 2006
Mai Po and Ting Kok Hong Kong	*Kandelia obovat*a	2.1 - 6.5	Tong *et al*. (2006)
Twin Cays, Coast of Belize	*Rhizophora mangle*	2.7 - 10.3	Feller & Chamberlain (2007)
Gazi Bay, Kenya, Africa	*Ceriops tagal* *Rhizophora mucronata* *Avicennia marina* *Bruguiera gymnorrhiza*	8.1 5.5 12.5 8.3	Kihia *et al*. (2012)
	Brazil		
Rio de Janeiro	*Avicennia schaueriana* *Laguncularia racemosa* *Rhizophora mangle*	0.5 - 1.5 3.2 5.5 – 6.2	Lacerda *et al*. (1986)
Mamanguape River Bar EPA, Paraiba	*Avicennia schaueriana* *Rhizophora mangle* *Laguncularia racemosa*	3.3 - 7.1 2.3 - 5.6 3.8 - 10.7	Araújo (2002)
Sepetiba Bay, Rio de Janeiro	*Laguncularia racemosa* *Avicennia schaueriana* *Rhizophora mangle*	12.1 8.3 6.2	Menezes & Peixoto (2009)
Mamanguape River Bar EPA, Paraiba	*Avicennia germinans* *Laguncularia racemosa*	0.2 - 3.6 1.8 - 12.1	Santos (2014)
Gramame River, Mamanguape River and Miriri River	*Avicennia schaueriana* *Laguncularia racemosa* *Rhizophora mangle*	0.36 - 0.91 3.17 - 7.07 0.77 - 1.76	Present study

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