

Relationships between host plant architecture and gall abundance and survival

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ABSTRACT. Relationships between host plant architecture and gall abundance and survival. The plant architecture hypothesis predicts that variation in host plant architecture influences insect herbivore community structure, dynamics and performance. In this study we evaluated the effects of *Macaírea radula* (Melastomataceae) architecture on the abundance of galls induced by a moth (Lepidoptera: Gelechiidae). Plant architecture and gall abundance were directly recorded on 58 arbitrarily chosen *M. radula* host plants in the rainy season of 2006 in an area of Cerrado vegetation, southeastern Brazil. Plant height, dry biomass, number of branches, number of shoots and leaf abundance were used as predicting variables of gall abundance and larval survival. Gall abundance correlated positively with host plant biomass and branch number. Otherwise, no correlation ($p > 0.05$) was found between gall abundance with shoot number or with the number of leaves/plant. From a total of 124 galls analyzed, 67.7% survived, 14.5% were attacked by parasitoids, while 17.7% died due to unknown causes. Larvae that survived or were parasitized were not influenced by architectural complexity of the host plant. Our results partially corroborate the plant architecture hypothesis, but since parasitism was not related to plant architecture it is argued that bottom-up effects may be more important than top-down effects in controlling the population dynamics of the galling lepidopteran. Because galling insects often decrease plant fitness, the potential of galling insects in selecting for less architectural complex plants is discussed.

KEYWORDS. Cerrado; insect galls; plant size; structural complexity.

RESUMO. Correlação entre a arquitetura da planta hospedeira e a abundância e sobrevivência de um inseto galhador. A hipótese da arquitetura de planta prediz que variações na arquitetura da planta hospedeira influenciam a comunidade de insetos herbívoros, sua dinâmica e performance. Neste estudo o efeito da arquitetura de *Macaírea radula* (Melastomataceae) na abundância de galhas induzidas por uma mariposa (Lepidoptera: Gelechiidae) foi avaliado. A arquitetura da planta e a abundância de galhas foram diretamente registradas em 58 indivíduos de *M. radula* arbitrariamente selecionados durante a estação chuvosa de 2006 em uma área de Cerrado no sudeste brasileiro. A altura da planta, biomassa seca, número de ramos e abundância de galhas foram utilizados como variáveis para prever a abundância de galhas e sobrevivência das larvas. A abundância das galhas foi positivamente correlacionada com a biomassa seca e o número de ramos secundários. Por outro lado, nenhuma correlação ($p > 0.05$) foi encontrada entre a abundância de galhas e ramos terciários e número de folhas por planta. De um total de 124 galhas analisadas, 67,7% sobreviveram, 14,5% foram parasitadas e 17,7% morreram por causas indeterminadas. No entanto, o parasitismo e sobrevivência das larvas não foram influenciados pela complexidade arquitetônica da planta hospedeira. Os resultados corroboram parcialmente a hipótese de arquitetura da planta, mas como o parasitismo não foi relacionado com a arquitetura da planta, os efeitos reguladores de níveis inferiores da cadeia alimentar possivelmente são mais importantes do que os efeitos de níveis superiores da cadeia alimentar na dinâmica populacional do galhador.

PALAVRAS-CHAVE. Cerrado; complexidade estrutural; galhas de insetos; tamanho de planta.

The preference for host plant species, individuals within a species, or traits of host plants, can influence the performance, distribution and abundance of insect herbivores and many trends have been reported worldwide. Not surprisingly, several hypotheses have been proposed to understand the described patterns of attack by herbivorous insects at several ecological scales. The “plant architecture hypothesis” states that the physical structure of the aerial parts of the host plant influences the community structure of herbivorous insects (Lawton 1983; Strong *et al.* 1984; Araújo *et al.* 2006). The plant architecture

encompasses plant size, growth form, variety of above-ground parts and persistence of these parts (Lawton 1983). A pattern of increased insect herbivore species richness and/or abundance with architecture host plant has been supported by several studies (e.g., Lawton 1983; Strong *et al.* 1984; Alonso & Herrera 1996; Haysom & Coulson 1998; Marquis *et al.* 2002; Rudgers & Whitney 2006; Woodcock *et al.* 2007). The mechanisms driving the reported pattern are argued to be i) the increase in size *per se*; ii) increase in resource diversity that provide herbivores with greater amount and diversity of

resources offered by high architectural complex plants; iii) lower herbivore mortality because larger plants provide enemy-free space (Jeffries & Lawton 1984); and/or reduced searching efficiency of parasitoids (Gingras *et al.* 2002; Riihimäki *et al.* 2006).

Based on a broad scale study, Espirito-Santo *et al.* (2007) stressed that plant architecture is usually a relevant factor influencing herbivore distribution and abundance, but that the determinant plant traits may vary between studies depending on the life history of the species involved. Indeed, the responses of gall-inducing insects to plant architecture is highly variable. As a result of their sessile habit, gall-inducing insects rely on the availability of young, undifferentiated tissue for gall induction and development (Mani 1964; Weis *et al.* 1988; Rohfritsch 1992). Therefore, plant architectural traits should have stronger effects on this guild when compared to free-feeding herbivores, which are allowed to leave the plant. Gall-forming sawfly species richness does not increase with plant height, and are richer on shrubs than on trees, independently on the geographic range of the host plant (Price *et al.* 1998). Moreover, gall-forming species richness is higher on woody than on herbaceous plants, but do not differ between shrubs and trees (Fernandes & Price 1988; Gonçalves-Alvim & Fernandes 2001; Lara *et al.* 2002). At the species level, Araújo *et al.* (2006) found that plant architecture positively influenced richness, abundance and survival of galls induced on the shrub *Baccharis pseudomyriocephala* Teodoro, while a similar result was obtained for several other *Baccharis* species (Espirito-Santo *et al.* 2007). Since no conclusions can yet be drawn at this moment on whether gall-forming insects positively respond to increase in plant architecture complexity, new studies are required to verify whether this hypothesis holds for different phylogenetically unrelated species. Therefore, the goal of this study was to test the hypothesis that gall abundance and larval survival increase with plant size and architectural complexity of the host *Macairea radula*.

METHODS

This study was conducted in the rainy season of 2006 in a 20-ha area of Cerrado vegetation in Dolores do Indaia (19° 27' 16.4" S; 45° 36' 09.5" W), Minas Gerais, southeastern Brazil at 716m a.s.l. The vegetation is characterized by scattered and sclerophyllous shrubs occurring among a well-developed herbaceous layer dominated by grasses and sedges. The climate is seasonal with rainy summers and dry winters. Mean annual temperature is 22°C and precipitation is 1.300mm.

Macairea radula DC. (Melastomataceae) is an evergreen shrub commonly found along the borders of gallery forests, but also occurs away from watercourses in the vegetation of Cerrado in southeastern Brazil (Gonçalves-Alvim *et al.* 1999). This species bears a conspicuous gall induced by an unidentified microlepidopteran (Lepidoptera, Gelechiidae) on the leaf axillary buds. Galls are spherical and covered by long green trichomes that become orange-reddish as gall matures. These authors also observed that galls are more abundant on

hosts in xeric habitats when compared to mesic ones. Moreover, number of leaves, inflorescence length, dry shoot biomass and length were significantly smaller on galled than on ungalled shoots, suggesting that galls decrease host fitness (Gonçalves-Alvim *et al.* 1999). Galls are large and conspicuous facilitating their counting and evaluation of their survival on hosts differing in architectural complexity.

Plant architecture and gall abundance were directly recorded on 58 arbitrarily chosen *M. radula* host plants in the field. The host plants were cut at soil level, placed in labeled plastic bags and then taken to the laboratory for measurements. Second-order branches were branches emerging from the trunk while shoots represented branches emerging from second-order branches. The total number of expanding leaves was recorded on all individuals. Number of second-order branches, shoots and leaves were used to evaluate *M. radula* architecture complexity, while plant biomass (weight of above-ground plant parts) and plant height indicated plant size (Araújo *et al.* 2006). After the removal of all lepidopteran galls, plants were dried in an oven at 70°C for seven consecutive days until they reached constant weight.

All galls were dissected in order to determine larvae survival. Mortality factors were classified into predation, parasitism, pathogens, and undetermined factors, following Fernandes & Price (1992).

All analyses were carried out using the procedure 'glm' in R_{2.4.0} (R Development Core Team 2006). To test the relationship of gall abundance (y-variables) with architectural complexity and plant size (x-variables), data were fitted into a multiple regression analysis with Poisson error corrected for overdispersion. The relationship between gall-inducing larvae survival and plant architecture were tested through regression analysis with binomial error corrected for overdispersion. In order to adjust for overdispersion a F test was used instead of a chi square test (Tjur 1998, Crawley 2002, Faraway 2006). The response variable was the proportion of surviving larvae and total number of galls, and the explanatory variables were the architectural complexity and plant biomass (x variables). A regression model with binomial error was used to test for the response of the proportion of parasitized / total galls per plant. Complete models were fitted and then simplified by removing non-significant variables in turn, and verifying the effect of removal on the deviance (Crawley 2002, Araújo *et al.* 2006). The analyses were followed by residual inspection to test for the suitability of the models and error distribution.

RESULTS

A significant relationship between architectural complexity of the host plant and gall abundance was observed (Fig. 1). Gall abundance was positively correlated with plant biomass ($F = 8.897$; $P = 0.004$) and with the number of branches ($F = 5.025$; $P = 0.03$). However, no correlation was found between number of galls with shoot number ($F = 3.154$; $P = 0.08$) or with the number of leaves of the host plant ($F = 2.359$; $P = 0.13$).

From a total of 124 analyzed galls, 67.7% survived, 14.5%

were attacked by parasitoids, while the remaining 17.5% died due to unknown factors. The number of surviving larvae did not vary statistically with architectural complexity of the host plant. The number of surviving larvae was not influenced by plant biomass ($F = 1.248$; $P = 0.27$), number of leaves ($F = 2.854$; $P = 0.10$), number of branches ($F = 0.0180$; $P = 0.90$), or by shoot number ($F = 0.78$; $P = 0.38$). Lack of correlation between parasitized larvae and plant biomass ($F = 0.297$; $P = 0.59$), number of leaves ($F = 1.190$; $P = 0.28$), number of branches ($F = 0.135$; $P = 0.71$), and shoot number ($F = 0.006$; $P = 0.94$) was also observed.

DISCUSSION

Gall abundance increased with increasing plant structural complexity and size. Plants with the lowest structural complexity (number of branches) and lowest size (plant biomass) supported lower gall abundance. Increasing the size of a host plant directly influence the size *per se* and resource diversity (Lawton 1983). As galling insects depend on young, undifferentiated plant tissue for gall induction and development, higher gall abundance on high architectural complex plants should be expected. In fact, several studies have found an increase in the richness and abundance of galling insects with increasing host plant biomass (Cornelissen & Fernandes 2001; Araújo *et al.* 2006; Rudgers & Whitney 2006). By assuming that galling insects rely on meristem availability, the estimated number of active meristems has been used as a strong predictive variable of gall abundance (Larson & Whitham 1997; Espírito-Santo *et al.* 2007).

Our data partially corroborate the “plant architecture hypothesis”. However, the mechanisms underlying the pattern are still uncertain. Host plant size *per se* should account for higher insect abundance on larger host plants. Insect density should increase with increase in host plant biomass per unit area, because of the relative rates of encounters between insects and plants (Haysom & Coulson 1998). Thus, taller *M. radula* individuals should be more apparent (*sensu* Feeny 1976) for gravid females and hence support higher gall abundance.

High meristem availability would explain higher colonization in more architectural complex plants. The increase in gall abundance with plant architecture complexity could be the result of an increase in the availability of oviposition sites in more complex plants. Furthermore, plants with higher architectural complexity should provide herbivores with an enemy-free space (Heisswolf *et al.* 2005; Riihimäki *et al.* 2006). Otherwise, our results did not support this assumption because the Gelechiidae larvae survival and mortality were not correlated with plant architecture. This result suggests that an increase in architectural complexity and plant size did not offer niches for escape from parasitoids or predators. Araújo *et al.* (2006) found similar results and proposed that bottom-up mechanisms are more important than top-down in determining the distribution and abundance of galling insects. Host plant architecture differentially determines the predation and parasitism of *Epirrita autumnata* (Borkhausen, 1794)

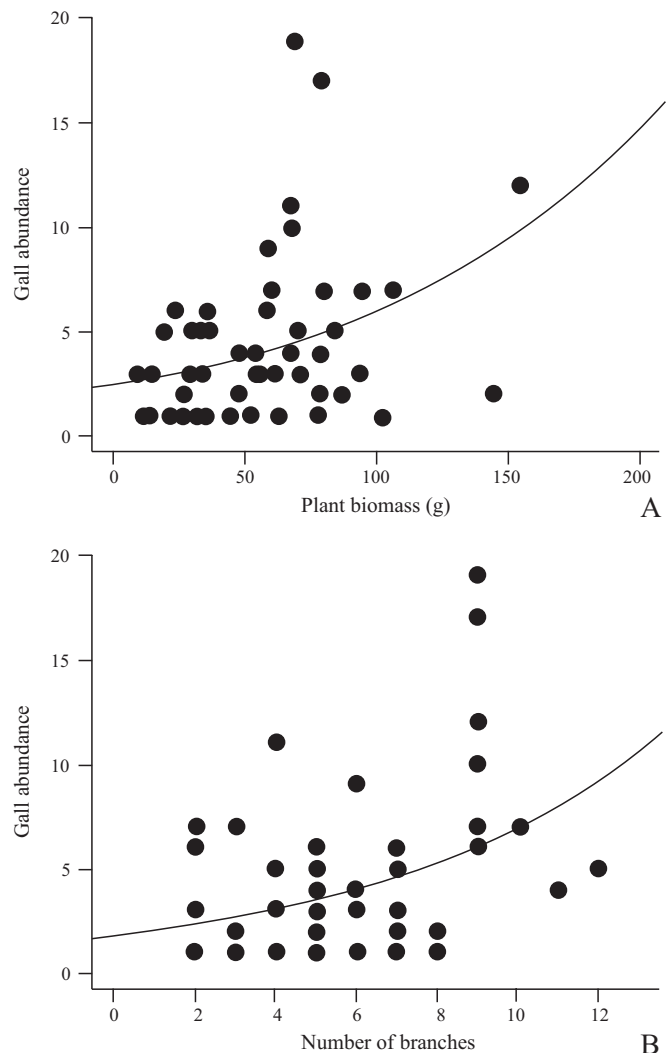


Fig. 1. Relationship between gall abundance and plant biomass (equation: $y = e^{0.882+0.009 \cdot \text{biomass}}$, $F = 8.897$; $P = 0.004$, $n = 58$, A) and number of branches (equation: $y = e^{0.604+0.134 \cdot \text{number branches}}$, $F = 5.025$; $P = 0.03$, $n = 58$, B) of the host plant, *Macairea radula*.

(Lepidoptera, Geometridae) on birches (Riihimäki *et al.* 2006). An unidentified passerine was observed preying galls on *M. radula* (L.A. Oliveira, pers. obs.) but the effect of plant architecture on larval predation remains unclear, as predated galls were not collected.

In a broader scale our study has an important implication. If galling insects negatively impact host fitness (e.g., Gonçalves-Alvim *et al.* 1999; Muniappan & McFadyen 2005), and gall abundance is higher on more complex plants, it should be expected that natural selection to favor low architectural complexity. Models that predict the evolution of plant architecture (Sussex & Kerk 2001) usually neglect the role of herbivores in plant architecture. Marquis *et al.* (2002) observed that leafyiting caterpillar abundance increased on *Quercus alba* L. individuals with increased number of touching leaves. They suggest that architectural traits that minimize leaf-to-leaf contact may be defensive against leafyiting caterpillar. Thus,

further investigations should be conducted to verify whether herbivores represent an important selective pressure on plant architecture (Whitham & Mopper 1985).

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