

## Leaf damage in a mangrove swamp at Sepetiba Bay, Rio de Janeiro, Brazil

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**ABSTRACT** – (Leaf damage in a mangrove swamp at Sepetiba Bay, Rio de Janeiro, Brazil). Leaf damage to *Rhizophora mangle* L., *Avicennia schaueriana* Stapf. & Leechman, and *Laguncularia racemosa* L. was studied in a two hectare mangrove swamp site in Sepetiba Bay. Seventeen arthropod morphospecies were identified as being responsible for the damage, and their species diversity was highest on *A. schaueriana*, followed by *R. mangle* and *L. racemosa*. Damage in terms of relative area was greatest in *L. racemosa*. Almost 9% of mangrove canopy leaf area demonstrated some damage. Loss of leaf area to herbivory was 12.1%, 8.3% and 6.2% in *L. racemosa*, *A. schaueriana* and *R. mangle* respectively. *L. racemosa* and *A. schaueriana* showed high percentages of leaf-margin damage in terms of the total damaged leaf area (82.2% and 56.3% respectively), while the most important type of damage in *R. mangle* was necrosis, representing 58.1% of the total damaged leaf area.

Key words - *Avicennia schaueriana*, herbivory, *Laguncularia racemosa*, mangrove, *Rhizophora mangle*

**RESUMO** – (Danos foliares em um mangue na Baía de Sepetiba, Rio de Janeiro, Brasil). Um trecho com 2 ha de mangue na Baía de Sepetiba foi estudado quanto ao dano foliar em *Rhizophora mangle* L., *Avicennia schaueriana* Stapf. & Leechman. e *Laguncularia racemosa* L. Foram reconhecidas 17 morfospécies de artrópodes causadoras de dano. *A. schaueriana* apresentou maior riqueza de morfoespécies danificadoras de folhas, seguida de *R. mangle* e *L. racemosa*. A área relativa de dano foi maior em *L. racemosa* e menor em *R. mangle*. Nossos resultados mostraram que 8,8% da área foliar do dossel do mangue estudado foi afetado pela predação. A perda de área foliar por herbivoria foi de 12,1%, 8,3% e 6,2% em *L. racemosa*, *A. schaueriana* and *R. mangle*, respectivamente. O consumo da borda da folha foi mais expressivo em *L. racemosa* and *A. schaueriana*, correspondendo a 82,2% and 56,3% de dano total na folha, respectivamente. Em *R. mangle*, o dano mais expressivo foi a necrose que correspondeu a 58,1% de toda a área de dano foliar.

Palavras-chave - *Avicennia schaueriana*, herbivoria, *Laguncularia racemosa*, mangrove, *Rhizophora mangle*

### Introduction

Mangrove forests serve as organic debris sources for coastal food chains, principally from their senescent leaves (Lugo & Snedaker 1974, Odum & Heald 1975, Boto & Bunt 1982). This organic production can vary between 1 and 10 t ha<sup>-1</sup> year<sup>-1</sup>, making mangrove swamps one of the principal factors responsible for the high fishery productivity of tropical waters (D’Croz & Kwiecinski 1980, IUCN 1983, Lacerda & Rezende 1990).

In spite of the pantropical distribution and importance of mangrove swamps the entomofauna associated with these environments is still only poorly known. The activities of leaf-consumer organisms have been examined in only a few localities in the world, and generally only moderate damage has been reported (not exceeding 50% of the leaf area) (Erickson *et al.* 2004,

Offenberg *et al.* 2004). Leaves of mangrove swamp plants are, in fact, considered to show relatively little damage because they are heavily protected by tannin compounds and other efficient inhibitors of insect herbivores (Huffaker *et al.* 1984, Hernes *et al.* 2001, Skov & Hartnoll 2002). Nonetheless, the literature also contains reports of severe leaf-loss events in some species found in mangrove swamps (Lee 1991, Anderson & Lee 1995, Elster *et al.* 1999, Menezes & Mehlig 2005).

Studies of leaf damage caused by insect herbivores generally refer to the quantification of the missing area leaf in relation to the potential (full) leaf area (Johnstone 1981, Lacerda *et al.* 1986, Dirzo 1987, Marquis 1987, Ellison & Farnsworth 1996) and have not taken into consideration many types of damage that do not necessarily cause a loss of the leaf area, such as necrosis, boring, galls and scraping (although these likewise signify the loss of photosynthetically active areas). Leaf damage in mangrove swamp plants can compromise the productivity of those environments (Lacerda *et al.* 1986) through the direct loss of photosynthetic area, reallocation of plant metabolic resources to herbivore defenses (Coley *et al.* 1985, Ernest 1989, Gange &

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Brown 1989) or, in extreme cases, the death of large numbers of a given species (West & Thorogood 1985, Whitten & Damanik 1986, Murphy 1990, Farnsworth & Ellison 1991, Anderson & Lee 1995). Additionally, herbivory can interfere with the developmental and/or reproductive patterns of the plants (Gange & Brown 1989, Gonçalves-Alvim *et al.* 2001) and seedling recruitment, and alter forest structures (McKee 1995, Farnsworth & Ellison 1997). In spite of the importance of these topics to mangrove ecology, few studies in these ecosystems have classified leaf damage or investigated their causal agents (Onuf *et al.* 1977, Farnsworth & Ellison 1991, Anderson & Lee 1995, McKee 1995, Stowe 1995).

The comparatively simple structure of a mangrove community allowed us to investigate the following questions: i) do the types of damage and total amount of leaf damage encountered in mangrove forest trees vary in terms of the different species? and, ii) does the amount of damaged leaf area demonstrate seasonal variations? The present study therefore sought to classify and compare the different types of leaf damage encountered in *Rhizophora mangle* L., *Avicennia schaueriana* Stapf. & Leechman., and *Laguncularia racemosa* L. and identify the causative agents of this damage in a mangrove forest in Sepetiba Bay, Rio de Janeiro State, Brazil.

## Material and methods

**Study area** – The present study was undertaken during the period between May 1991 and April 1992 in an area of two hectares in a mangrove swamp located on the right bank of the mouth of the Piraquê River as it flows into Sepetiba Bay along the southern border of the Guaratiba Biological and Archaeological Reserve (RBAG) (23°01' S, 43°38' W) in Rio de Janeiro State, Brazil. This bay covers an area of 305 km<sup>2</sup> and mangrove swamps are located primarily along its eastern edge (Roncarati & Barrocas 1978). The mangrove swamps in this region are populated principally by *Rhizophora mangle*, *Laguncularia racemosa*, and *Avicennia schaueriana* (which will be referred to here by their generic names) and these plants are distributed throughout the area without any apparent defined zonation. *Hibiscus pernambucensis* and *Acrostichum aureum* can also be found in areas with slightly higher elevations in the mangrove swamp. Two basic vegetation types can be identified in the region: a dominant form with trees reaching up to 5 m tall that extends through the entire forest; and a second form that is well represented in the rivers and tidal canals and is dominated by individuals of *Rhizophora* that can reach 25 m in height, with trunks measuring up to 50 cm of diameter at breast height. In other regions of the RBAG mangrove swamp that are located further from the canals, *Rhizophora* dominates in terms of the numbers of trees, but *Avicennia* is represented by much larger

individuals. The species *Laguncularia* is less common, and almost always associated with *Rhizophora* and *Avicennia*. This latter taxon has the widest distribution, occupying areas that are both saltier and more elevated (Dias-Brito & Zaninetti 1979).

**Climate** – The study area macroclimate is classified as Aw (Tropical Rainy) according to the Köppen system, with air temperatures typical of tropical coastal zones. The average annual temperature is 23.7 °C, with February being the warmest month (average 26.9 °C) while August is the coldest (average 20.9 °C). The average annual rainfall is 1237.7 mm, with 37% occurring during the summer and condensed into about 40 rainy days. The winter months are drier, accounting for only 15% of the average annual rainfall, which is distributed in about 21 days. The average monthly rainfall during July and August is between 40 and 55 mm, although in dry years it can drop to less than 30 mm, corresponding to an accentuated drought for the region (Mattos 2005). The climatic data utilized here was furnished by the Instituto Nacional de Meteorologia (INMET) based on information from the Marambaia meteorological station (23°03' S, 43°36' W) located approximately 7 km from the study area.

**Sampling strategies** – At monthly intervals during the study period ten adult individuals of *Avicennia*, *Laguncularia*, and *Rhizophora* having diameters at breast height (DBH) > 2.5 cm were chosen at random and five leaves were collected from each plant. The individuals sampled were then marked so that they would not be sampled again in the following months. As herbivore damage is not distributed uniformly in the plant crown and can vary greatly among different branches and leaves or according to the age of the plant (Coley 1980, 1983, Lowman 1985, Ernest 1989, Basset 1991, Coley & Aide 1991, Loyola Jr. & Fernandes 1993, Nascimento & Hay 1993), the sampling was standardized to collect only the third pair of leaves on randomly chosen branches (Filomeno & Castellani 1990). In order to collect the highest branches an extendable pruning pole was used (with a 15 m reach).

Leaf damage was classified as follows: damage caused by gall-forming arthropods were denominated “galls”; predation on the leaf margins was denominated “leaf-margin” damage; rasping of the leaf cuticle (on either the dorsal or ventral face of the leaf) was denominated “rasping”; predation part of the leaf blade without damaging the leaf margin was denominated a “hole”; necrosis of the leaf tissue was generically denominated “necrosis”; spots not larger than 1 mm<sup>2</sup> that were infested by fungi were denominated “fungal spots”; and predation of the leaf mesophyll while maintaining the integrity of the cuticle was denominated “leaf-mining”. Damage that did not fit perfectly into any of these classes and that had not been caused by herbivores (as, for example, deformities caused by mechanical stress) was denominated “undefined damage”.

The complete area of each leaf was obtained by drawing its outline on a piece of paper, and in the case of

leaves with damaged borders, their presumed original shapes were completed by drawing dotted lines. These drawings were subsequently cut out with a scissors and their areas quantified using a Li-Cor model Li – 3.100 Area Meter (Beerling & Fry 1990). The outline of each type of damage visible on each leaf was also outlined on paper, cut out, and subsequently quantified using the Area Meter apparatus (with the exception of the fungal dots). The areas of the fungal spots were standardized at 1 mm<sup>2</sup> each (this value was never exceeded) and the total density of these points corresponded to the damaged area.

In parallel with the collection of the leaf samples, any invertebrates observed consuming the leaves were also collected. Any lepidopteron larvae found were taken to the laboratory (and maintained on the same leaves they were observed consuming in the field) and allowed to metamorph into adults for identification. The herbivores and pathogens responsible for leaf damage were identified by specialists at the Entomology Department of the National Museum – Federal University of Rio de Janeiro and in the Phytopathology Department of Federal Rural University of Rio de Janeiro. All entomological material collected during the course of the field work was deposited in the Ângelo Moreira da Costa Lima Collection of the Federal Rural University of Rio de Janeiro.

In performing the statistical analysis, the homogeneity of the variance and the normality of the frequency distributions of the data were verified using the Cochran & Bartlett and Lilliefors tests respectively. Variables that did not satisfactorily approximate normality or homogeneity were mathematically transformed (as indicated in the tables and figures). Variance analysis was used to compare averages, followed by the Tukey test at 5% (Zar 1999). All analyses were performed using the SAEG statistical software package of the Arthur Bernardes Foundation.

Any given type of damage was considered to be present if it was observed on the leaf, independent of its extent or density.

## Results and discussion

Climate – December was the warmest month during the study period (26.3 °C) and September the coldest (17.8 °C) (figure 1). Rainfall was greatest during the month of January (322.4 mm) and least during April (15.5 mm). The study period was marked by three dry periods: during months of June and August; the month of November; and from February to April. The period from November through February was marked by high rainfall levels.

Types of damage and their causative agents – Eight types of damage were recognized as affecting the mangrove tree leaves (table 1). The damage we encountered was

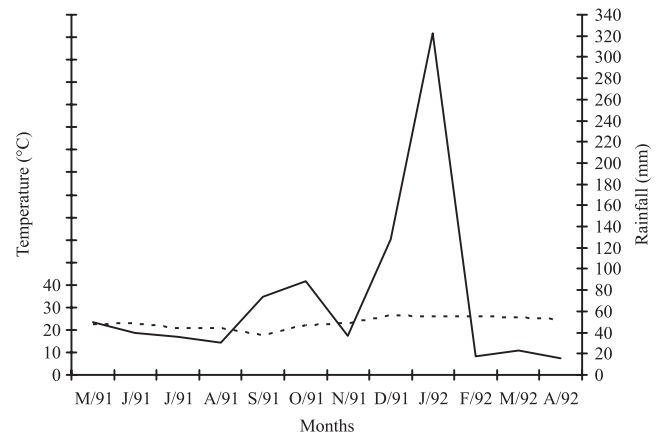


Figure 1. Gausse-Bagnouls ombrothermic diagram for an area of mangrove swamp at the mouth of the Piraquê River, Sepetiba Bay, Rio de Janeiro State, Brazil, during the period from May 1991 to April 1992. Climatological data was obtained from the Marambaia Weather Station (Instituto Nacional de Meteorologia) located approximately 5 km from the study area. (— = Rainfall; --- = Average temperature).

similar to that reported in other mangrove swamps in Brazil, Pakistan, the United States, the Bahamas, Belize, China, as well as other localities around the globe (Johnstone 1981, Schoener 1988, Filomeno & Castellani 1990, Farnsworth & Ellison 1991, Lee 1991, Stowe 1995, Gonçalves-Alvim *et al.* 2001, Erickson *et al.* 2004, Saifullah & Mahera 2004). Undefined damage caused by deformities of *Rhizophora* leaves appeared as corky structures, but without any signs of pathologies resulting from fungal or bacterial infections. An exaggerated growth of trichomes on the adaxial surface of the leaves of *Avicennia* was sometimes observed, but without the presence of external or internal structures that would suggest a fungal origin.

Seventeen predator morphospecies causing leaf damage (table 1) were recognized, with *Avicennia* being the taxon with the greatest predator diversity (9 morphospecies). *Rhizophora* and *Laguncularia* were observed to have equal numbers (5) of morphospecies responsible for leaf damage.

Adults of four species of lepidopterons were frequently collected on mangrove trees during the study period: *Amorbia* sp., Olethreutinae (Tortricidae); *Motyra abseuzalis* (Walker, 1859) (Noctuidae); and *Spoladea recurvalis* (Fabricius, 1775) (Pyralidae), although it was not possible to determine which plant species served as the true food source for their larvae, nor to determine the type of damage caused by these insects. Adult specimens of the coleopterans *Eumolpus* sp. (Chrysomelidae) and



Table 1. Types of damage and their respective causal agents encountered on *Laguncularia racemosa*, *Avicennia schaueriana* and *Rhizophora mangle* in a mangrove swamp at the mouth of the Piraquê River, Sepetiba Bay, Rio de Janeiro State, Brazil.

Type of damage	Plant damaged	Causal agent	Classification
Fungal spots	<i>Laguncularia racemosa</i>	<i>Septoria</i> sp.	Fungi
Necrosis	<i>Avicennia schaueriana</i>	Reduviidae 1	Hemiptera (Reduviidae)
	<i>Rhizophora mangle</i>	Reduviidae 2	Hemiptera (Reduviidae)
	<i>Laguncularia racemosa</i>	Reduviidae 1	Hemiptera (Reduviidae)
Rasping	<i>Avicennia schaueriana</i>	<i>Junonia evarete</i> (Cramer, 1775)	Lepidoptera (Nymphalidae)
	<i>Rhizophora mangle</i>	<i>Melampus coffeus</i> (Linnaeus, 1758)	Molusca (Ellobidae)
	<i>Laguncularia racemosa</i>	Geometridae 1	Lepidoptera (Geometridae)
Holes	<i>Avicennia schaueriana</i>	<i>Hyblaea puera</i> (Cramer, 1777)	Lepidoptera (Hyblaeidae)
	<i>Rhizophora mangle</i>	Geometridae 2	Lepidoptera (Geometridae)
	<i>Laguncularia racemosa</i>	<i>Oiketicus kirbyi</i> (Guilding, 1827)	Lepidoptera (Psychidae)
Leaf-mining	<i>Avicennia schaueriana</i>	Lepidoptera 1	Lepidoptera
	<i>Laguncularia racemosa</i>	Lepidoptera 1	Lepidoptera
Leaf-margin	<i>Avicennia schaueriana</i>	<i>Junonia evarete</i> (Cramer, 1775)	Lepidoptera (Nymphalidae)
		<i>Rothildia aurota</i> (Cramer, 1775)	Lepidoptera (Saturnidae)
		<i>Madoryx oiclus</i> (Cramer, 1779)	Lepidoptera (Sphingidae)
		<i>Oiketicus kirbyi</i> (Guilding, 1827)	Lepidoptera (Psychidae)
		<i>Hyblaea puera</i> (Cramer, 1777)	Lepidoptera (Hyblaeidae)
		<i>Aratus pisonii</i> (H. Milne Edwards, 1837)	Crustacea (Grapsidae)
		<i>Stilpnochlora marginella</i> (Serville, 1839)	Orthoptera (Tettigoniidae)
	<i>Laguncularia racemosa</i>	<i>Oiketicus kirbyi</i> (Guilding, 1827)	Lepidoptera (Psychidae)
	<i>Rhizophora mangle</i>	Lymantridae 1	Lepidoptera (Lymantridae)
		Geometridae 2	Lepidoptera (Geometridae)
	<i>Aratus pisonii</i> (H. Milne Edwards, 1837)	Crustacea (Grapsidae)	
Galls	<i>Avicennia schaueriana</i>	<i>Cecidomyia avicenniae</i> (Cook, 1909)	Diptera (Cecidomyiidae)
Undefined	<i>Avicennia schaueriana</i>	Deformities	Mechanical stress
	<i>Rhizophora mangle</i>		
	<i>Laguncularia racemosa</i>		

*Stroglyium* sp. (Tenebrionidae) were collected numerous times on the leaves of *Laguncularia*, although it was not possible to determine if they used that plant as a food source. The greatest densities of herbivore species encountered were among the lepidopterons, as has been reported for other mangrove swamps in Brazil and Hong Kong (Filomeno & Castellani 1990, Lee 1991).

In the laboratory, the lepidopteron species *Junonia evarete* (Nymphalidae) and *Madoryx oiclus* (Sphingidae) restricted their diets to the consumption of *Avicennia* leaves (table 1). These insects did not accept the substitution of these leaves for those of other species growing in the mangrove swamp, most likely due to the presence of different secondary plant defense compounds (Farnsworth & Ellison 1991).

Variations in total leaf damage area – significant differences were confirmed (ANOVA:  $F = 29.31$ ;  $P = 0.0001$ ) between the averages of the total damaged leaf areas among the different species studied (Tukey test  $P < 0.05$ ) (table 2). As we always consider the proportion of the damage in relation to the leaf size, and not the absolute damaged leaf area, a given type of damage that might cover the same area in each of the three mangrove species studied would still generate distinct proportions in relation to the total area of the different leaves.

*Laguncularia* demonstrated the greatest percentage of damaged leaf area among the three species examined (12.1%), although this value was not statistically different from *Avicennia* (8.3%) ( $P > 0.05$ ) (table 2). These two species, however, did suffer significantly more

Table 2. Total leaf area, average total leaf area, total damaged leaf area, and percentage of damaged leaf area in *Laguncularia racemosa*, *Avicennia schaueriana* and *Rhizophora mangle* in a mangrove swamp at the mouth of the Piraquê River, Sepetiba Bay, Rio de Janeiro State, Brazil.

Species	Total leaf area in cm <sup>2</sup> (N = 600)	Average total leaf area in cm <sup>2</sup> (N = 600)	Total damaged leaf area (cm <sup>2</sup> )	Percentage of damaged leaf area (relative area damaged)
<i>Laguncularia racemosa</i>	14.931,2	24,9 b ± 3,3	1.808,7	12,1% (0,076 a*)
<i>Avicennia schaueriana</i>	13.592,3	22,7 c ± 2,8	1.124,1	8,3% (0,068 a*)
<i>Rhizophora mangle</i>	16.509,4	27,5 a ± 3,8	1.025,2	6,2% (0,053 b*)
Total	45.032,9	–	3.958,0	8,8%

Transformed data: \* relative area damaged (arcsine of the square root of the percentage). Averages followed by the same letters in any column do not differ significantly by the Tukey test at 5%.

damage than *Rhizophora* (6.2%) ( $P < 0.05$ ). The lower percentage of herbivory seen in *Rhizophora* is probably related to the physical and chemical defenses of this species (Robertson & Duke 1987). The leaves of this species are known to be extremely resistant (Robertson & Duke 1987, Fernandes 1994) and their especially high concentrations of soluble tannins as well as the high proportions of carbon/nitrogen in their leaves seem to render them especially unpalatable (Feeny 1976, Fox & Macauley 1977, Lowman & Box 1983, Farnsworth & Ellison 1991).

Studies in other mangrove swamps in Brazil and the world that quantified leaf area loss due to herbivores demonstrated variable (and even contrasting) levels of predation among the same species studied here. In an earlier examination of two mangrove sites near the present study area, for example, Lacerda *et al.* (1986) found that *Avicennia* demonstrated a lower herbivory rate (0.5 and 1.5%) than *Rhizophora* (5.5 and 6.2%). *Laguncularia* was found to be the most heavily damaged species in Santa Catarina during both the summer (7.5%) and winter (20.9%) months (Filomeno & Castellani 1990). Herbivory resulted in the loss of 5.7% of the leaf area *Laguncularia* (Stowe 1995) in the Caribbean region, while in Belize this rate varied from 4.3 to 25.3% in *Rhizophora* (Farnsworth & Ellison 1991). Even higher values for these and other species have reported in the mangrove swamps of Florida and tended to oscillate between 26% and 47% of the total area of the leaf (Onuf *et al.* 1977, Erickson *et al.* 2004). The variations reported for leaf area loss may be related to the different methodologies used or to temporal alterations of some environmental conditions that in turn influence herbivory rates. More widespread and standardized

sampling will be necessary in order to be able to detect herbivory patterns in these ecosystems. In the mangrove swamp examined in the present study during the period between May/91 and May/93, for example, a population boom of *Hyblaea puera* (Lepidoptera: Hyblaeidae) was detected that resulted in the widespread defoliation of *Avicennia* trees, and the death of many individuals. This same species of lepidopteron was responsible for the marked defoliation of *Avicennia germinans* (L.) Stearn in mangrove areas in Pará State (Menezes & Mehlig 2005). Similar defoliations also caused by lepidopterons were observed affecting *Avicennia marina* (Forssk.) Vierh in Australia (West & Thorogood 1985), Hong Kong (Anderson & Lee 1995), and Singapore (Murphy 1990); affecting *Avicennia alba* Blume in Thailand (Piyakarnchana 1981); *Excoecaria agallocha* L. in Indonesia (Whitten & Damanik 1986) and Singapore (Murphy 1990); and damaging *Aegiceras corniculatum* (L.) Blanco in Singapore (Murphy 1990).

The total loss of leaf area due to herbivory in the entire arboreal community in the present study was 8.8% (table 2). Data available in the literature concerning damage caused by insects and arboreal crabs on living leaves among tree species in mangrove swamps demonstrate variations of from 1% to 47% of the total leaf area of a forest (Lacerda *et al.* 1986, Filomeno & Castellani 1990, Farnsworth & Ellison 1991, Feller 1995, Feller & Mathis 1997, Erickson *et al.* 2004). Herbivory levels are generally quite low in the Caribbean (Onuf *et al.* 1977, Beever *et al.* 1979), while in the Indo-Pacific region these levels can be quite contrasting, varying from 2.1% in Australia (Robertson & Duke 1987) to 20% in the mangrove swamps of Papua, New Guinea (Johnstone 1981).

Distribution of the different types of damage among the plant species examined – Galls were only observed on *Avicennia* (induced by *Cecidomyia avicenniae* [Diptera: Cecidomyiidae]) (figure 2). Galls have been reported in mangrove swamps in Brazil in *Laguncularia racemosa* (induced by *Brachendus enodis* [Acari, Eriophyidae]) (Santos-Mendonça & Almeida-Cortez 2007), and in *Avicennia germinans* Learn. (induced by *C. avicenniae*) (Gonçalves-Alvim *et al.* 2001). In mangrove swamps in Belize, galls on the leaves of *A. germinans* were induced by unknown agents and were restricted only to that tree species (Farnsworth & Ellison 1991).

Fungal spots were only seen on *Laguncularia*, and they were caused by *Septoria* sp. (which probably

infested the plant following insect predation). Fungal infestations by *Colletotrichum* sp. and *Ascochitia* sp. were observed on *Avicennia* in necrotic areas that were formed by predation by hemipterons.

Leaf-margin damage was previously reported as being most expressive in *Laguncularia* and in *Avicennia*, and represented 82.2% and 56.3% of their total damaged leaf areas respectively. Both species demonstrated significantly more of this type of damage than was seen in *Rhizophora* ( $P < 0.05$ ); this latter species demonstrated most damage due to necrosis (58.1%) (figure 2). Leaf margin damage was most representative in *Laguncularia* in the mangrove swamps of Santa Catarina State (Filomeno & Castellani 1990).

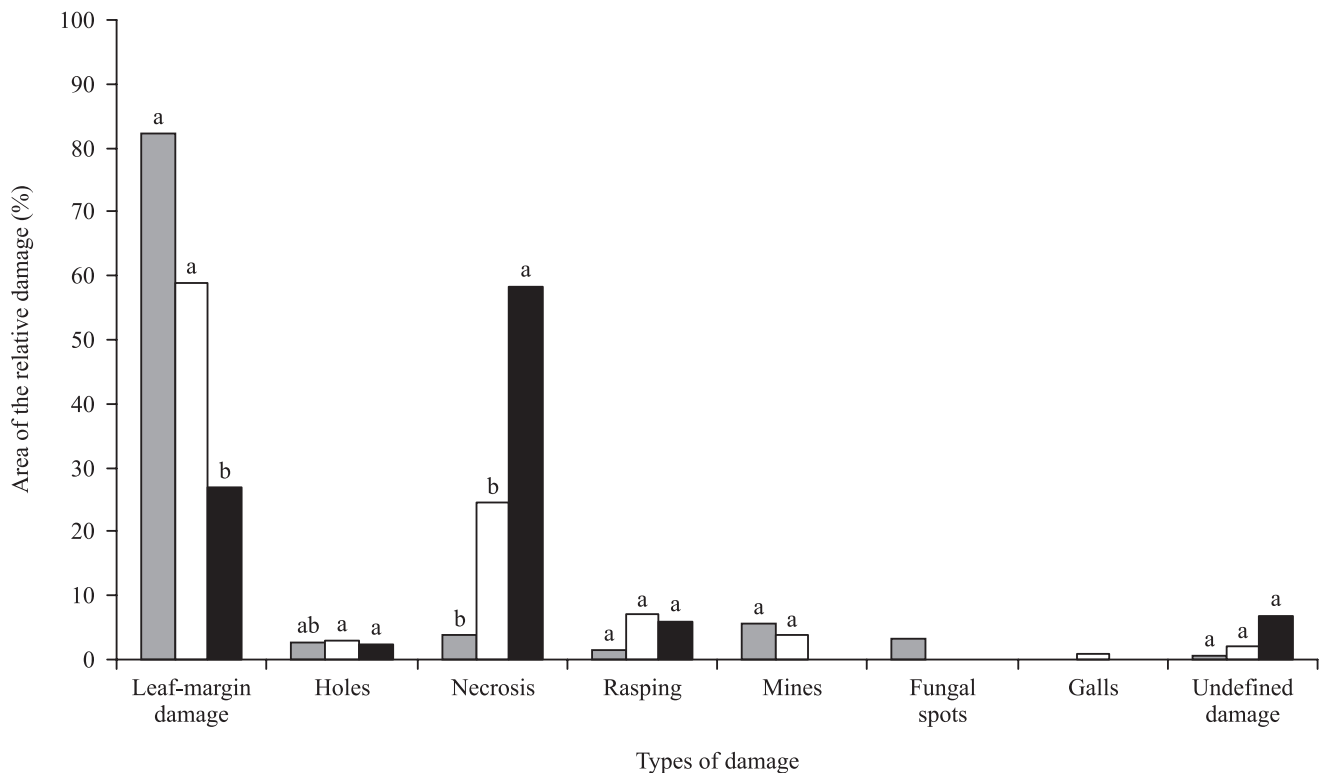


Figure 2. Representivity of the area of each type of leaf damage in relation to the total damaged area in *Laguncularia racemosa* (■), *Avicennia schaueriana* (□) and *Rhizophora mangle* (■) in a mangrove swamp at the mouth of the Piraquê River, Sepetiba Bay, Rio de Janeiro State, Brazil. Transformed data: arcsine of the  $\sqrt{\%$  of the relative area of the damage. Averages followed by the same letters do not differ significantly by the Tukey test at 5%. The comparisons are valid among the species for each types of damage.

The percentage of leaf damage caused by “holes” was greatest in *Avicennia*; *Laguncularia*, however, showed significantly greater absolute numbers of leaves with holes than the other species ( $P < 0.05$ ) (figure 3). This same type of damage was also reported for *Laguncularia* in mangrove swamps in Belize, and was

caused by predation by hemipterons (Farnsworth & Ellison 1991).

Rasping damage appeared greatest in *Avicennia*, although there were no statistically significant difference among the different species ( $P > 0.05$ ). Leaf mines were observed in *Avicennia* and *Laguncularia*, and were most

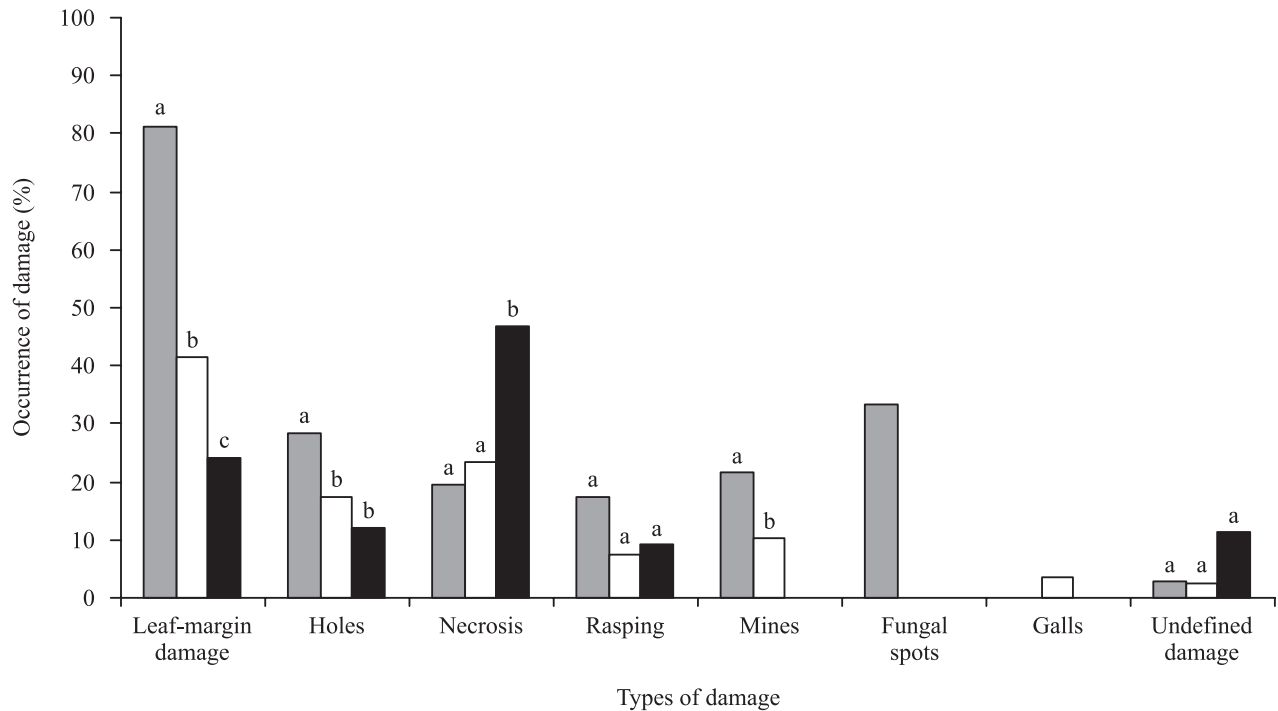


Figure 3. Percentage of the occurrences of each type of damage to *Laguncularia racemosa* (■), *Avicennia schaueriana* (□) and *Rhizophora mangle* (■) in a mangrove swamp at the mouth of the Piraquê River, Sepetiba Bay, Rio de Janeiro State, Brazil. (N = 600). Transformed data: arcsine of the  $\sqrt{\%}$  of the relative area of the damage. Averages followed by the same letters do not differ significantly by the Tukey test at 5%. The comparisons are valid among the species for each types of damage.

expressive in the former, although these differences were not statistically significant ( $P > 0.05$ ). Both rasping and leaf-mining damage have been reported from mangrove swamps in Papua – New Guinea (Johnstone 1981) and Belize (Farnsworth & Ellison 1991).

In general, the greatest levels of leaf damage among the three species studied were observed during the months of May to November (figure 4). *Avicennia* demonstrated greatest damaged in June and July, and less predation in April, while August and March represented the months with the greatest and least rates of damage respectively for *Rhizophora*, although these differences were not statistically significant ( $P > 0.05$ ) in either of the two species. *Laguncularia* demonstrated the greatest total leaf damage in September and October and least damage during the month of February, with these differences being statistically significant ( $P < 0.05$ ).

The differences observed in terms of leaf damage during the different months of the year in the study area were principally due to leaf fall and the subsequent production of new leaves during the rainy season (which occurs between the months of November and January) (Souza *et al.* 2000, Fernandes *et al.* 2005). As such, sampling the third pair of leaves included young leaves –

and consequently leaves that were exposed to agents of damage for much less time.

Little variation was observed in terms of the relative damaged areas among the three species during the course of the study (figure 4). During March, August, September and October the relative damaged areas of *Laguncularia* differed significantly from *Rhizophora*. *Avicennia* differed from *Laguncularia* only during the month of September, but did not differ from *Rhizophora* during the course of the study ( $P < 0.05$ ).

The damage types of galls and fungal spots (as well as their causative agents) were restricted to *Laguncularia* and *Avicennia* respectively in the mangrove area examined, and even the damage types common to all three species studied here demonstrated different intensities among the different taxa – indicating that some species were more susceptible to predator damage than others. Although damage caused by chewing insects (principally lepidopteron) represented almost all of the damage seen in *Laguncularia*, and more than half of that seen in *Avicennia*, chewing damage resulting in the death of leaf tissue was more significant in *Rhizophora*.

The levels of herbivory observed in the present study area can be considered low, even though comparisons

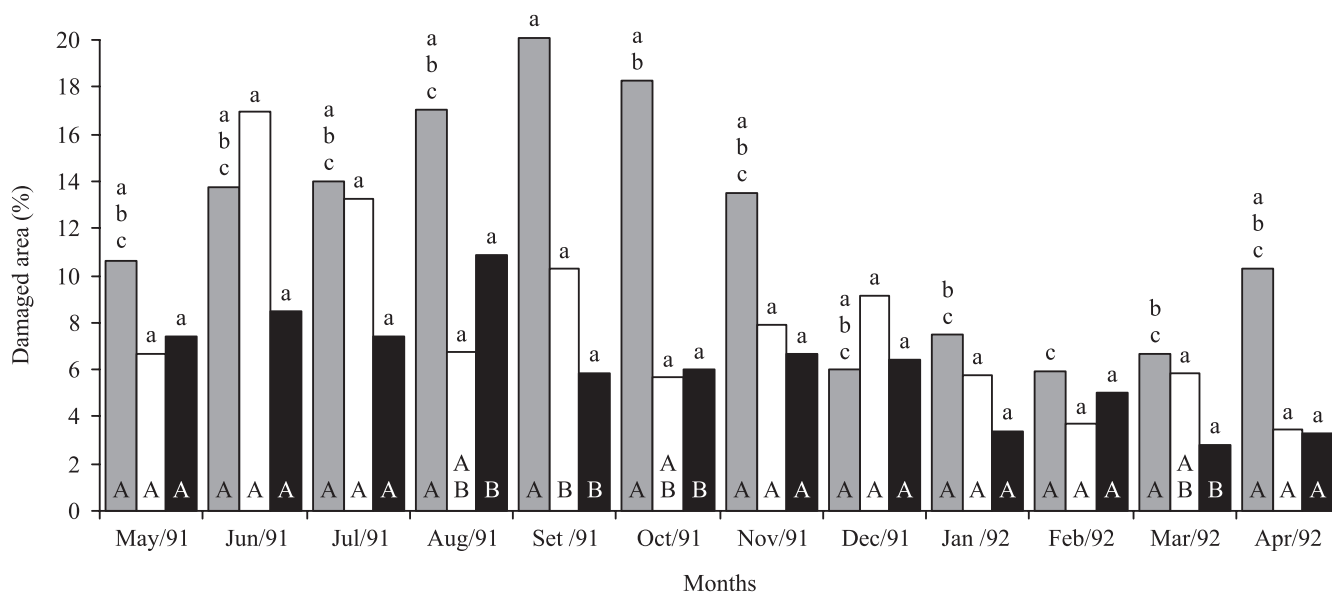


Figure 4. Monthly percentages of the damaged areas of *Laguncularia racemosa* (■), *Avicennia schaueriana* (□) and *Rhizophora mangle* (■) during each month of the year in a mangrove swamp at the mouth of the Piraquê River, Sepetiba Bay, Rio de Janeiro State, Brazil. Transformed data: arcsine of the  $\sqrt{\%}$  of the relative area of the damage. Averages followed by the same letters do not differ significantly by the Tukey test at 5%. Capital letters compare averages between the species for each month. Lower case letters compare the averages of each species between the months.

with other mangrove areas are still incipient, due to the lack of data from many regions and to the fact that reported differences in herbivory rates may only reflect different leaf-sampling methodologies. In order for these comparisons to be more robust, additional long-duration studies are needed that will accompany fluctuations in environmental conditions and herbivore insect populations.

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