



PLANT ARCHITECTURE AND GALL ABUNDANCE ON TWO PLANT SPECIES FROM RESTINGA, RJ, BRAZIL

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Abstract: Several hypotheses have been proposed to explain the distribution pattern and abundance of herbivorous insects on its host plants. For example, the plant architecture hypothesis predicts that variation in host plant architecture influences insect herbivore community structure, dynamics and performance. This study aimed to test the plant architecture hypothesis and its relation with gall abundance on two Brazilian endemic plant species, *Clusia lanceolata* (Clusiaceae) and *Monteverdia obtusifolia* (Celastraceae) in Maricá Restinga, Rio de Janeiro. Plant architecture and gall abundance were directly recorded on 30 individuals from each plant species. Plant height, soil height circumference, number of second and third level ramifications, treetop area, plant volume, and leaf number were all used as predicting variables of gall abundance. A total of 922 insect galls were registered on *C. lanceolata* and 1.139 on *M. obtusifolia*. Variations on plant architecture did not explain gall abundance for both plant species. Results can be explained the plastic potential of the species studied. In this sense, the morphological changes in *C. lanceolata* and *M. obtusifolia* caused by the galls may have been buffered to maintain the vigor of the species. The difference between the variables in relation to gall abundance indicates that species studied can tolerate and minimize the presence of galling insects, revealing a high capacity for homeostasis in the face of biotic stress.

Keywords: gall inducing insects; super-host; architectural complexity; Atlantic Forest.

INTRODUCTION

Insect galls are structures formed by cellular multiplication (hiperplasia) and/or an increase in cellular size (hypertrophy). They are known for providing shelter and food to their inductors. A few studies focusing on gall induction have already demonstrated that the insect is responsible for determining the gall morphology, not the plant, moreover, these inductors can redirect the nutritional tissue production for their own benefit (Cook & Gullan 2008). Galling insects are considered one of the most specialized herbivores, showing high specificity of host plant species and plant organ (Carneiro *et al.* 2009). Galls encompass

an important element in identifying ecological patterns and processes since they constitute units, delimited in time and space, they are easily sampled and have species-specific relation with their host plant (Fernandes *et al.* 1996, Price *et al.* 1998, Stone & Schönrogge 2003, Fagundes *et al.* 2005).

Plant selection by insect herbivores encompasses choices regarding the plant's physical and chemical characteristics that ultimately influence insect population dynamics and community organization. It has been long recognized that plant traits influence herbivore dynamics, distribution and abundance and intra-specific variation in plant size; chemistry and

appearance can have profound effects on herbivore selection and herbivory levels experienced by host plants (Price 1997, Cornelissen & Stiling 2008).

Sessile and host-specific herbivores, such as gall-inducing insects, are usually patchily distributed within the populations of their host plants, and it has been suggested that both bottom-up and top-down effects explain variations in gall abundance (Araújo *et al.* 2006, Barbosa & Fernandes 2014), distribution (Lara *et al.* 2008; Bergamini *et al.* 2017) and survivorship (Hosaka *et al.* 2009). Given the specific features of insect–plant interactions, a number of hypotheses have been proposed to account for the patterns of distribution and abundance of gall morphotypes, and of insects that induce these galls on their respective plant hosts (Fleck & Fonseca 2007).

Plant architecture hypothesis predicts greater richness and abundance of insect galls on plants with greater structural complexity, i.e., larger plants with more branches represent greater resource availability (Lawton 1983); greater visibility and number of oviposition sites (Fernandes & Price 1988); and lower risk of attack by parasitoids (Collevatti & Sperber 1997). Plant architecture may be defined as plant biomass, presence/absence and number of leaves, plant height, shoot diameter, shoot and flower density, and ramification level (Denno & Roderick 1991, Haysom & Coulson 1998, Price *et al.* 1998).

The plant architecture is usually a relevant factor influencing the abundance and distribution of herbivores. However, the determinant traits of the plant may vary among studies depending on the life history of the species involved (Espírito-Santo *et al.* 2007). As a result of the sessile habit, galling insects depend upon young undifferentiated tissue availability for the induction and development of the galls (Mani 1964, Rohfritsch 1992). Therefore, plant architectural traits may have stronger effects upon gall insects when compared to free-living insects, which can leave the plant at any time.

Several studies on endophyllous herbivores have identified a positive relationship between richness and abundance of gall inducing insects and the structural complexity of the plant host (Lara *et al.* 2008, Araújo & Santos 2009, Gonçalves-Alvim *et al.* 2010). However, other studies have pointed out that structural complexity does not significantly affect the distribution of such group

of herbivores, especially in forest environments (Price *et al.* 1998, Miller & Weis 1999, Lara *et al.* 2002, McGeoch & Price 2004, Costa *et al.* 2010).

In this context, the main goal of this study is to test the plant architectural hypothesis and its relation with gall abundance on two plant species endemic to Brazil, in Maricá Restinga, Rio de Janeiro. Thus, we expect that gall abundance may be positively related to plant architecture, as predicted by the Plant Architecture Hypothesis. This is the first study approaching plant architecture and gall abundance in a Restinga environment in Brazil.

MATERIALS AND METHODS

Study area

The field research was accomplished in August 2017 in the Área de Proteção Ambiental de Maricá (22°57'42"S/ 42°51'54"W), a protected area located in Maricá municipality, Rio de Janeiro, southeast Brazil with a total area of 8.3 km² (Figure 1). The area comprises about 800 hectares of Restinga vegetation, including 379 plant species and nearly 100 species of galling insects (Silva & Oliveira 1989, Maia 2001, Silva 2011).

The climate of the Maricá region was classified by Nimer (1972) as warm, super humid, with sub-tropical. Meteorological data come from the municipality of Niterói (National Department of Meteorology, period 1931-1968), with the average annual temperature being 23.2 °C, the average of the warmest month (February) 32.2 °C and the minimum from the coldest month (July) 15.1 °C. The average annual rainfall is 1.230 mm, with 69.2 % occurring from November to April.

Analyzed species

Clusia lanceolata Cambess. and *Monteverdia obtusifolia* (Mart.) Biral are perennial shrubs or small trees with great frequency and abundance in the study area (Maia 2001). *Clusia lanceolata* (Figure 2a) hosts two gall morphotypes, both on leaves, one induced by an unidentified Lepidoptera species, rare and occurring in low abundance (Maia 2013); the other induced by *Clusiamyia nitida* Maia 1996 (Diptera, Cecidomyiidae), which is very abundant, common and occurs throughout the year (Figure 2b) (Maia 2001). *Monteverdia obtusifolia* (Figure 2c) hosts two gall morphotypes,

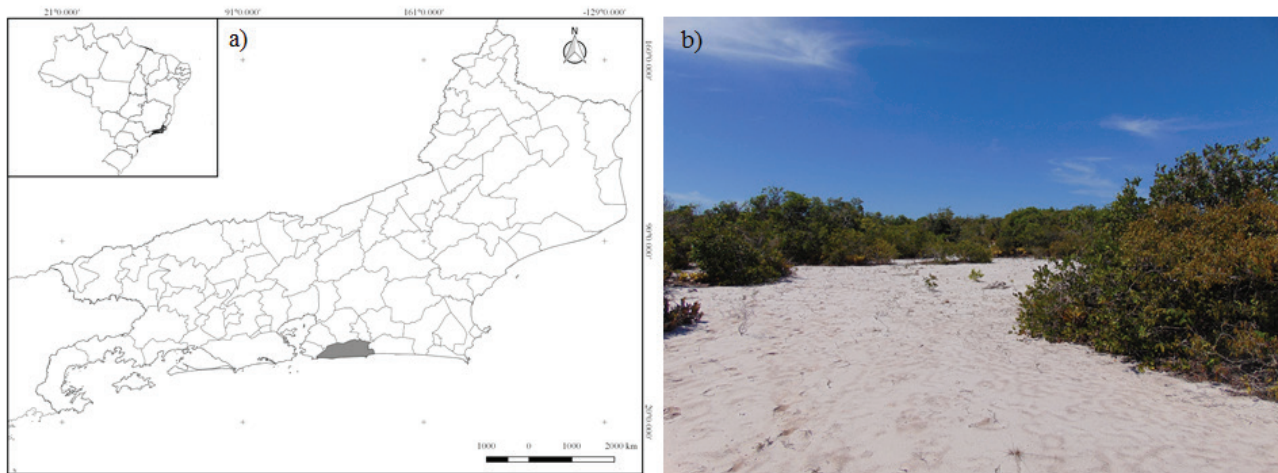


Figure 1. (a) Maricá municipality, Rio de Janeiro, Southeast Brazil. (b) Area of study: Área Protegida Ambiental de Maricá.



Figure 2. Plants and galling insect species. (a) *Clusia lanceolata* Cambess., (b) *Clusiamyia nitida* Maia, 1996, (c) *Monteverdia obtusifolia* (Mart.) Biral, (d) *Mayteniella distincta* Maia, 2001.

one on fruits induced by *Bruggmanniella maytenuse* Maia & Couri 1992 and the other on leaves induced by *Mayteniella distincta* Maia 2001 (Figure 2d), the first is very rare, while the second is common and abundant (Maia 2001). Both galls are induced by the Cecidomyiidae (Diptera) mosquito family.

Experimental design

During the months of September and November 2017, 30 individuals of each plant species were randomly selected in the studied area. For each individual the following parameters were measured: height, CAS (soil height circumference), number of second and third level ramifications, treetop area, plant volume and number of leaves from 10 terminal branches (Espírito-Santo *et al.* 2007). Plant volume was measured through the cone volume formula:

$$V = [(\pi \cdot r^2 \cdot h) / 3]$$

, and the treetop area through the ellipse area:

$$A = (\pi \cdot a \cdot b / 4)$$

, where “a” and “b” are the larger and smaller widths respectively (Cintrón & Schaeffer-Novelli 1984). The abundance of each gall morphotype was determined through its direct counting in 10 terminal branches from each treetop plant, totaling 300 branches per species.

Statistical analyzes

To test the relationship of gall abundance (y-variables) with plant architecture (x-variables), data were fitted into generalized linear models analysis (GLM) with Poisson error corrected for overdispersion. Since this model was overdispersed, we used a negative binomial distribution family, a commonly used distribution for such cases (Hilbe 2011). Given that the number of ramifications of second and third level, height, volume and treetop variables were too correlated (> 90 %), we included in the model only the height, number of second level ramifications and treetop. The analyses were followed by residual inspection to test for the suitability of the models and error distribution, and were carried out using the procedure ‘glm’ in software R (R Development Core Team 2006).

RESULTS

For *C. lanceolata* individuals, 922 galls were registered on 2496 leaves with an average of 31 galls per individual, varying from 1 to 73. Plant height varied from 0.6 to 4.9 m (2.06 ± 1 / mean \pm standard deviation), CAS varied from 0.05 to 0.6 m (0.15 ± 0.14), number of ramifications: second level from 1 to 8 (4 ± 1.94) and third level from 3 to 15 (6 ± 2.69), treetop from 0.06 to 2.01 m² (0.52 ± 0.49), volume from 0.26 to 41.68 m³ (8.07 ± 11.27) and leaf number varied from 40 to 175 (83.2 ± 26.44) per plant.

For *M. obtusifolia*, 1139 galls were registered on 3010 leaves with an average of 38 galls per individual, varying from 0 to 254. Five plants were registered without galls. Plant height varied from 0.9 to 4.44 m (2.24 ± 0.97), CAS from 0.06 to 0.33 m (0.16 ± 0.09), the number of ramifications varied: second level from 1 to 6 (4 ± 1.5) and third level from 2 to 12 (6 ± 2.46), treetop from 0.04 to 1.73 m² (0.5 ± 0.42), volume from 0.27 to 41.01 m³ (7.71 ± 9.24) and the number of leaves varied from 64 to 154 (100.3 ± 24.6) per plant.

The variables did not explain the gall abundance for both studied species (Table 1). Thus, the number of galls did not respond to the increase of height, soil height circumference, treetop area and volume, that is, plant size. In this same way, the complexity characterized by the presence of secondary and tertiary branches and leaf number, did not influence the abundance of the insects.

DISCUSSION

In the present study, variables did not explain gall abundance on both studied species. One possible explanation concerns the plastic potential of the species studied. Phenotypic plasticity is the ability of an organism to change its physiology or morphology in response to an unstable and heterogeneous environment as a way of maintaining vigor (Debat & David 2001). Lomônaco and Germanos (2001) points out that biotic factors are also involved in the mechanisms underlying phenotypic plasticity. In this sense, the morphological changes in *C. lanceolata* and *M. obtusifolia* caused by the galls may have been buffered to maintain the vigor of the species (Alves-Silva 2012). The difference between

Table 1. Relation between architectural variations and gall abundance on both plant species studied in Maricá, RJ, Brazil.

Variance	<i>Clusia lanceolata</i>				<i>Monteverdia obtusifolia</i>			
	estimate	standard error	z	p	estimate	standard error	z	p
Intercept	-0.935	0.306	-3.058	0.002	-19.716	0.645	-3.057	0.002
Height	-0.022	0.134	-0.16	0.871	0.378	0.265	1.427	0.153
Intercept	-12.007	0.281	-4.266	0.001	-20.080	0.673	-2.983	0.003
Second level	0.059	0.068	0.862	0.389	0.243	0.171	1.416	0.156
Intercept	-10.628	0.193	-5.513	0.003	-11.059	0.410	-2.696	0.007
Treetop	0.157	0.272	0.575	0.565	0.089	0.629	0.143	0.886

the variables in relation to gall abundance indicates that *C. lanceolata* and *M. obtusifolia* can tolerate and minimize the presence of galling insects, revealing a high capacity for homeostasis in the face of biotic stress.

Costa *et al.* (2010) also did not observe significant relation between gall diversity associated to *Copaifera langsdorffii* Desf. (Fabaceae) and the size or ramification pattern of the host plant. The authors invoked the predictability of the resource and galling specificity to support the results. In fact, if a single tree supports most of the galling insects due to resource predictability and the galling specialist habit, it would be expected that plant architecture could explain very little of the total variation. McGeoch and Price (2004) demonstrated evidence that the vigor of the *Baccharis pilularis* plant (Asteraceae) is not a determining factor for colonization of the galling insect *Rhopalomyia californica* (Ceccidomyiidae). Miller and Weis (1999) also found no evidence in favor of the hypothesis since the condition (vigor) of individuals of the host species *Salix lasiolepis* (Saliaceae) did not alter the susceptibility to galling hymenoptera (Tenthredinidae) attack.

Other studies showed that plant architecture has partially influenced gall richness and abundance (Lara *et al.* 2008, Costa *et al.* 2010, Silva *et al.* 2017). Lara *et al.* (2008) partially corroborated the plant architecture hypothesis finding correlation between number of galls and number of branches and biomass, but not with number of sprouts and leaves of the host plant *Macairea radula* DC. (Melastomataceae). However, there are some studies where a positive relation between the increase of host plant complexity and the galling

insect diversity was found (Alonso & Herrera 1996, Marquis *et al.* 2002, Espírito-Santo *et al.* 2007, Woodcock *et al.* 2007, Araujo & Santos 2009, Silva *et al.* 2017).

Silva *et al.* (2017) have shown that the plant structural complexity has a significant influence on the number of galls on *Avicennia germinans* L. (Acanthaceae). Araújo and Santos (2009) observed a strong relation between height, leaf number and gall number per individual. According to these authors, plant size is synonymous of resource availability, because the larger the plant and its structural complexity, the higher is the number of insects that it may host.

Araújo *et al.* (2006) showed that plant architecture has also positively influenced richness, abundance and survival of galls induced on *Baccharis pseudomyriocephala* Teodoro (Asteraceae) shrubs. Similar results were found for other species of the *Baccharis* (Espírito-Santo *et al.* 2007) genus. Vrcibradic *et al.* (2000) confirm as a strategy of galling insect reproduction, the oviposition on plants with greater number of leaves. These authors also mention that such strategy lowers the risk of attacks by natural enemies and parasitoids. Plants with greater number of leaves offer more oviposition site availability and as a consequence, suffer with more galling attacks (Collevatti & Sperber 1997).

Other host plant characteristics, such as the nutritional quality, may also influence the settling and colonization success of gall-inducing insects. Gall-inducing insect communities might also respond to host plant phenology, which may induce seasonal changes in nutritional quality (Yukawa 2000). According to Basset & Burckhardt (1992), the abundance of gallers related to a host species

depends more on its chemical characteristics than on its structural complexity, which is plausible given the degree of specialization of this group. We believe that these issues should be considered in future studies regarding the subject (Araújo & Santos 2008).

ACKNOWLEDGEMENTS

To CNPq (Proc. 301481/2017-2) for the financial support, to Dr. Marco A. A. Carneiro for the AID with statistical analysis, and to Dra. Gabriela Thomaz da Silva for revision the English version.

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Submitted: 25 June 2019

Accepted: 27 March 2020

Published on line: 05 April 2020

Associate Editor: Pedro Villa