Natural History of a Gall-Inducing Weevil *Collabismus clitellae* (Coleoptera: Curculionidae) and Some Effects on its Host Plant *Solanum lycocarpum* (Solanaceae) in Southeastern Brazil

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ABSTRACT The phenology, general characteristics, and mortality factors acting upon the weevil *Collabismus clitellae* Boheman in a population of *Solanum lycocarpum* St. Hil. (Solanaceae) were investigated in southeastern Brazil, as well as its distribution and impact on the host plants. Mating and oviposition of the weevils were observed in the beginning of the summer, with larval development until the autumn and emergence in spring. Most galls were found toward the base on plants 0.9-1.2 m high, a distribution perhaps the result of physiological differences between plants of different height. Natural enemies also may influence this pattern; logistic regressions showed that greater gall size and increased height above the ground increased mortality caused by the woodpecker *Colaptes campestris* (Vieillot). Larger galls also were more frequently attacked by the fungus *Penicillium* sp. Gall attack rates were correlated with *S. lycocarpum* stem mortality (43.4% of plants analyzed), because galls could act as nutrient sinks or favor the breaking of stems. The possible effect of *C. clitellae* on the population dynamics of *S. lycocarpum* is discussed.

KEY WORDS *Collabismus clitellae*, Coleoptera, Solanaceae, plant-insect interactions, gall mortality

GALL-INDUCING INSECTS are extremely diverse and have interesting and complex life histories. Most of their life is spent embedded within tissues of their host plants, with which they have perhaps the most intimate relationship of all organisms (Mani 1964, Mattson et al. 1988, Fernandes 1990). The understanding of the natural history of Neotropical galling insects is tremendously poor, most studies having centered on the ecological aspects of gall distribution (Fernandes et al. 1988; Fernandes and Price 1988, 1991). In addition, there are few studies on the frequency and kind of impacts caused by galling insects on their host plants, especially for shoot galls (Sacchi et al. 1988).

The weevil *Collabismus clitellae* Boheman forms galls on shoots of the lobeira tree, *Solanum lycocarpum* St. Hil. (a synonym of *S. grandiflorum* Benth. variety [Carvalho 1985]) (Solanaceae), a woody shrub that grows to a height of 3 m. This plant is a common weed in central and southeastern Brazil, occurring along highways, pasture, grasslands, and disturbed areas (Carvalho 1985). This association also was recorded for *S. grandiflorum* in Minas Gerais State (Bondar 1923, Lima 1956).

Here we describe the phenology, general characteristics, and mortality factors acting upon *C. clitellae* in a population of *S. lycocarpum* in southeastern Brazil. We also provide data on the distribution of galls within and between plants and discuss some aspects of the impact of these galls on the host plant.

Materials and Methods

The study was conducted between May 1991 and July 1992 in a population of *S. lycocarpum* located along highway MG-010 (km 89), near Serra do Cipó, Minas Gerais, 840 m above sea level. The dominant vegetation is cerrado, which is regularly cut as a management practice for cow grazing. Plants of *S. lycocarpum* were cut at 5 cm above the ground every other year, and were last pruned in January 1990. The population studied consisted of clones with several ramets patchily distributed. Ramets were 16-18 mo old and varied from single small shoots (<10 cm from the ground) to 1.6 m high. Ramets up to 3 m high also were found and examined in the study area.

We randomly collected 385 galls from 97 individuals of *S. lycocarpum*. To identify possible patterns of gall distribution within and between plants, we measured plant height and gall height on the plant relative to the ground. Because plant height was variable, the distribution of galls on different plant parts was analyzed using the height ratio. The distribution on the plants was then measured by dividing gall locations into basal (0-0.33), median (0.33-0.66), and apical (0.66-1.00) parts of the plant. We also recorded the diameter of the galled stems and whether they were wilting or dead, to evaluate the impact of galls on stem survival, using the gall attack rates (see below).
In the laboratory, we measured the length and diameter of galls and estimated their volume with the formula volume = length \times (\text{diameter}/2)^2. To test whether this measure provided a statistically reliable estimate of gall size, we randomly subsampled 67 galls whose volume we measured by immersing each gall in a graduated tube filled with water and recording the volume of water displaced. As the relationship between both measurements was linear \(y = 1.88 + 8.01x, r^2 = 0.83, P < 0.001\), the former method was used to estimate gall size throughout this study.

The attack rate per stem was evaluated as the sum of chambers in all galls found per stem; later, all galls were dissected and the chambers were counted and opened. This approach was needed because the number of chambers per gall and number of galls per stem was highly variable. Furthermore, there is only 1 beetle larva per chamber, which would be a better estimate of the attack rates.

During oviposition by females of *C. citellae*, we randomly marked 175 egg batches on 48 plants. Of these, we measured the stem diameter, plant height, and the number of scars left by the females on the epidermis of the stem oviposited upon. We also recorded the number of stems that were broken exactly where the eggs were deposited.

The mortality factors acting upon *C. citellae* in relation to plant height, gall height in relation to ground, and gall volume were analyzed with logistic regressions (Hosmer and Lemeshow 1989, Steinberg and Colla 1991). The odds ratio \((\psi)\) was calculated according to an increase of \(c\) units of the independent variable analyzed, with the following equation:

\[
\psi = e^{\beta c}
\]

and 95% confidence limits set by the relation

\[
CI = e^{(\beta c \pm 1.96 SE_{\beta}\sqrt{c})}
\]

where \(\beta\) is the parameter estimate and \(SE_{\beta}\) is the standard error of the estimate (Hosmer and Lemeshow 1989). A similar model was used to analyze stem survival in relation to beetle attack rates and stem diameter. The relationship between these factors and stem diameter categories on the breaking off of stems was analyzed using the G test (Sokal and Rohlf 1995). Voucher specimens of *C. citellae* were deposited in the Museu de História Natural, Universidade Estadual de Campinas.

Results

Biology of *C. citellae*. Mating and oviposition of *C. citellae* occur in the beginning of summer (November-December). Ovipositing females use their mouthparts to perforate the epidermis of nonwoody stems (shoots) of *S. lycocarpum* to lay their eggs. Each hole is quickly sealed off after egg deposition, leaving a conspicuous scar on the stem. We collected several newly oviposited stems for dissection in the laboratory, and only 1 egg was deposited in each hole. Therefore, the number of eggs laid corresponded to the number of scars left on the surface of the stem. We observed 3-181 (29.3 ± 21.46 [mean ± SD]) eggs per oviposition. Eggs were deposited around the entire circumference of a stem, but in a spiral formation. Thus, the length of the oviposition bout varied both with the number of eggs deposited by a female and stem diameter.

Each larva of *C. citellae* (Fig. 1A) was concealed within a single chamber (Fig. 1E), developing between December and May. Galls continued to grow as larvae fed on the galled tissue until larvae terminated feeding and pupated, which occurred in May. Pupae (Fig. 1B) were found from May to July, and adults were found inside galls between July and September. Emergence of adults from their galls (Fig. 1C) took place from late September to October.

The adults of *C. citellae* (Fig. 1D) are pale yellow with a dark spot on the elytra. This color matches the pale yellow of the stem of their host plant. Adults are very abundant in the field from October to December, where they are found commonly feeding on newly growing shoots, leaves, and flowers of *S. lycocarpum*, as well as ovipositing on new shoots.

Newly formed galls are green, juicy, and soft (Fig. 1F). Their internal tissues have many fibers and a large amount of water. They are glabrous, globular, or ellipsoid and may occur singly or in coalescence. As galls age, their tissue becomes drier, woody, and brownish.

Galls were very variable in size, ranging from 1.26 to 16.85 cm (3.55 ± 1.96, \(n = 385\)) long and from 0.59 to 4.65 cm (2.41 ± 0.81, \(n = 385\)) wide. Their volume varied from 0.34 to 139.84 cm\(^3\) (21.74 ± 24.59, \(n = 385\)). The number of chambers also was highly variable, ranging from 1 to 70 chambers per gall.

Gall Distribution Between and Within Plants. Galls were distributed on plants that ranged between 40 and 200 cm high, only 3% being recorded on plants higher than 160 cm and the greatest proportion (42%) on plants 80-120 cm tall (Fig. 2a). Within the host plants, they occurred mostly on the median and basal parts, greater numbers in the latter region (\(G = 9.7, df = 3, P = 0.02\)). Because only 15 galls were found on apical stems, they were excluded from the analysis.

Of all galls collected, 249 (65%) were smaller than 20 cm\(^3\), containing from 1 to 8 chambers. Large galls (>40 cm\(^3\)) might have up to 68 chambers, more of them occurring on the basal stems of the plants than on the median region (\(G = 15.6, df = 3, P = 0.001, \text{Fig. 2b}\)). All galls located on the apical region were <40 cm\(^3\).

Mortality Factors. An unidentified species of the fungus *Penicillium* was the major mortality factor acting upon *C. citellae* during our study (35.9% of all dead galls). The external morphology of the gall was not altered by the presence of the pathogen, whereas its growth inside the gall damaged larval chambers and killed the galling larva. On 38.2% of the galls attacked by *Penicillium* sp., we observed 1–3 larvae of an unidentified species of Cerambycidae (Coleoptera). These larvae formed tunnels inside the pathogen-damaged galls. The occurrence of the fungus was most frequent in the largest galls, but was independent of plant and gall height (Table 1). According to the analysis, an increase in 10 cm\(^3\) in gall size increased the chance of a gall being attacked by a factor of 1.22. For example, if the chance of a gall being attacked in the field is 10%, an increase of 10 cm\(^3\) will raise this chance to 12.2%.
Fig. 1. Several phases of the galls caused by *C. clitellae* on *S. lycocarpum*. (A) Larva. (B) Pupa. (C) Adult excavating the gall walls to emerge. (D) Adult. (E) View of a gall chamber located close to the gall external wall. (F) Gall on the basal portion; holes were drilled by adults that left the gall successfully.

Galls also were attacked by the woodpecker *Colaptes campestris* (Vieillot) (Piciformes: Picidae). These birds perforated the gall walls to reach the juicy larvae inside the chambers, partially or even entirely destroying galls. *C. campestris* was frequently observed on branches of the host plant, and attacks were commonly recorded in the field. Birds most frequently attacked the largest galls or those located on the superior portion of the host plant (Table 1). Analysis indicated that an increase of 10 cm in gall height increased the chance of being attacked by *C. campestris* by a factor of 1.36, and a 10 cm³ increase in gall volume led to a factor of 1.17. Despite the fact that plant height had an important effect on the decision of the woodpecker to attack a given gall, plant height alone was not a risk factor because the lower confidence limit of the odds ratio was <1.0 (e.g., Hosmer and Lemeshow 1989). Therefore, the most important factors influencing the pattern of attack by *C. campestris* were gall size and gall height from the ground.

Galls also were attacked by 2 species of parasitic hymenopteran; both leave their cocoons inside the gall after emergence. This study did not focus on the relationship between the parasitoids and gall distribution patterns within plants because parasitism rates were much lower than other mortality factors (14.4%). A large percentage of galls was killed by undetermined factors, possibly including nematodes, ants, and plant resistance (30.7% of galls attacked).
Fig. 2. Number of galls in (a) plant height classes and (b) gall size classes in different parts of plant. Dark bars represent galls located in apical portion, hatched bars in median portion, gray bars in basal portion.

Impact on Host Plant. The number and size of galls varied enormously among stems. Many galled stems died, probably as a consequence of gall induction; death began with the wilting and drying of the apical region. Of 76 randomly collected stems on 76 plants, 33 (43.4%) were dead. The probability of stem death was positively associated with attack rates and negatively associated with stem diameter (Table 2). Therefore, the number of larvae per stem was an important factor influencing stem survival; an increase in 10 chambers per stem (10 individuals) increased 2.4 times the probability of stem death, whereas an increase of 1 cm in stem diameter decreased the probability of death by 0.042 times. Thus, thinner stems without galls are more likely to survive, as would larger stems, even if galled.

Drilling by females during oviposition frequently resulted in stem breakage by mechanical factors such as wind, rain, and by passing animals. Among the stems analyzed, 24.4% were broken exactly at the site of oviposition. Breaking was frequently observed in the thinnest stem classes ($G = 11.63, df = 4, P = 0.02$, Fig. 3).

Discussion

The mortality of C. clitellae from external agents is independent of plant height. Thus, the greater occurrence of galls on smaller plants may be caused by inherent factors of the interaction between the galling insect and S. lycocarpum. First, plants or parts of the plant may be in different phenological or developmental stages, which could influence the survival and performance of C. clitellae larvae and consequently the attack rates observed (e.g., Kearsley and Whitham 1989). The aging of host plants can lead to differences in the nutritional quality of young and mature tissues because of distinct chemical or mechanical defense levels, which influences the distribution of herbivorous insects (Frankie and Morgan 1984, Whitham et al. 1984, Craig et al. 1986, Akimoto and Yamaguchi 1994).

Second, the pattern observed could result from female behavior when choosing oviposition sites as attempts to maximize the survival and performance of her offspring (Thompson 1988, Craig et al. 1989, Price 1991) (but see Burstein and Wool 1993). A 3rd hypothesis is that this distribution may result from the impact of galls on plants, reducing their growth (Fernandes 1986, 1987). Whether these hypotheses explain the pattern observed will be clarified only with further experiments.

In addition to the limitation on the distribution among plants of different heights, galls of C. clitellae occur more frequently on the basal portions of the attacked plants, where galls attain the largest sizes. An

Table 1. Logistic regression results for the explanatory variables of C. clitellae mortality

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>SE</th>
<th>P</th>
<th>Odds ratio</th>
<th>95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Upper</td>
<td>Lower</td>
</tr>
<tr>
<td>Constant</td>
<td>-1.916</td>
<td>0.565</td>
<td>0.001</td>
<td>1.09</td>
<td>0.86</td>
</tr>
<tr>
<td>Penicillium sp.</td>
<td></td>
<td></td>
<td></td>
<td>1.62</td>
<td>1.30</td>
</tr>
<tr>
<td>Plant height</td>
<td>-0.003</td>
<td>0.006</td>
<td>0.658</td>
<td>0.97</td>
<td>1.22</td>
</tr>
<tr>
<td>Gall height</td>
<td>0.004</td>
<td>0.006</td>
<td>0.602</td>
<td>1.04</td>
<td>1.22</td>
</tr>
<tr>
<td>Gall size</td>
<td>0.020</td>
<td>0.005</td>
<td>0.001</td>
<td>1.22</td>
<td>1.35</td>
</tr>
<tr>
<td>Colaptes campestris</td>
<td></td>
<td></td>
<td></td>
<td>1.37</td>
<td>1.11</td>
</tr>
<tr>
<td>Constant</td>
<td>-0.877</td>
<td>0.703</td>
<td>0.212</td>
<td>1.69</td>
<td>0.61</td>
</tr>
<tr>
<td>Plant height</td>
<td>-0.030</td>
<td>0.010</td>
<td>0.002</td>
<td>0.74</td>
<td>1.76</td>
</tr>
<tr>
<td>Gall height</td>
<td>0.031</td>
<td>0.013</td>
<td>0.013</td>
<td>1.36</td>
<td>1.06</td>
</tr>
<tr>
<td>Gall size</td>
<td>0.016</td>
<td>0.008</td>
<td>0.039</td>
<td>1.17</td>
<td>1.06</td>
</tr>
</tbody>
</table>

$G = 10$ for all variables analyzed.

$^a G = 13.04, df = 3, P = 0.005$.

$^b G = 14.18, df = 3, P = 0.003$. 

(a)
important factor determining these distribution patterns was the attack of the woodpecker C. campestris, because the chances of being attacked increase with gall size and height on the plant. Birds of the family Picidae search for insect larvae, mainly beetles in wood, which constitute the preferred food item of many Brazilian species (Sick 1984). Generally, insectivorous birds hunt by visual search, and individuals of this species should detect the galls most easily visualized at greater distances. Attack of insect galls by the woodpecker Picoides pubescens on the Canadian goldenrod, Solidago canadensis, also were intensive on large galls on tall stems (Confer and Paicos 1985). The attack rates recorded for C. campestris (19% of all attacked galls) seems to be relatively high and may assume a larger importance for those galls located on the higher portions of the plants, where gall occurrence is lower than on the basal region.

Mortality caused by fungi also was higher on the largest galls. In 38.2% of the attacked galls, we observed larvae of a cerambycid that probably fed on the mycelia, and adults may be acting as a dispersal agent of this pathogen. Fungal transport by several coleopteran families has been recorded. Vectors of plant diseases have been recorded in Scolytidae (Levieux et al. 1991), Curculionidae (Nevill and Alexander 1992), Nitidulidae (Currie 1995), and Anobiidae (Hoover et al. 1995). Thus, the behavior of this cerambycid could influence the distribution of Penicillium sp. and ultimately gall survival.

Solanum lycocarpum stems died according to a balance between gall infestation rate and stem diameter. The stem dries progressively from the apex, modifying or interrupting the development of galls located at greater heights. This suggests the possibility of competition among C. clitellae galls. Those in the basal parts of the plants may be draining resources otherwise available for galls in the apical parts (e.g., galls on different leaf parts [Whitham 1980]). These galls not only contributed to stem breaking, they also reduced plant fitness; stem mortality caused by intense gall attack was 43.4%. The direct effect of herbivores on plants can be very strong, influencing the net production of inflorescences and seeds, modifying plant architecture or sex expression (or both), or inducing shoot mortality (Craig et al. 1986, Sacchi et al. 1988, Whitham et al. 1991). The presence of galls can influence the physiology of the host plants, acting as metabolic sinks for energy and mineral nutrients and modifying tissues that otherwise could serve for growth and reproduction (Abrahamson and Weis 1987, Price and Louw 1996). Indirect effects include the susceptibility to other herbivore species because of the modification of plant tissue and/or plant resistance caused by a specific herbivore (Whitham et al. 1991, Price and Louw 1996, McGeoch and Chown 1997).

The damage of herbivores to the reproductive characteristics of plants may depend on the phenology of the plant (Harper 1977). Because gall frequency was higher on smaller plants, young dead plants were observed several times. In larger plants, the infestation rates were smaller, and there was less damage to the plants. Sacchi et al. (1988) observed that the sawfly Euura lasiolepis influenced the production of inflorescences by Salix lasiolepis only during the year of infestation, rather than in subsequent years. The artificial cut of S. lycocarpum keeps a high resource availability to C. clitellae, maintaining young branches highly susceptible to attack by the herbivore. Thus, the pruning season of those agricultural and pasture fields should influence the effect of C. clitellae on S. lycocarpum when adjusted to the life cycle of this insect.

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