# Pattern of attack of a galling insect reveals an unexpected preference-performance linkage on medium-sized resources

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ABSTRACT. Pattern of attack of a galling insect reveals an unexpected preference-performance linkage on medium-sized resources. The Plant Vigor Hypothesis (PVH) predicts oviposition preference and higher offspring performance on longer and fast-growing shoots, and although several studies have tested its predictions, long-term studies concerning the patterns of host selection by galling species are still lacking. The PVH was tested in this study using *Bauhinia brevipes* (Fabaceae) as the host of a leaf gall midge, *Asphondylia microcapillata* (Diptera, Cecidomyiidae) during three consecutive years. Shoots were collected from the same 80 plants between 2001 and 2003 and shoot length, number of healthy and galled leaves, gall number, and mortality factors were recorded. Nearly 600 galls were found on the 5,800 shoots collected. Medium-sized shoots supported from 46 to 70% of all galls, with greater gall survival rate in 2002 and 2003. A decrease in parasitism rate coupled with an increase in gall predation lead to a constant similar gall survivorship rate in all years ($\bar{x} = 22.7\%$). Although gall abundance varied among years (122 in 2001, 114 in 2002 and 359 in 2003) preference for longer shoots was not observed because the percentage of galled shoots and galled leaves were higher on medium shoot length classes in all years. The observed distribution of gall abundance and galled shoots were always greater than the expected distribution on medium shoot length classes. These findings do not support the PVH, and show that *A. microcapillata* can maximize the female preference and larval performance on medium-sized shoots of *B. brevipes*.

KEYWORDS. Host selection; insect galls; mortality factors; Plant Vigor Hypothesis; top-down effect.

RESUMO. Padrão de ataque de um inseto galhador revela uma inesperada ligação entre preferência e performance sobre recursos de tamanho médio. A Hipótese do Vigor de Plantas (HVP) prevê uma oviposição preferencial e alta performance da prole em ramos longos e de crescimento rápido da planta hospedeira. Embora diversos estudos tenham testado suas predições, estudos de longa duração focados no padrão de seleção de planta hospedeira por insetos galhadores ainda são escassos. A HVP foi testada neste estudo usando *Bauhinia brevipes* (Fabaceae) como planta hospedeira de uma galha foliar induzida por *Asphondylia microcapillata* (Diptera: Cecidomyiidae) por três anos consecutivos. Ramos foram coletados das mesmas 80 plantas entre 2001 e 2003 e o tamanho do ramo, número de ramos galhados e sadios, número de galhas e fatores de mortalidade foram registrados. Aproximadamente 600 galhas de *A. microcapillata* foram coletadas em 5.800 ramos de *B. brevipes*. Ramos médios suportaram entre 46% e 70% do total de galhas, e a taxa de sobrevivência das galhas foi maior em 2002 e 2003. Uma diminuição da taxa de parasitismo associada com um aumento da taxa de predação de galhas resultou em uma sobrevivência similar em todos os anos ($\bar{x} = 22{,}7\%$). A abundância de galhas variou entre os anos (122 em 2001, 114 em 2002 e 359 e 2003). A preferência por ramos longos não foi observada porque a porcentagem de ramos galhados e folhas galhadas foram maiores em ramos de classes de tamanho intermediário por dois anos. A distribuição observada da abundância de galhas e ramos galhados foi sempre maior do que a distribuição esperada em classes de ramos médios. Estes resultados não suportam a HVP, e mostram que *A. microcapillata* pode maximizar a preferência da fêmea e a performance larval em ramos de tamanho médio de *B. brevipes*.

PALAVRAS-CHAVE. Efeito topo-base; fatores de mortalidade; Hipótese do Vigor de Plantas; insetos galhadores; seleção de planta hospedeira.

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The last decades have witnessed an enormous growth in studies dealing with patterns of host plant selection by herbivorous insects. Many of these studies have addressed the relationship between female oviposition preference and offspring performance in an attempt to shed light in the evolution of interactions between insect herbivores and their host plants (see Thompson & Pellmyr 1991). Although several hypotheses were raised to explain the described patterns of attack by herbivorous insects at several ecological scales (Price 1997), a consensus on the likely mechanisms and processes involved may be premature; perhaps owing to the enormous diversity of taxa and feeding modes of herbivores and their derived results. The Plant Vigor Hypothesis (PVH; Price 1991) predicts that insect herbivores will choose preferentially large, more vigorously growing plants or plant modules (preference prediction) and that offspring performance will be greater on these more vigorous plants or plant modules (performance prediction). Several studies support both PVH predictions (Price *et al.* 1987a,b; Craig *et al.* 1989; Kimberling *et al.* 1990; Price & Ohgushi 1995; Stein & Price 1995; Woods *et al*. 1996; Inbar *et al.* 2001; Bruyn *et al.* 2002), while other studies have partially supported the preference prediction (Cornelissen *et al.* 1997; Prado & Vieira 1999; Fritz *et al.* 2000; Cornelissen & Fernandes 2001; Ferrier & Price 2004; Cunningham & Floyd 2006; Cornelissen *et al.* 2008) or even refuted both PVH predictions (Bruyn 1995; Faria & Fernandes 2001; Rehill & Schultz 2001).

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Amongst the few opposing evidences against the PVH, Faria & Fernandes (2001) argued that the amount of resources has been underestimated in shoots belonging to larger size classes (see Price 1991 for details). In their study, the higher attack rates of females of *Baccharopelma dracunculifoliae* Burckhardt (Hemiptera, Psyllidae) on the longest shoots of *Baccharis dracunculifolia* DC. (Asteraceae) were due to the higher availability of resources (leaves) on longer shoots compared to shorter shoots. When they incorporated the amount of resources on the shoot to estimate the random probability of attack, the pattern of attack on vigorous shoots disappeared. Here we tested the PVH using two methods based in shoot (Price 1991) and leaf distribution (Faria & Fernandes 2001) to find the estimated distribution of attack.

For three consecutive years the attack by the leaf galling species, *Asphondylia microcapillata* Maia (Diptera, Cecidomyiidae) on *Bauhinia brevipes* Vogel (Fabaceae) was studied. The genus *Asphondylia* comprises 82 neotropical univoltine or multivoltine species inducing galls only when young undifferentiated plant tissue is available; generally these galls are induced on flowers and fruits (Gagné 1994). Some gall midges on this genus represent exceptions to the general rule of gall feeding on the nutritious gall tissues. These insects feed upon the spores of symbiotic fungi which are probably introduced by the egg-laying female (Stone & Schönrogge 2003). *Asphondylia microcapillata* is univoltine and induces galls only when immature expanding or unfolded *B. brevipes* leaves are available. *Asphondylia microcapillata* is the second most abundant gall-former species on *B. brevipes*, whereas another leaf-galling midge, *Schizomyia macrocapillata* Maia (Diptera, Cecidomyiidae) is the dominant species (Cornelissen & Fernandes 1998, 2001; Cornelissen *et al.* 2002; Santos *et al.* 2008).

Previous studies on these two galling herbivores showed that *S. macrocapillata* has a strong preference for longer shoots (Cornelissen *et al.* 1997; Fernandes 1998; Cornelissen & Fernandes 2001, Santos *et al.* 2008) while *A. microcapillata* lacks a pattern of attack on shoots (Cornelissen *et al.* 1997). In this 3-yr study we tested the preference-performance predictions of PVH that gall induction and survivorship of *A. microcapillata* are significantly greater on larger shoots and we analyzed the effects of top-down mortality factors on the performance of *A. microcapillata*. Here, we enlarged the sampled variables and added a temporal effect, thereby generating a wider scenario to describe insect-plant interactions. Three questions were asked: a) what are the effects of top-down mortality factors on the survivorship of *A. microcapillata*?; b) what are the effects of shoot size in the oviposition preference of *A. microcapillata* on *B. brevipes*?; and c) what is the effect of *B. brevipes* shoot size in *A. microcapillata* offspring survival?

## MATERIAL AND METHODS

Study area.

This study was performed in the Estação Ecológica de Pirapitinga - IBAMA (EEP) in Três Marias, Minas Gerais, southeastern Brazil. The EEP is a 1.100ha man-made island, built in 1965 in the Três Marias reservoir (18°23'S, 45°20'W), at an altitude of 560m a.s.l. (Azevedo *et al.* 1987). The average annual temperature varies from 21 to 25°C and the average annual precipitation is 1.200mm, with rainy summers and dry winters. The vegetation is primarily cerrado (Brazilian savanna) with sandy, shallow and nutrient-poor soils, with high aluminum saturation (Gonçalves-Alvim & Fernandes 2001).

The system.

*Bauhinia brevipes* is a deciduous shrub, growing up to 3m high and abundant in the cerrado vegetation (Vaz & Tozzi 2003). Blooming occurs between June and September whereas fructification peaks between September and October. Leaf flushes starts at the onset of the rainy season in October and lasts until the end of the rainy season in March. Leaf fall takes place during the dry season, beginning in May and ending up in August; during September all individuals are leafless (Silveira F. A. O. *unpublished data*).

*Bauhinia brevipes* is attacked by seven galling species (three leaf gall midges and four stem gallers - one Cecidomyiidae, one Lepidoptera, and two Curculionidae (Coleoptera) (Cornelissen *et al*. 1997; Cornelissen & Fernandes 1998, 2001). The three gall midges, *A. microcapillata*, *S. macrocapillata* and one undetermined species induce leaf galls. Gall induction and formation were observed in October when leaves are flushed synchronously. The spheroid leaf galls of *A. microcapillata* are covered with short, whitish trichomes. The gall is positioned between the adaxial leaf lamina and has a single chamber where a single galling larva is found. The two polar regions of the spheroid galls collapse the two-lobed leaves of *B. brevipes*. At the beginning of gall formation, the trichomes are whitish but may change color as the galls mature, and when exposed to direct sunlight present reddish tones at the distal portion of the trichomes (Maia & Fernandes 2005).

Table I. *Asphondylia microcapillata* (Diptera, Cecidomyiidae) abundance and density on the host plant *Bauhinia brevipes* (Fabaceae) during three consecutive years (2001, 2002, and 2003) in a cerrado vegetation (Três Marias, Minas Gerais). Numbers in parentheses represent the amount of galled shoots or galled leaves in relationship to the respective abundance of shoot or leaves in each year.

| Year | Number of shoots | Number of leaves | Galled shoots | Galled leaves | Gall abundance | Galls/shoot |
|---|---|---|---|---|---|---|
| 2001 | 1,947 | 12,344 | 55 (2.82%) | 59 (0.48%) | 122 | 0.06 |
| 2002 | 1,996 | 14,192 | 41 (2.05%) | 48 (0.34%) | 114 | 0.06 |
| 2003 | 1,848 | 12,291 | 111 (6.01%) | 147 (1.20%) | 359 | 0.19 |
| Total | 5,791 | 38,827 | 207 (3.57%) | 254 (0.65%) | 595 | 0.10* |

* mean for all years

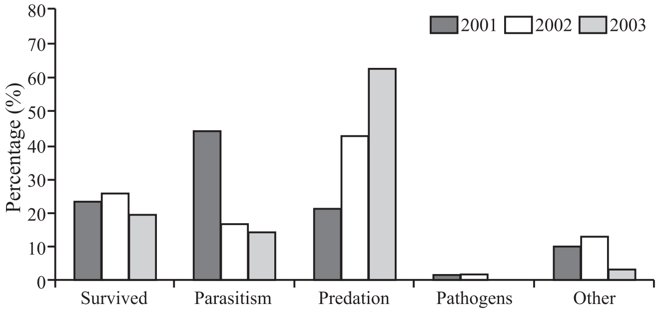

Fig. 1. Mortality factors across shoot length classes in three consecutive years of attack by *Asphondylia microcapillata* (Diptera, Cecidomyiidae) on *Bauhinia brevipes* (Fabaceae) in a cerrado vegetation (Três Marias, Minas Gerais). 2001 (black bars), 2002 (white bars) and 2003 (grey bars).

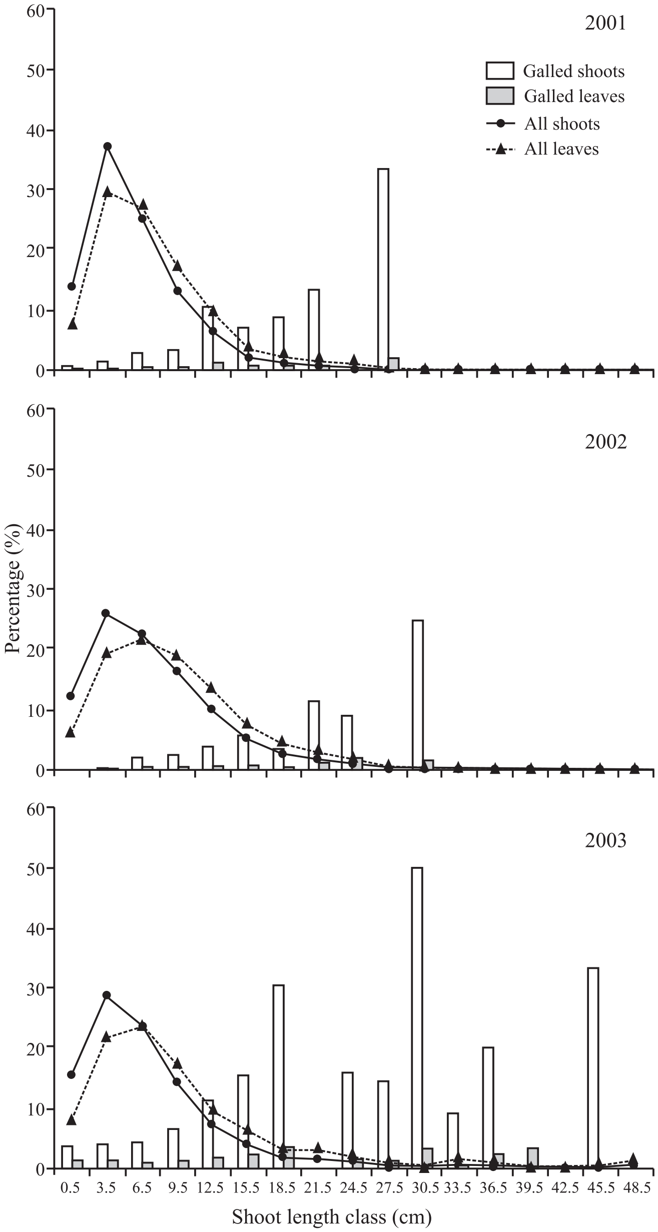

Fig. 2. Frequency distribution expressed as the percentage of total shoots, total leaves, attacked shoots and attacked leaves of *Asphondylia microcapillata* (Diptera, Cecidomyiidae) in each shoot length class of *Bauhinia brevipes* (Fabaceae) during three consecutives years (2001, 2002, and 2003) in a cerrado vegetation (Três Marias, Minas Gerais).

Sampling and statistical analysis.

Patterns of attack were determined over a 3-yr period (2001, 2002 and 2003) by randomly collecting each year, up to 25 shoots around the canopy of the same 80 randomly selected individuals of *B. brevipes*. Shoot collection was always performed early in December when most shoots and galls were mature. Shoots were bagged, numbered and taken to the laboratory where their length, total number of leaves, number of galled leaves, number of galls, and gall diameter were recorded. Shoots were then divided into 3cm classes based on previous studies in this system (e.g., Fernandes 1998; Santos *et al.* 2008). Mortality factors acting upon the gall were grouped into the following categories (Fernandes & Price 1992): parasitism, predation, pathogens and unidentified factors. In an attempt to relate the plant vigor with gall mortality, all mortality factors were plotted as a function of shoot length class (see Fernandes 1998) and they were compared with preference (galled shoots, galled leaves or galls) and performance (larvae survival) distributions observed along shoot length classes. Preference was defined as non-random oviposition on plant resources offered simultaneously and performance was defined as a measure of offspring survival (egg, larval or pupal), growth, or reproduction (Singer 1986; Thompson 1988).

To test shoot preference and to estimate the number of galled shoots, galled leaves, and galls of *A. microcapillata* we used two methods to find the estimated distribution. In *Method a*, shoot length was considered as an indicator of plant vigor and their frequency distribution used to find the estimated distribution (Price 1991). In *Method b*, the leaf distribution was used to find the estimated distribution because a leaf is needed for each gall to be formed, and the number of leaves in each size class was taken as a measure of the availability of resources, one leaf being the smallest parcel of resource liable to be used as an oviposition site by any single *A. microcapillata* female by shoot length classes (see Faria & Fernandes 2001 for details). We used *Method b* with the objective of inserting the amount of resources available (leaves) (Faria & Fernandes 2001) that was not estimated by *Method a* from PVH (Price 1991). Thus, let $P$ be the probability of any particular shoot and leaf being galled:

$$P = \frac{\text{Total sum of } G \text{ in the sample}}{\text{Total sum of } R \text{ in the sample}}$$

Where $G$ was defined as galled shoots, galled leaves or galls and $R$ was defined as resource, shoots or leaves. Thus, the ratio between $G$ and total of $R$ in a sample is taken as a measure of the probability of attack ($P$). If a size class $i$ is made of $M$ shoots, then $MP$ shoots will be galled. Subsequently, the preference prediction was tested by comparing the expected and observed distribution along shoot length classes using a Chi-square distribution (see Faria & Fernandes 2001). Shoot length classes with smaller sample sizes were combined to form classes containing at least five shoots per class in the expected distribution (Zar 1996). Proportion of larvae survival and gall diameter at each shoot length classes and their distribution along shoot length classes were used to estimate

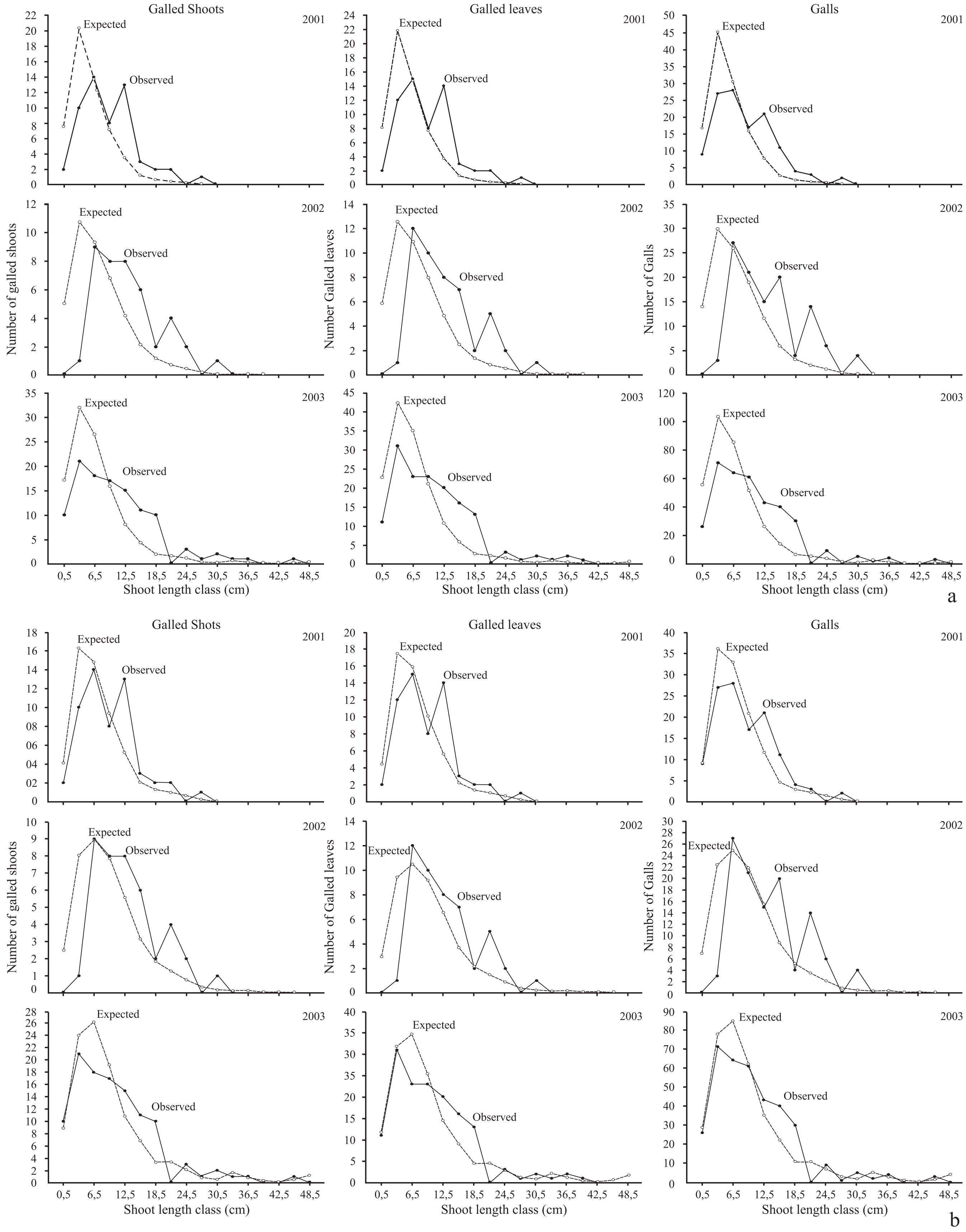

Fig. 3. Observed and expected distributions of total number of galled shoots (left column), galled leaves (middle column) and total number (right column) of *Asphondylia microcapillata* (Diptera, Cecidomyiidae) galls on *Bauhinia brevipes* (Fabaceae) during three consecutive years (2001, 2002, and 2003) in a cerrado vegetation (Três Marias, Minas Gerais). a) Preference estimated using shoots, see *Method a* by Price (1991) and b) Preference estimated using leaves abundance per shoot length classes (probability of attack though of abundance of resource, *Method b*).

the performance prediction. Differences in the proportion of larvae survival and gall diameter among shoot size classes of *B. brevipes* were analyzed by Kruskal-Wallis test or Mann-Whitney Test. We used non-parametric tests because the data did not present normal distribution (Zar 1996; STATISTICA 6.0 - StatSoft 2001).

## RESULTS

Temporal variation of attack, survivorship and mortality factors.

A total of 595 galls were found on 38,827 leaves and 5,791 *B. brevipes* shoots collected during the 3-yrs study period (Table I). Approximately three galls were found per galled leaf ($\overline{X}$ = 2.87 ± 2.00; range: one to 13 galls/leaf; n = 207). Overall, only 3.57 % and 0.65% of total amount of shoots and leaves sampled were galled, respectively. Gall abundance, galled shoots, and galled leaves were similar in 2001 and 2002, but increased in 2003. In 2003, the number of galled shoots and number of galls per shoot increased almost 3-fold in relation to 2001 (Table I).

Nearly one quarter of *A. microcapillata* larvae that successfully induced galls survived. Survival rates of *A. microcapillata* were 23.0%, 25.4%, and 19.5% in 2001, 2002, and 2003, respectively (Fig. 1). In 2001, parasitism was the most important mortality factor acting upon *A. microcapillata* larvae, accounting for 44.3% of killed larvae; followed by predation which killed 21.3% of total larvae. An increase in predation rate was observed in subsequent years (43.0% in 2002 and 62.7% in 2003). Unidentified parasitoid wasps killed 16.7% and 14.5% of larvae in 2002 and 2003, respectively. Mortality due to unknown factors reached its peak in 2002 (13.2%) but decreased in the following year to 3%. Few pathogenic fungi hyphae were found inside galls indicating that pathogens did not represent a strong mortality factor against *A. microcapillata* during the studied period (Fig. 1).

Resource distribution and oviposition preference.

Smaller shoots of *B. brevipes* were always more abundant whereas longer shoots were rare (Fig. 2). The percentage of galled shoots and galled leaves in each shoot length class increased with decreasing shoot length until the medium-size shoots (9.6-24.5 cm) in all years (Fig. 2). Larger shoots were rarely attacked, except in 2003 (Fig. 2). This trend was not expected by the PVH, which predicts higher herbivore attack rates on larger shoots classes.

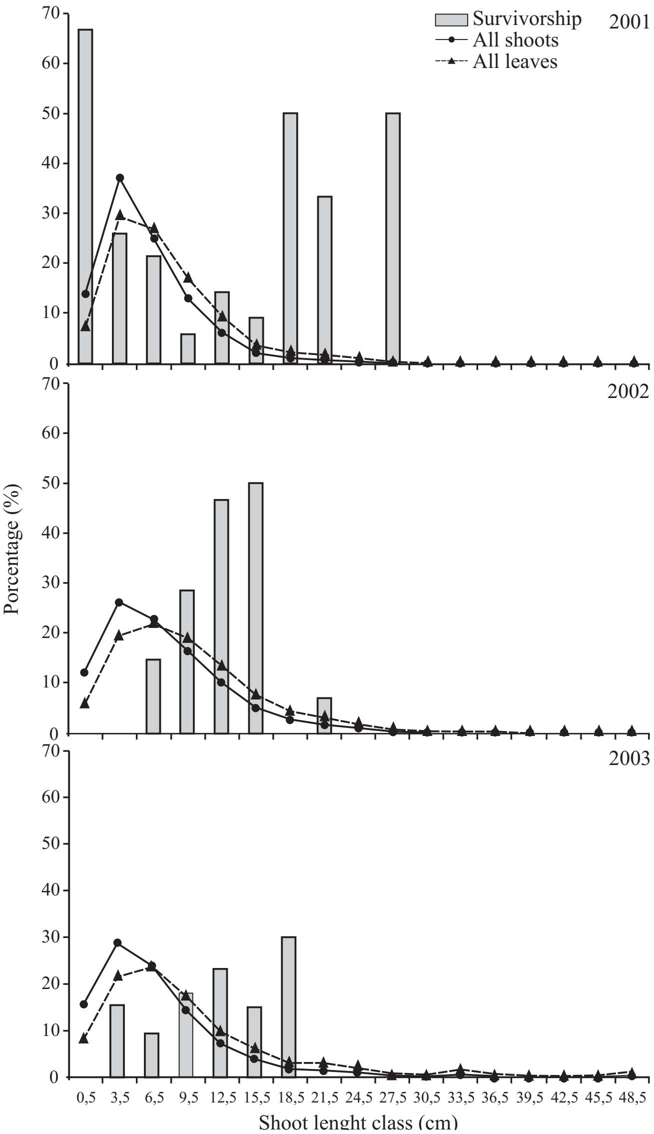

Fig. 4. Frequency distribution expressed as the percentage of total shoots, total leaves, and survivorship of *Asphondylia microcapillata* (Diptera, Cecidomyiidae) in each shoot length class of *Bauhinia brevipes* (Fabaceae) during three consecutives years (2001, 2002, and 2003) in a cerrado vegetation (Três Marias, Minas Gerais).

The analysis of oviposition preference based in *Method a* (shoot abundance) on the pattern of attack of *Asphondylia* showed that the observed number of galled shoots in each shoot length class differed from the expected value in all years (2001 - $\chi^2$ = 45.25 df = 4 $p < 0.0001$; 2002 - $\chi^2$ = 35.43 df = 4 $p < 0.0001$ and 2003 - $\chi^2$ = 45.44 df = 5 $p < 0.0001$; Fig. 3a). This same trend was observed for the number of galled leaves (2001 - $\chi^2$ = 44.94 df = 4 $p < 0.0001$; 2002 - $\chi^2$ = 41.19 df = 5 $p < 0.0001$ and 2003 - $\chi^2$ = 59.35 df = 6 $p < 0.0001$; Fig. 3a) and gall abundance (2001 - $\chi^2$ = 67.53 df = 5 $p < 0.0001$; 2002 - $\chi^2$ = 126.10 df = 6 $p < 0.0001$ and 2003 - $\chi^2$ = 198.21 df = 8 $p < 0.0001$; Fig. 3a).

When *Method b* (resource availability) was used, the number of galled shoots in each shoot length class differed from the expected value in 2001 ($\chi^2$ = 16.74 df = 4 $p < 0.002$) and 2002 ($\chi^2$ = 15.77 df = 4 $p < 0.003$), but not in 2003 ($\chi^2$ = 8.44 df = 6 $p = 0.208$; Fig. 3b). The same trend was observed for the number of galled leaves galls in 2001 ($\chi^2$ = 16.88 df = 4 $p < 0.002$), 2002 ($\chi^2$ = 17.22 df = 4 $p < 0.002$) and 2003 ($\chi^2$ = 12.18 df = 6 $p = 0.058$; Fig. 3b). The observed number of galls differed from the expected value in all years (2001 - $\chi^2$ = 21.09 df = 6 $p < 0.002$; 2002 - $\chi^2$ = 67.71 df = 7 $p < 0.001$, and 2003 - $\chi^2$ = 68.71 df = 9 $p < 0.001$; Fig. 3b).

Results shown by both methods indicate that the number of observed galled shoots and leaves and the number of galls

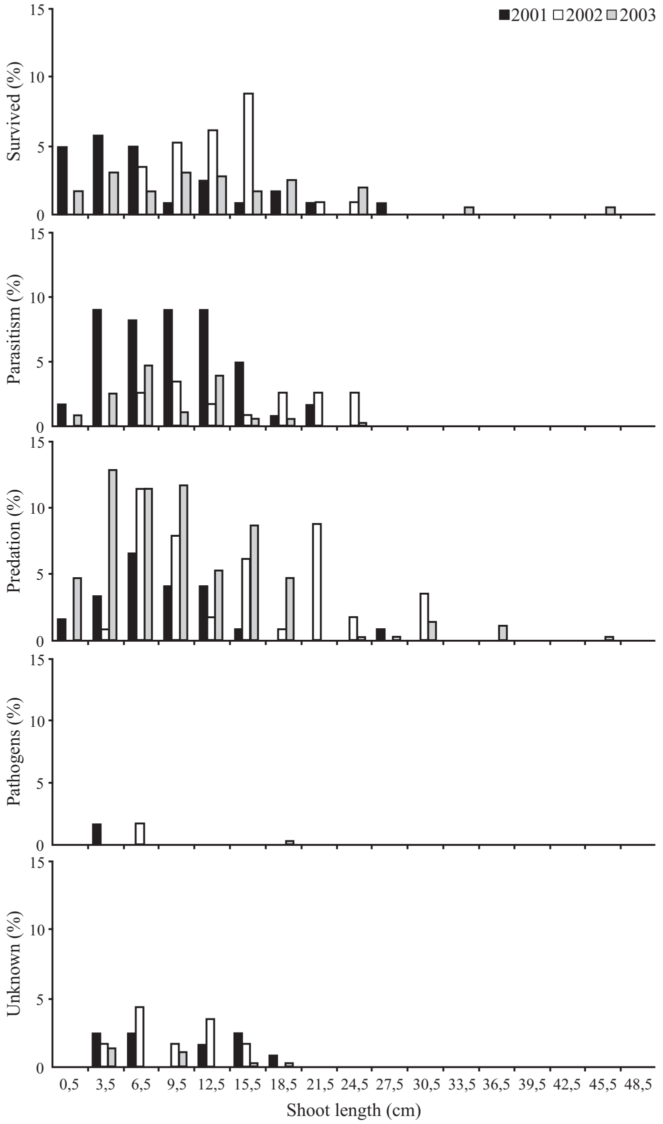

Fig. 5. Temporal variation of percent survivorship and mortality of the gall midge *Asphondylia microcapillata* (Diptera, Cecidomyiidae) in each shoot length class of *Bauhinia brevipes* (Fabaceae) during three consecutives years (2001, 2002, and 2003) in a cerrado vegetation (Três Marias, Minas Gerais).

were always smaller than expected on the smaller shoot classes. However, this pattern did not hold from the 9cm shoot length class upward. The observed gall abundance and galled shoots were always greater than expected on intermediate shoot length classes. Therefore, high levels of attack were observed on medium-sized shoots (9.5-24.5 cm). These results also suggest a lack of preference for smaller shoots because the attack rate on these shoot length classes was smaller than expected.

### Attack on medium-sized shoots.

Due to the higher preference for intermediate shoot length classes (9.5 cm-24.5cm), the data were further analyzed by separating the shoot length classes into three main classes: small (0.5–9.5cm), medium (9.6-24.5cm), and large (24.6-48.5cm) (Table II). More than 50% of the attacked shoots and galled leaves were concentrated on medium-sized class shoots. Medium-sized shoots supported from 46% to 70% of the total galls sampled during the three years of study. When the effect of resource availability was taken into account by dividing the number of galls per number of leaves in each shoot class, medium-sized shoots supported from 47% to 57% of all galls.

Furthermore, during two consecutive years *A. microcapillata* survival was greater on medium-sized shoots (2002 - Kruskal-Wallis test: $H_{(2, N=17)} = 9.492$, $p = 0.009$ and 2003 - Kruskal-Wallis test: $H_{(2, N=17)} = 9.659$, $p = 0.008$; Fig. 4-5, Table II). In 2001, higher survival was achieved on the smaller shoots (Fig. 4-5, Table II) (Kruskal-Wallis test: $H_{(2, N=17)} = 12.117$, $p = 0.002$). The percentage of larvae killed by natural enemies varied widely among shoot length classes, without a consistent pattern (Fig. 5, Table II). However, gall diameter, another indicator of larval performance, did not differ among shoot size classes in 2001 ($U = 326.5$, $p = 0.532$), 2002 (Kruskal-Wallis test: $H_{(2, N=17)} = 2.237$, $p = 0.327$) or 2003 (Kruskal-Wallis test: $H_{(2, N=17)} = 2.2$, $p = 0.333$).

## DISCUSSION

The relative importance of the mortality factors acting upon *Asphondylia* galls varied during the study period. In 2001, the attack by parasitoid wasps represented the strongest mortality factor acting upon *A. microcapillata*, while in the following years, predators killed most of larvae. In different plant-herbivore-parasitoid systems the attack of parasitoid wasps are regarded as the main mortality factor of galling insects (Weis *et al.* 1985; Price & Clancy 1986; Espírito-Santo *et al.* 2004). The consumption of gall tissue by Lepidoptera larvae, adult Coleoptera and Orthoptera may kill the galling larva or lead to a desiccation process (Fernandes & Price 1992). Interestingly, the mortality factors acting upon the other gall midge, *S. macrocapillata*, differed significantly from that acting upon *A. microcapillata* on the same host plant. On *S. macrocapillata*, an induced resistance mechanism, hypersensitive reaction (a bottom-up effect) accounted for more than 90% of the mortality, making few galls available to be found and killed by natural enemies (Fernandes 1990, 1998; Fernandes *et al.* 2000; Santos *et al.* 2008). Pathogenic fungi accounted for no more than 3% as predicted by Fernandes & Price (1992) in xeric environments. In general, we observed that the *A. microcapillata* mortality ratio by natural enemies is in agreement with that found for many other galling species (e.g., Weis *et al.* 1985; Price & Clancy 1986; Abrahamson & Weis 1987; Espírito-Santo *et al.* 2004). Regardless of the strength of each individual mortality factor, the population dynamics of *A. microcapillata* was not affected because survival ratio was relatively constant. Our results also indicate an important role of temporal variability of natural enemies on the performance of *A. microcapillata*.

*Asphondylia microcapillata* oviposited and survived preferentially on medium-sized shoots (9.6-24.5 cm). This result does not corroborate the predictions of the PVH, which predicts a strong female preference and increased larval survival on the largest plant modules (Price 1991). However, these results are similar to those reported by Craig *et al.* (1999),

Table II. Percentage of galled shoots and leaves, galls, gall survival rate, and mortality factors rates of *Asphondylia microcapillata* (Diptera, Cecidomyiidae) in different group of shoot length classes of *Bauhinia brevipes* (Fabaceae) during three consecutive years (2001, 2002, and 2003) in a cerrado vegetation (Três Marias, Minas Gerais).

| Year | Shoot size Classes | Shoot Classes | Preference | | | | Performance | Mortality factors | | | | Performance |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Galled Shoots | Galled Leaves | Galls | Galls/ leaves | Survival | Parasitism | Predation | Pathogens | Others | Gall Diameter |
| 2001 | Small | 0.5-9.5 | 47.27 | 49.15 | 52.46 | 18.13 | 67.86 | 42.59 | 53.85 | 100 | 50 | 3.32 |
| | Medium | 9.6-24.5 | 50.91 | 49.15 | 45.90 | 55.09 | 28.57 | 57.41 | 42.31 | 0 | 50 | 3.50 |
| | Large | 24.6-48.5 | 1.82 | 1.69 | 1.64 | 26.78 | 3.57 | 0 | 3.85 | 0 | 0 | 2.06 |
| 2002 | Small | 0.5-9.5 | 24.39 | 27.08 | 26.32 | 5.87 | 13.79 | 15.79 | 28.57 | 100 | 46.67 | 2.87 |
| | Medium | 9.6-24.5 | 73.17 | 70.83 | 70.18 | 56.62 | 86.21 | 84.21 | 63.27 | 0 | 53.33 | 3.14 |
| | Large | 24.6-48.5 | 2.44 | 2.08 | 3.51 | 37.51 | 0 | 0 | 8.16 | 0 | 0 | 0.58 |
| 2003 | Small | 0.5-9.5 | 44.14 | 44.22 | 44.85 | 14.85 | 32.86 | 55.77 | 46.22 | 0 | 45.45 | 3.32 |
| | Medium | 9.6-24.5 | 50.45 | 51.02 | 50.97 | 46.59 | 61.43 | 44.23 | 48.89 | 100 | 54.55 | 3.03 |
| | Large | 24.6-48.5 | 5.41 | 4.76 | 4.18 | 38.55 | 5.71 | 0.00 | 4.89 | 0 | 0.00 | 2.06 |

who reported that *Eurosta solidaginis* (Diptera, Tephritidae) survival was highest on ramets with intermediate growth rates of *Solidago altissima* (Asteraceae). Our results also support the parabolic curves relationship reported by Mckinnon *et al.* (1999) who found that *Adelges abietis* (Linnaeus, 1758) (Hemiptera, Adelgidae) gall abundance and density were higher on intermediate-sized trees and shoots of the white spruce *Picea glauca* (Moench) Voss (Pinaceae). Additionally, they speculated that *A. abietis* lacks the necessary resources for successful gall formation on smaller shoots and that it is unable to produce a stimulus strong enough to induce gall formation on large shoots. Recently, Flaherty & Quiring (2008) proposed the optimal module size hypothesis (OMSH) using this same model systems; a shoot galling adelgid on white spruce. The OMSH predicts that galler performance will be greatest on intermediate-sized modules, based on a tradeoff between ease of gall induction on small modules and increased resource availability in large modules. After evaluating the predictions of the PVH and OMSH during a two-year field study examining gall induction and full gall development success; Flaherty & Quiring (2008) found more support to the OMSH than the PVH (but see Cornelissen *et al.* 2008). In the present study, our ecological data do not allow a physiological interpretation on the differential capacity of *A. microcapillata* to stimulate the different size classes of *B. brevipes* shoots to respond gall induction.

The relationship between oviposition preference and offspring performance is crucial to understand the evolution of interactions between herbivorous insects and their host plants (Thompson & Pellmyr 1991). A strong link between female preference and larval performance of *A. microcapillata* was found on medium-sized shoots on *B. brevipes*. Higher survival rates resulted from the female preferential attack on medium-sized shoots can provide an evolutionary mechanism for the maintenance of preference on intermediate shoots. Otherwise, this pattern should be further studied in relation to the other herbivore insects in the community that feed on similar resources.

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