

Are *Laguncularia racemosa* galled leaves less attractive to chewing herbivores?

Folhas de *Laguncularia racemosa* com galhas são menos atrativas para herbívoros mastigadores?

Isabela Vieira Santos-Mendonça¹

isabelaic@gmail.com

Julio Marcelino Monteiro²

juliomonteiro@yahoo.com

José Roberto Botelho Souza³

jrbSouza@ufpe.br

Jarcilene Silva Almeida-Cortez^{1*}

cortez_jarcy@yahoo.com

Abstract

Evolutionary interactions between herbivores and plants have resulted in an impressive variety of adaptations, and herbivory pressure has led to the evolution of chemical, mechanical and phenological defense in plants. Coastal mangrove forests provide a very tractable system in which to study the dynamics of herbivory. The objective of this work was to evaluate if galled leaves of the mangrove tree *Laguncularia racemosa* (L.) Gaerten (Combretaceae) are less consumed by chewing insects. Monthly excursions were carried to the Maracaípe Mangrove in Pernambuco, to collect adult leaves from 60 plants of *L. racemosa*: 240 ungalled leaves consumed by chewing insects (CL), 240 galled leaves consumed by chewing insects (CLG) and 240 galled leaves not consumed by chewing herbivores (LG). Other leaves were collected in August, in order to quantify total phenolic concentration: 40 intact leaves of individuals with low rate of infestation by galls (LL) and 40 of individuals with high infestation (HL) were thus collected. CLG displayed a lesser loss of foliar area to chewing herbivores. The results show a significant amount of phenols in HL (35.63 mg) and LG (32.7 mg). This high phenol concentration is probably repelling chewing phytophagous. It is known that herbivores tend to avoid leaves that were previously predated by another herbivore. Possibly galls are influencing the feeding performance of the chewing insects.

Key words: chemical defenses, total phenolic, mangrove.

Resumo

Interações evolutivas entre herbívoros e plantas resultaram numa impressionante variedade de adaptações, e uma pressão de herbivoria levou a evolução de defesas químicas, mecânicas e fenológicas em plantas. Manguezais são sistemas excelentes para estudos da dinâmica de herbivoria. O objetivo deste trabalho foi investigar se há interação entre a galha induzida por ácaro e herbívoros mastigadores em folhas de *Laguncularia racemosa* (Combretaceae). Foram realizadas excursões mensais (Novembro/2004 a Outubro/2005) ao manguezal de Maracaípe (PE), para coletar 240 folhas expandidas de cada categoria: consumidas por mastigadores (CL), consumidas e com galhas (CLG) e apenas galhadas (LG), provenientes de 60 plantas. Para as folhas que apresentavam indícios da atividade alimentar de mastigadores foi mensurada a porcentagem de herbivoria. A fim de testar se

¹ Dept.. Botânica, Programa de Pós-Graduação em Biologia Vegetal, Universidade Federal de Pernambuco, Av. Profº Moraes Rêgo, s/n, Cidade Universitária, 50670-901 Recife PE, Brazil.

² Dept. Biologia/Área de Botânica, Universidade Federal Rural de Pernambuco, Rua Dom Manoel de Medeiros s/n, Dois Irmão, 52171-900 Recife PE, Brazil.

³ Dept. Zoologia, Universidade Federal de Pernambuco, Av. Profº Moraes Rêgo, s/n, Cidade Universitária, 50670-901 Recife PE, Brazil.

* Author for correspondence.

ocorre defesa induzida nas folhas de *L. racemosa* pela presença da galha foram quantificados os compostos fenólicos totais em folhas de cada categoria. Uma coleta de 40 folhas sem galhas foi realizada em indivíduos com baixa infestação (LL) e em indivíduos com alta infestação (HL) para quantificar os fenóis a fim de analisar se a defesa induzida seria sistêmica ou localizada. CLG obteve menor área foliar perdida pelo herbívoro mastigador. Foi registrada uma quantidade maior de fenóis em HL e LG. Uma alta concentração de fenóis provavelmente está repelindo os mastigadores. Sabe-se que herbívoros tendem a evitar folhas previamente herbivoradas, pois podem conter maior concentração de defesas químicas. Possivelmente a galha está influenciando o desempenho alimentar do inseto mastigador.

Palavras-chave: defesa química, compostos fenólicos totais, manguezal.

Introduction

Herbivory in natural communities can be high, decreasing the growth and reproduction rates of individual plants, and influencing competitive outcomes and community composition. Studies of herbivory in terrestrial tropical forests have attempted to identify host plant properties that influence herbivore foraging preference, for example host plant quality and secondary chemistry (Coley, 1983, and references therein). Evolutionary interactions between herbivores and plants have resulted in an impressive variety of adaptations, and herbivory pressure has led to the evolution of chemical, mechanical and phenological defense in plants (Coley, 1983). Chemicals produced by plants may be more important than any other single factor controlling insect behavior in nature (Baldwin and Preston, 1999). Furthermore, plants resistance to herbivory may also be involved with different strategies such as constitutive resistance and induced resistance (Almeida-Cortez, 2005; Kaplan *et al.*, 2008).

Agrawal and Karban (1999) define induced resistance to herbivory as a plant response that leads to a reduction in the performance or preference of an herbivore that feeds on a damaged plant. The same author showed several potential benefits of induced responses to herbivory and the allocation costs seem to be the key factor. Changes in plant secondary metabolites induced by an animal may alter nutritional quality and palatability, increase toxicity and alter anatomy, phenology and physiology of the host plant. These changes may affect other herbivores (Inbar *et al.*, 1995).

The action of two distinct herbivore species over one plants host, according to Straus (1991), can be shown in two ways: (i) one herbivore's presence facilitates the action of the other, in which case this activity set is physiologically more stressful for the plant (additive effect) or (ii) the feeding of a species reduces the performance of the other, either by

interspecific competition, either by unchaining an induced defense in the plant hostess.

The resistance to herbivory is a phenomenon registered in leaves previously attacked by chewing insects as well as in phytophagous mites (Karban and Myers, 1989). Diverse works have dealt with interspecific interaction between a great variety of herbivores, for example: Fritz (1990) studied competition between four different insects forming galls in the same plant hostess (*Salix lasiolepis*); Gómez and González-Megías (2002) analyzed the competitive relation between a vertebrate herbivore, *Capra pyrenaica*, Capridae, and a phytophagous beetle, *Timarcha lugens*, Chrysomelidae in the host plant *Hormathophylla spinosa* (Cruciferae), and Denno *et al.* (2000) studied competition between two chewing insects, *Prokelisia dolus* and *P. marginata* in the plant hostess *Spartina alterniflora*.

Mangroves forests occur in the intertidal region between sea and land in the tropical and sub-tropical latitudes and provide important ecosystem good and services (Tomlinson, 1986). The forests help stabilize shorelines and reduce the devastating impact of natural disasters, such as tsunamis and hurricanes. They also serve as breeding and nursing grounds for marine species, and are sources of food, medicine, fuel, and building materials for local communities. The high productivity rate of these fens, in many places, exceeds 2 t.ha⁻¹.year⁻¹ (Ellison, 2000), and support an entire community of pelagic organisms (Robertson *et al.*, 1992), and dense assemblages of migratory and sedentary birds (Klein *et al.*, 1995). However, the forests have been declining at an alarming rate — perhaps even more rapidly than inland tropical forests — and much of what remains is in a degraded condition. The remaining mangrove forests are under immense pressure from clear cutting, encroachment, hydrological alterations, chemical spills, storms, and climate change.

Mangroves show species-specific differences to gradients in certain physical factors such

as temperature, inundation and salinity (Ball, 1988), water movement (Rabinowitz, 1978; Nickerson and Thibodeau, 1985), nutrients (Feller, 2002), and soil sulfide content (Thibodeau and Nickerson, 1986).

Laguncularia racemosa, white mangrove, is present in the median zone of mangrove forests in America and Occidental Africa (Sobrado, 2004). It has broad, flat oval leaves up to 7 cm long that are rounded at both ends (Schaeffer-Novelli and Cintrón, 1986). Two salt glands are found at the base of each leaf at the apex of the petiole (Medina, 1999), opposing leaves, thick and leathery, oblong or elliptical, with apexes rounded off and margined (Tomlinson, 1986). The leaves of the study species are infested by inducing mite galls (Acari: Eriophyidae, *Brachendus enodis* n. sp.) (Flechtmann *et al.*, 2007). This green gall crossing both leaf faces is characterized by presenting an average size of length and width of 1.5 by 1.0 mm (Santos-Mendonça and Almeida-Cortez, 2007, Figure 1).

We predict that *L. racemosa* galled leaves are less attractive to chewing phytophagous because the galls induce production of secondary metabolites. To test this prediction we addressed three questions: Does the galling damage to *L. racemosa* stimulate the induced responses in its leaves? If so, is induction systemic or localized? If the answer to the first question is positive, then does the induced defense caused by galls in leaves of *L. racemosa* affect free-feeding insects?

Material and methods

Study area

The work was carried through the Maracaípe Mangrove (08°32'24"S; 35°00'27" W), Ipojuca, located on the southern coast of the Pernambuco State, Brazil. The mangrove of the Maracaípe River's estuary is physiographical characterized, according to Cintrón *et al.*

(1985), classification as a fringe forest of fen, as it is developed on the edges of protected coasts, not evidencing strong physic-chemical gradients. The precipitation and the temperature averages of the last five years are 175 mm and 26.7°C respectively, with a dryer period going from September to February, and a rainy season between March and August (ITEP/LAMEPE). The Maracaípe estuary covers an area of 329,532 m², where approximately 19,800 m² corresponds to the area occupied by the *Laguncularia racemosa* species. Figure 2 reports the precipitation and the temperature averages for the study year.

Induced defense test

The phenolic acids, a class of carbon based secondary metabolites, are one of the most widespread defense compounds (Whittaker and Feeny, 1971; Porter *et al.*, 1985; Hagerman and Butler, 1991, Philip *et al.*, 1994), and contain an alcohol group attached to a benzene ring. The total phenolic concentration in leaves of *L. racemosa* were quantified for each of the different categories to verify if galled leaves stimulated the induced responses: (i) 240 ungalled leaves consumed by chewing insects (CL), (ii) 240 galled leaves consumed by chewing insects (CLG), and (iii) 240 galled leaves not consumed by chewing herbivores (LG).

Forty ungalled leaves were collected from plants with low density of galls per leaf (LL) and 40 leaves from plants with high density of galls per leaf (HL) in order to analyze the total phenolic concentration. These analyses were carried out to test if the defense is induction systemic or localized.

Leaves of different categories (CL, CLG, LG, LL and HL) were dried at 40 °C for 3 days. The dried material was pulverized into fine powder using a grinder. For each category, 500 g from each group were extracted with 80% methanol (5 mL). After filtration, methanol was removed under reduced pressure in a rotary evaporator. The extracts were triplicates for each sample type. Triplicates of the samples were analyzed for total phenolic concentration by the Folin-Ciocalteu method (Folin and Ciocalteu, 1927; Mueller-Harvey, 2001; Read *et al.*, 2001; Queiroz *et al.*, 2002). The standard calibration curve was plotted using tannic acid in the following concentrations: 0.1; 0.5; 1.0; 2.5 and 3.75 µg.mL⁻¹, with an adjustment error of R² = 0.9941 and straight y line = 0.0523x + 0.0023. The amount of phenols was expressed in mg of dried leaf.

The total phenolic concentrations among three categories (CL, CLG and LG) and between

ungalled leaves (HL, LL) were analyzed with Chi-Square test (Zar, 1999).

Testing the influence of the galls on the feeding of free-feeding insects

The second and/or third mature leaves, exposed to the sun were collected to test the hypothesis of induced defense affecting free-feeding insects in galled leaves of *L. racemosa*. According to Downum (1992), UV light may affect expression of defenses and so it is necessary to standardize samples.

Leaves of *L. racemosa* were collected monthly from November 2004 to October 2005. Each month 240 leaves were collected according to the categories: CL, CLG and LG. Damages by chewing herbivores were measured with UTHSCSA IMAGETOOL 3.0, calculating values for remaining and consumed portions. The total lost area was measured according to Schaeffer-Novelli and Cintrón's methodology (1986), which consists of reconstituting the area consumed by chewing herbivore. In galled leaves, the total number of galls for each leaf was recorded. The Percentage lost leaf area was submitted to variance analysis, using the

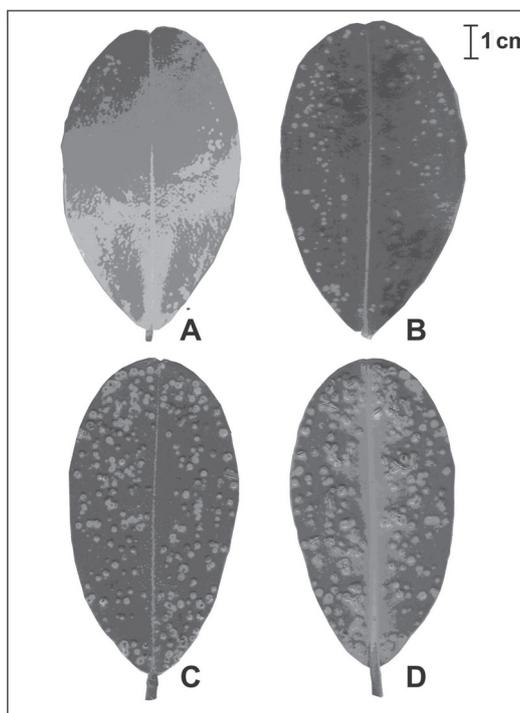


Figure 1. Galled leaves of *Laguncularia racemosa*. **A.** Young leaf with young galls. **B.** Mature leaf bearing older galls; **C.** Adaxial leaf blade with gall; **D.** Abaxial leaf blade with gall.

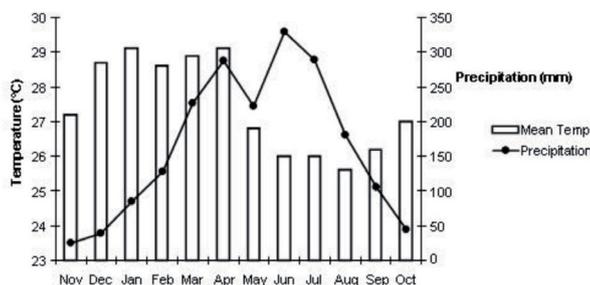


Figure 2. Precipitation and temperature average of each study area during the rainy and dry season (2004/2005) in each plot into the Maracaípe mangrove, Pernambuco.

square root arc sen transformation. The number of galls between LG and CLG was analyzed by ANOVA followed by Tukey's post-hoc test (Zar, 1999).

Results

Induced defense test

The total phenol concentrations for each analyzed leaf category of *Laguncularia racemosa* differed significantly among them ($\chi^2_{(2; 0.01)} = 34.26$). The leaves displaying mite induced galls (LG) had the highest concentration and were significantly different from leaves consumed by chewing herbivores (CL) and leaves with galls and chewing herbivores (CLG) (Tab. 1). When analyzing leaves from plants with different density of galls, we observed that ungalled leaves from plants with high density of galls (HL) presented a significant higher total phenolic concentration (35.63 ± 0.44 mg) than leaves belonging to low density of galls (14.09 ± 0.38 mg) ($\chi^2_{(1; 0.01)} = 9.33$). The LG and HL presented similar phenol concentrations.

Testing the influence of galls on the feeding of free-feeding insects

The chewing insect observed is a species of grasshopper (Orthoptera) and an unidentified caterpillar (Lepidoptera). These herbivores mainly feed on young *L. racemosa* leaves. The herbivory percentage was significantly higher ($F_{(1, 5258)} = 32.611, p < 0.0001$) in the CL when compared to the CLG, with significant differences throughout the year ($F_{(10, 5258)} = 16.726, p < 0.0001$; Figure 3), but without a clear pattern. The number of galls found in the LG was significantly higher than the number found in CLG ($F_{(1, 5245)} = 373.86, p < 0.0001$). This difference was significant in the most part of the year (Tukey, Figure 4).

Discussion

Data gathered from total phenolic concentration point out the likelihood that the presence of galls induces defenses, as can be seen from Table 1. Leaves with *Brachendus enodis* galls (Flechtmann *et al.*, 2007) had the highest concentration of total phenolic concentration. Several studies have demonstrated that phenolic acids levels are inducible in some species (Karban and Baldwin, 1997). For example, poplar trees have been shown to

induce phenolics in response to leaf damage (Baldwin and Schultz, 1983). The first studies with host plant and galling insects suggested that phenolics were produced by plants as a defense mechanism against them (Tjia and Houston, 1975; Westphal *et al.*, 1981). Abrahamson *et al.* (1991) demonstrated that host phenolic concentrations are not associated with plant resistance against galling insects. Some authors suggest that the increase in concentration could be caused by the presence of gallic acid, phenolic compounds frequently found in association with galls' tissues (Motta

et al., 2005; Cornelissen and Fernandes, 2001b). Otherwise, the high concentration of total phenolic acids seen in ungalled leaves that were taken from individuals displaying high density of galls (HL) when compared to ungalled leaves harvested from plants bearing a low number of galled leaves is a strong evidence of an induced defense in *L. racemosa* plants. Our data corroborated to the work of Pascual-Alvarado *et al.* (2008) that studied the interactions between galling insects and leaf-feeding insects. This research found that the concentration of phenolics was greater in

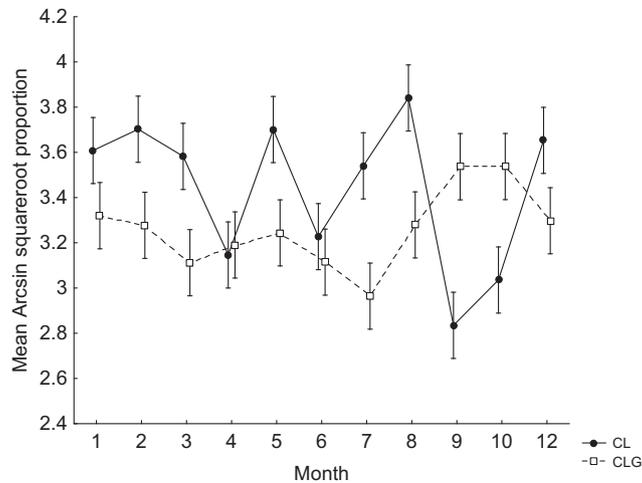


Figure 3. Percentage lost leaf area (arcsin squareroot transformed) of *Laguncularia racemosa*: consumed leaf (CL) and consumed leaf and with galls (CLG), n = 240 leaves per month, during one year of observation (2004/2005) at Maracaípe mangrove, Pernambuco (G test contingency table monthly). Vertical bars denote 0.95 confidence intervals.

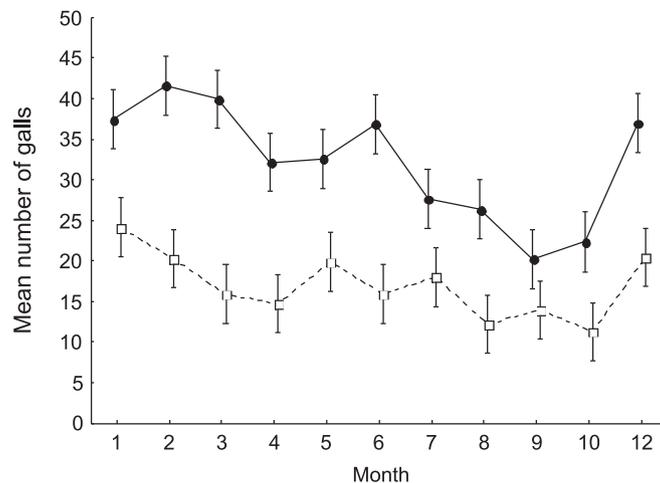


Figure 4. Galls' means observed in leaves of *Laguncularia racemosa*: (LG) with galls (●) and (CLG) leaves consumed and with galls (□) during twelve months of observation (2004/2005) at Maracaípe mangrove, Pernambuco. Vertical bars denote 0.95 confidence intervals.

galled than ungalled leaves in five species of plant (*Achatocarpus gracilis*, *Cordia alliodora*, *Guapira macrocarpa*, *Guettarda elliptica* and *Ruprechtia fusca*) that occur in both hillside and riparian sites at Chamela-Cuixmala tropical dry forest in western Mexico.

This is the first attempt to study induced chemical defenses in *L. racemosa* using the total phenols quantification from its leaves. Total phenolic acids served as a good marker of induced defenses due to galls' infestation in leaves of the host-plants in the Maracaípe Mangrove.

When analyzing if the induction is systemic or localized, we observed that *L. racemosa* defenses induced by acari galls are probably systemic due to the larger concentration levels obtained for HL, thus demonstrating that healthy leaves already had a high total phenolics concentration.

The fact that the herbivory percentage was significantly higher for CL when compared to CLG, suggests that galled leaves may be less attractive to the free-feeding insects. Cornellisen and Fernandes (2001a) suggest that herbivores tend to avoid leaves already damaged by the action of other phytophagous, due to the possible presence of a larger chemical composites' concentration. Westphal *et al.* (1992) demonstrated that gall induction by *Aceria cladophthirus* mites induced resistance to subsequent attack by *A. cladophthirus* as well as by the rust mite, *Thamnacus solani*. However, Agrawal and Karban (1999) demonstrated that plants infested with galling mites may become more susceptible to other herbivores. Westphal *et al.* (1992) found leaves of *S. dulcamara* damaged by galling mites more susceptible to the generalist Two-Spotted Spider Mite, *Tetranychus urticae*. Moreover, our results contrasted with those: the total number of galls quantified in each month was bigger in LG than in CLG and in several months it was significantly higher. This probably happened because the leaves with less gall densities may contain less secondary metabolites, suggesting that galls induce plants to produce secondary metabolites

Several studies pointed out the existence of induced defense in plants as an answer to herbivory (Wool and Hales, 1996; Agrawal and Sherriffs, 2001) and this mechanism affects negatively the feeding habits of other phytophagous (Inbar *et al.*, 1999; Denno *et al.*, 2000). For example, Inbar *et al.* (1999) studied the response type of *Lycopersicon esculentum* (tomato), in relation to the interspecific interaction of two herbivores: *Bemisia argentifolli* (Homoptera) and

Table 1. Total phenolic acids concentration of adult leaves of *L. racemosa*: leaves consumed by chewing insects without galls (CL), leaves consumed with galls (CLG) and galled leaves (LG). Maracaípe Mangrove, Pernambuco.

Leaves	Total phenolic acids concentration (mg)	%
LG	32.7 ± 0,55	6.54 ± 0
CL	7.4 ± 0,5	1.48 ± 0
CLG	3.64 ± 0,39	0.79 ± 0

Liriomiza trifolli (Diptera), and he concluded that the leaves previously consumed by *B. argentifolli* (teething ring) were avoided by the leaf miner (*L. trifolli*). Other experiments have positively correlated the phenolic acids concentration with gall infestation (Motta *et al.*, 2005; Cornelissen and Fernandes, 2001b) and negatively correlated the intensity of herbivory for chewing phytophagous (Furlan *et al.*, 2004). Most studies of feeding-induced changes by one species and their future consequences for other herbivores have been conducted using chewing phytophagous (Tallamy and Raupp, 1991).

Few studies have evaluated the effects of gall induction on host defensive chemical compounds and the subsequent effects of these changes on the incidence of folivorous insects (Pascual-Alvarado *et al.*, 2008). While studying the interspecific interaction between the host *L. racemosa* and mite leaf-gall, we concluded that we are probably facing a competition between this gall and the phytophagous insects. We are able to infer that during the observed period we verified an inverse correlation for the presence of galls and leaf removal by chewers. Total phenolic compounds served as a good marker for induced defense in *L. racemosa*, since individuals hosting high gall infestation levels displayed healthy leaves with high concentrations of phenolic compounds. In this case, galling insects decrease of folivorous and consequently the consumed leaf area.

Acknowledgements

Thanks to Claudio Vinicios V. Magalhães and two anonymous readers for reviewing the manuscript.

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Submitted on October 13, 2008.

Accepted on May 14, 2009.