Abundance and Impact of a Lepidopteran Gall on *Macarea radula* (Melastomataceae) in The Neotropics

SILMARY DE J. GONÇALVES-ALVIM1,2, ELENA CHARLOTTE LANDAU3, MARCÍLIO FAGUNDES1,2, VÂNIA G. DA SILVA2, YULE R.F. NUNES2 AND WILSON FERNANDES1

1Ecologia Evolutiva de Herbívoros Tropicais/DBG, ICB/Universidade Federal de Minas Gerais, CP 486, 30161-970 Belo Horizonte MG Brazil.
2Pós-graduação em Ecologia, Conservação e Manejo de Vida Silvestre, CP 486, ICB/Universidade Federal de Minas Gerais, 30161-970 Belo Horizonte MG Brazil.

ABSTRACT

We explored two hypotheses to explain the pattern of attack by a galling Heliodinidae (Lepidoptera) on *Macarea radula* (Melastomataceae) in Serra do Cipó, Brazil. The harsh environment hypothesis predicts higher attack rates on plants in xeric habitats than on plants in mesic habitats. We found that plants in xeric habitats supported more galls than plants in mesic habitats in 1996 and in 1997, corroborating the hypothesis. Rates of attack per plant did not differ significantly between years in the two habitats. The number of galls in 1996 was consistent with the number of galls produced in 1997 in both habitats. The host plant size hypothesis predicts a positive relationship between the area of the host plant and gall density. The number of galls per plant did not vary with host plant area; leading to the rejection this hypothesis. We also tested the hypothesis that galling insects have a negative impact on plant growth. Number of leaves, inflorescence length, dry biomass of shoot, and shoot length were significantly smaller on galled than on ungalled shoots. The gall influenced the growth of attacked shoots negatively, corroborating the hypothesis that galls negatively impact their host plants.

Key Words: Gall impacts, Habitat stress, Heliodinidae, Herbivory, Insect galls.

INTRODUCTION

The environment, the abundance and biomass of herbivore populations, and traits and physiology of host plant influence the impact of herbivory on plants (Grahan 1963, Knight 1967, Schowalter et al. 1986). Plant’s nutritional status can strongly influence its rates of herbivory and its capacity to regenerate following damage by herbivores. Plant nutritional quality affects herbivore growth rate (Washburn et al. 1987, Herms and Mattson 1992, Marquis 1996), fecundity (Mopper and Whitham 1992), and survivorship (Kemp and Moody 1984, Waring and Cobb 1992, Bentz et al. 1993). Plants grown under...
better light, water and nutrient conditions react more quickly to herbivore damage than plants grown under adverse conditions (e.g., Fay et al. 1996). Nevertheless, a complex feedback loop exists in plant-herbivore interactions that affects the performance of the host plant and the associated herbivore fauna (Craig and Price 1986).


Casual observation indicated that galls induced by a species of sun moths (Lepidoptera: Heliothidae) are common on leaf axillary buds of Macairea radula (Bompl.) DC. (Melastomataceae) in Serra do Cipó, Minas Gerais, southeastern Brazil. The host plant is widely distributed in xeric and mesic habitats and its galls are large and conspicuous. These features stimulate our interest to address several questions on the interactions between host and galling herbivore. We tested three hypotheses related to the interaction between the galling Lepidoptera and its host plant: (i) The harsh environment hypothesis that predicts higher rates of attack on plants in xeric habitats than on plants in mesic habitats (Fernandes and Price 1988, 1991, 1992), (ii) The host plant size hypothesis that predicts a positive relationship between the area of host plant and the density of galls (Feeny 1976, Lawton 1983) and (iii) The gall impact hypothesis that predicts a negative impact of the gall on the growth of the host plant (Price et al. 1987, Larson and Whitham 1991).
Tests of Hypotheses

The Flora Environment Hypothesis

To determine whether gall abundance was greater in xeric habitats than in mesic habitats, we counted all galls found on 41 randomly chosen plants in xeric (n = 20) and mesic (n = 21) habitats. Two generations of galls were sampled. Galls of green-orange coloration with the galling larva inside were assumed to represent the 1997 generation while galls of dark brown or black coloration with no larva were assumed to represent the 1996 generation. Difference in gall abundance per plant between habitats and generations were tested through analysis of variance (Zar 1996). A logarithmic transformation was used to obtain a better fit to the normal distribution. In addition, a regression analysis was performed on gall abundance per plant to test if abundance of the parental generation (1996) could be used as a predictor for abundance of the following generation (1997), indicating some consistency in the pattern of gall attack.

The Host Plant Size Hypothesis

To test the host plant size hypothesis, we measured the height and the largest diameter of the 41 sampled plants. We calculated the plant external area with the cone formula:

\[ \text{Plant area} = \pi \times \left( \frac{h^2}{2} \times r \right) \]

where \( \pi = 3.14, r = \) larger tree canopy diameter/2, and \( h = \) total height. The rate of attack per plant was obtained by dividing the number of galls formed during 1997 by the external area of the respective plant, yielding the number of galls per square centimeter. The relationship between area and intensity of attack on each plant was evaluated through regression analysis and linear correlation.

The Gall Impact Hypothesis

To test the gall impact hypothesis, we sampled 72 galled and ungalled shoots (36 per habitat) selected at random on the studied plants. Galled shoots and their nearest ungalled neighboring shoot were collected; 1-3 pairs of shoots were collected per plant. Only shoots with one gall were considered in this analysis as shoots with two or three galls occurred with less frequency in the galled shoot population. In all cases, the nearest ungalled shoot was on the opposite side of the galled shoot, indicating similar age. Shoots of different habitats (xeric and mesic) did not show significant differences in length (t test \( t = 1.01, n = 36, p > 0.05 \)), biomass (t test \( t = 0.60, n = 36, p > 0.05 \)), number of leaves (t test \( t = 0.04, n = 36, p > 0.05 \)), or inflorescence length (t test \( t = 0.41, n = 12, p > 0.05 \)). Therefore, shoots of the two different habitats were pooled in the analysis.

Once collected, shoots were cut to separate the growth area of the previous season. Growth of the 1997 season was separated easily from growth of the 1996 season by its green-reddish coloration. We recorded the inflorescence length (cm), number of leaves, and length (cm) of each shoot. Dry biomass (g) of shoots and galls were obtained by drying the samples at 80°C for three days and then weighing them with an analytical scale.

Impact of Insect

The impact of galls on plant growth was evaluated by comparisons of growth rate increment biomass, production of leaves, and length of the inflorescence between galls and its nearest ungalled neighbour shoot. Differences were compared through paired t test. Inflorescence length was analyzed only for those shoots that bore inflorescence \( t = 25 \). Regression tests and linear correlation indicated a strong correlation between the number of flowers and inflorescence length \( r^2 = 0.77, n = 50, p < 0.01 \). Thus, the length of the inflorescence was used as an indicator of the number of flowers per inflorescence.

We hopped to determine the diameter or biomass of galls affected shoot growth performance. However, since gall diameter and biomass were strongly correlated \( r^2 = 0.66, n = 71, p < 0.01 \) only the diameter was used for this study. Hence, correlation at linear regression tests were performed on diameter of galls and differences of measurement (length, biomass, inflorescence length, and number of leaves) on galled and ungalled shoots.

RESULTS

Although plant size was not affected by habitat type (t test \( t = 0.27, n = 41, p > 0.05 \)), plants in xeric habitats were approximately twice as likely to be attacked by the gall herbivore than plants in mesic habitat. Plants supported an average of 2.32 galls \( \pm 0.3 \) of the 1996 herbivore generation in xeric habitat and 1.20 galls \( \pm 0.27 \) in mesic habitat. Plants supported an average of 2.49 galls \( \pm 0.34 \) of the 1997 herbivore generation in xeric habitat and 1.08 galls \( \pm 0.21 \) in mesic habitat. However, differences in gall abundance per plant did not differ between generations within habitats (Figure 2).

![Figure 2. Average number of galls (log) on Macrocephalus radula in mesic and xeric habitats in 1996 at 1997 generations in Serra do Cipó, Brazil. Lines represent the standard error. Averages with different letters are significantly different (one way ANOVA, \( F = 6.90, p = 0.01 \). Tukey test \( p < 0.05 \)).](image-url)
The number of galls per plant in a previous generation was a good predictor of the number of galls in the following generation in the xeric habitat \( (y = 0.252 + 0.963x, r^2 = 0.84, F = 93.74, p<0.01) \) as well as in the mesic habitat \( (y = 0.559 + 0.435x, r^2 = 0.31, F = 8.50, p<0.01) \) (Figure 3). These findings indicate that gall abundance of the parental generation could be used as a predictor for gall abundance in the next generation, though better in xeric than in mesic. The abundance of galls in 1997 season was not influenced by the area of the host plant \( (y = 1.53 + 0.0314x, r^2 = 0.01, F = 0.26, p>0.05) \), therefore rejecting the host plant size hypothesis.

![Figure 3. Relationship between gall abundance per plant in 1996 generation and gall abundance per plant in 1997 generation on *M. radula* in mesic and xeric habitats (\( \star \) = mesic habitat; \( \square \) = xeric habitat).](image)

Table 1. Comparison of shoot length, inflorescence length, number of leaves and shoot biomass between galled and ungallled shoots of *M. radula* in mesic and xeric habitats \( (x = \text{average}; SE = \text{standard error}, n = \text{total number of shoots}, p\text{-value} = \text{probability}) \).

<table>
<thead>
<tr>
<th>Variables</th>
<th>Ungalled shoots</th>
<th>Galled shoots</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shoot length (cm)</td>
<td>7.16 ± 0.89</td>
<td>4.99 ± 0.86</td>
<td>7.98</td>
</tr>
<tr>
<td>Inflorescence length (cm)</td>
<td>4.59 ± 0.85</td>
<td>4.92 ± 1.05</td>
<td>1.09</td>
</tr>
<tr>
<td>Number of leaves</td>
<td>9.33 ± 0.73</td>
<td>8.12 ± 0.55</td>
<td>2.00</td>
</tr>
<tr>
<td>Shoot biomass (g)</td>
<td>2.98 ± 0.21</td>
<td>2.35 ± 0.18</td>
<td>1.31</td>
</tr>
</tbody>
</table>

Galled shoots had less leaves, shorter inflorescences, weighed less, and were shorter than ungalled shoots (Table 1), indicating that lepidopteran galls influence the growth pattern of shoots. However, none of the measured parameters of the shoots were influenced by gall diameter (Table 2), indicating that gall size did not influence shoot growth.

Table 2. Relationship between gall diameter and shoot length, inflorescence length, number of leaves, and shoot biomass, between galled and ungalled shoots on *M. radula* \( (r^2 = \text{percentage of explained variation}, n = \text{total number of shoots}, p\text{-value} = \text{probability}) \).

<table>
<thead>
<tr>
<th>Shoot variables</th>
<th>Regression Equation</th>
<th>( r^2 )</th>
<th>( n )</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shoot length (cm)</td>
<td>( y = 1.48 - 0.048x )</td>
<td>0.00</td>
<td>71</td>
<td>0.801</td>
</tr>
<tr>
<td>Inflorescence length (cm)</td>
<td>( y = -0.086 - 0.661x )</td>
<td>0.12</td>
<td>25</td>
<td>0.087</td>
</tr>
<tr>
<td>Number of leaves</td>
<td>( y = 1.57 - 0.105x )</td>
<td>0.00</td>
<td>71</td>
<td>0.768</td>
</tr>
<tr>
<td>Shoot biomass (g)</td>
<td>( y = 2.11 - 0.204x )</td>
<td>0.00</td>
<td>71</td>
<td>0.658</td>
</tr>
</tbody>
</table>

DISCUSSION

The abundance and diversity of gallers are higher on plants that grow in nutritionally and hydrothermically stressed habitats (Fernandes and Price 1988, 1991). Mechanisms that produce different herbivore abundance between mesic and xeric habitats are related to the differential survival of immature stages and differential preference of the galling females for specific oviposition sites (Fernandes and Price 1992). The effects of predators, parasites, pathogens and plant resistance on the galling insect are more effective in mesic environments (Fernandes and Price 1992). In the studied system, the abundance of the herbivore was strongly affected by the habitat of host plant, corroborating the hypothesis of environmental stress. Because gall abundance per plant did not illustrate significant variation between generations, this trend apparently is consistent from year to year.

White (1969, 1984) argued that plants that suffer water or nutritional stress constitute food of better quality to herbivores because they have a larger content of soluble nitrogen and smaller concentrations of chemical defenses. In fact, many phytophagous insects frequently reach larger population densities on plants under some type of stress (White 1969, 1976, 1984; Cobb et al. 1997). However, not all herbivores respond equally to plant stress (see Larsson 1989, Mopper and Whitham 1992). Some prefer and perform better on vigorous plants (e.g., Price et al. 1990; Price 1991), while others may attack plants indiscriminately (Prie 1994). This study lends some support to the hypothesis that some galling herbivores attack a greater number of plants in more stressed habitats where plants may be suffering from lack of nutrients and water when compared to plants living in comparatively resource rich habitats.
Plant architecture may directly affect the richness and abundance of herbivorous insects (Lawton 1983, Marquis 1996). Hartman (1985) studied the differential infestation of a galling Gelechiidae (Lepidoptera) on "Tetrastigma stenolepis" (Asteraceae) of different sizes and found higher rates of galling on larger plants. On the other hand, Alonso and Herrera (1996) studied the variation of herbivory on "Daphne laureola" (Thymelaeaceae) and found that the total number of leaf verticils and basal diameter of stems positively influenced rates of herbivory. Our results do not corroborate the hypothesis that the number of galls per plant is directly influenced by plant size. Factors such as oviposition site availability may be more important than for host plant (Waring and Price 1990).

Some studies have shown the negative effect of herbivory on inflorescence length (e.g. Zimmerman 1990, Wyatt 1982). Stephenson (1979) studied the effect of leaf damage by herbivores on "Catalpa speciosa" (Bignoniaceae) and verified that inflorescence size, fruit maturation, and seed weights were affected negatively by the presence of galls. Willson and Price (1977) observed that the largest inflorescences of "Asclepias" (Asclepiadaceae) generally received more pollen and a higher average number of visitors. Furthermore, the number of mature fruits produced was correlated positively with inflorescence length. We observed that galled shoots had smaller inflorescences, which could affect overall plant performance. However, a closer look at the reproductive biology of "Macarea radula" is necessary to completely understand the effects of galls on host plant fitness.

To develop and maintain galls, the galling herbivore creates a resource sink at the galling site (Hartnett and Abrahamson 1979, Raman 1991, Larson and Whitham 1991). Thus, gall formation probably disrupts physiological processes provoking a negative impact in the growth of "Macarea radula". Our results suggest that the presence of galls affect "Macarea radula" performance, negatively influencing its growth. On the other hand, we did not find any relationship between diameter and biomass of galls and the intensity of the damage caused to the host shoots.

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