

Long term oviposition preference and larval performance of *Schizomyia macrocapillata* (Diptera: Cecidomyiidae) on larger shoots of its host plant *Bauhinia brevipes* (Fabaceae)

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Abstract The Plant Vigor Hypothesis (PVH) proposes that natural selection on female oviposition choice results from higher fitness of larvae on more vigorous and larger plant modules. For six consecutive years we tested the PVH predictions by investigating the effect of shoot size of *Bauhinia brevipes* (Fabaceae) on the oviposition preference and offspring survival of the gall-midge *Schizomyia macrocapillata* (Diptera: Cecidomyiidae). Additionally, we analyzed the effects of bottom-up and top-down mortality forces on the system. The hypersensitive reaction (bottom-up effect) accounted for more than 90% larval mortality of *S. macrocapillata*, making available few galls to be found and killed by natural enemies (top-down effect). Smaller shoots were always more abundant while longer shoots were rare. Nevertheless, the percent number of galls induced by *S. macrocapillata* was up to 10-fold greater on the largest shoots, corroborating the preference prediction of the PVH. *Schizomyia macrocapillata* should use over-exploit larger shoots to maximize the preference for, and consequently increase the performance on these shoots. Our results partially support the performance prediction of the PVH: (1) the observed survival was higher than expected on longer shoots, and (2) the ratio of survival per shoot was positively related with shoot length only in 2 years. Thus, we found a link between female preference and larval performance on large-sized shoots, at least in some years. The gall-midge attack pattern in this study might be an evolved response to maximize the female preference and increased larval performance on longer shoots of the host plant.

Keywords Bottom-up and top-down forces · Herbivory · Host selection · Insect galls · Mortality factors · Plant Vigor Hypothesis · Preference–performance

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Introduction

A current goal in plant–insect ecology is the understanding of the selective factors accounting for the use of host plants by insect herbivores. The linkage between preference and performance is a key factor in the evolutionary ecology of herbivores (Thompson 1988) and can be influenced by top-down forces, such as natural enemies (Bernays and Graham 1988), by bottom-up forces, such as environmental variation (White 1978) and even by plant resource limitation (Price 1990). The preference of insect herbivores for host plant species, individuals within a species, or traits of host plants, such as module size, can influence the performance, distribution and abundance of herbivores. In this warm field many hypotheses have been proposed to understand the described patterns of attack by herbivorous insects at several ecological scales (Price 1997).

For galling insects, adult reproduction and larval survival depend on successful female oviposition in plant tissue (Abrahamson and Weis 1987). The Plant Vigor Hypothesis (PVH; Price 1991) predicts that insect herbivores will choose preferentially large, more vigorously growing plants or plant modules and that offspring performance will be greater on these more vigorous plants or plant modules. Its predictions have been widely tested in diverse ecosystems around the world, being either fully supported (Price et al. 1987a, b; Craig et al. 1989; Kimberling et al. 1990; Price and Ohgushi 1995; Stein and Price 1995; Woods et al. 1996; Carr et al. 1998; Inbar et al. 2001; de Bruyn et al. 2002), partially supported (Cornelissen et al. 1997; Prado and Vieira 1999; Cornelissen and Fernandes 2001c; Fritz et al. 2000; Ferrier and Price 2004), or refuted (de Bruyn 1995; Faria and Fernandes 2001; Rehill and Schultz 2001). Faria and Fernandes (2001) argued that the amount of resources has been generally underestimated in large size class shoots. In their study, the high attack rates of females of *Baccharopelma dracunculifoliae* (Hemiptera: Psyllidae) on the longest shoots of *Baccharis dracunculifolia* (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 preference for longer, fastest growing shoots disappeared.

Bauhinia brevipes Vogel (Fabaceae) supports a rich and phylogenetically unrelated insect herbivore fauna (Cornelissen et al. 1997; Cornelissen and Fernandes 1998, 2001c), therefore offering an excellent opportunity for the study of preference and performance of galling insects and to understand general patterns of attack by herbivores. For six consecutive years, the attack and performance by a leaf galling species, *Schizomyia macrocapillata* Maia (Diptera: Cecidomyiidae) (Maia and Fernandes 2005) on *B. brevipes* was studied. *Bauhinia brevipes* leaf flush occurs once a year, and because this gall midge requires immature expanding or unfolded leaves for gall induction, high quality host organs are only available during a short period (Fernandes 1998; Silveira FAO et al. submitted). In addition, an inverse relationship between shoot growth rates and tannin concentration was reported by Cornelissen and Fernandes (2001a, b), who showed that mature leaves had higher concentrations of tannins than young leaves, and that young leaves are approximately 60% more likely to be attacked than mature leaves by free-feeding herbivores.

Previous work on *S. macrocapillata* failed to find any positive relationship between female preference and larval performance for longer and more vigorous shoots (Cornelissen et al. 1997; Fernandes 1998; Cornelissen and Fernandes 2001c).

Asphondylia microcapillata, another *B. brevipes* leaf gall midge, and a free-feeding geometrid also lacked a consistent pattern of module preference (Cornelissen et al. 1997). The goal of this study was to test the PVH on a long term basis by addressing two questions: (1) what is the effect of shoot size on the oviposition preference by *S. macrocapillata*?; and (2) what is the effect of shoot size on *S. macrocapillata* off-spring survival? We tested the prediction that gall induction is significantly higher on larger shoots and that larval fitness is positively associated with larger shoots. In addition, we analyzed the effects of bottom-up and top-down mortality factors on preference and performance of *S. macrocapillata*.

Methods

Study area

This study was performed at the Estação Ecológica de Pirapitinga—IBAMA (EEP) in Três Marias, Minas Gerais, southeastern Brazil. The EEP is a 1,100 ha man-made island, built in 1965 in the Três Marias reservoir (18°23'S, 45°20'W), at an altitude of 560 m a.s.l. (Azevedo et al. 1987). The average annual temperature varies from 21°C to 25°C and the average annual precipitation is 1,200 mm, with rainy summers and dry winters (Silveira FAO et al. submitted). The vegetation is primarily cerrado (Brazilian savanna) with sandy, shallow and also nutrient-poor soils, with high aluminum saturation (Gonçalves-Alvim and Fernandes 2001).

The system

Bauhinia brevipes is a deciduous shrub, growing up to 3 m high and is abundant in Cerrado vegetation (savanna) but is also found at the Caatinga (seasonally dry forest) (Vaz and Tozzi 2003). Blooming takes place between June and September and fruiting 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. Xylem water potential values below -1.0 MPa suggest the presence of a shallow root system and deciduousness is required to reestablish water status prior to flowering and leaf flushing (Silveira FAO et al. submitted).

Bauhinia brevipes is attacked by at least seven species of galling insects. Three species of leaf gall midges (Diptera: Cecidomyiidae) attack the host plant: *Schizomyia macrocapillata*, *Asphondylia microcapillata*, and a new species yet to be described (see Maia and Fernandes 2005). The most abundant galls on *B. brevipes* are those induced by *A. microcapillata* and *S. macrocapillata*. Four insect species induce stem galls: one Cecidomyiidae, one Lepidoptera, and two Curculionidae (Coleoptera) (Cornelissen et al. 1997; Cornelissen and Fernandes 1998, 2001c; Cornelissen et al. 2002). *Bauhinia brevipes* is also attacked by free-feeding herbivores: *Pantomorus* sp. (Coleoptera: Curculionidae), *Naupactus lar* (Coleoptera: Curculionidae) (Cornelissen and Fernandes 2001c; Cornelissen et al. 2002), an unidentified species of Geometridae (Lepidoptera) (Cornelissen et al. 1997), four species of grasshoppers (Acrididae) and eight species of termites (Murcia SL et al. submitted).

Our study focused on the spherical, reddish-orange and one-chambered gall induced by *Schizomyia macrocapillata* on the adaxial leaf surface. *Bauhinia brevipes* strongly reacts to *S. macrocapillata* gall induction by eliciting a rapid and lethal response to the developing larvae. The hypersensitivity against gall formation is the most important host-driven mortality factor (bottom-up force) in the population dynamics of *S. macrocapillata* (Fernandes 1998). More than 90% of the larvae fail to induce galls due to the effectiveness of this induced resistance by the host plant (Cornelissen and Fernandes 1997; Cornelissen et al. 2002). A preliminary description of the morphological and anatomical changes that occur in the leaf tissues during the elicitation of hypersensitivity against *S. macrocapillata* is provided by Fernandes et al. (2000). Because galls represent a strong sink to host plant photosynthates, the preclusion of gall-induction at this initial phase results in a decrease in the impact of gall impinged against the host plant (Fernandes 1990).

Sampling and statistical analysis

Patterns of attack were determined over a 6-year period (1999–2004) by randomly collecting 25 shoots around the canopy of the same 159 randomly selected *B. brevipes* individuals. *Bauhinia brevipes* leaf flush occurs at the onset of the rainy season (mid-October) when oviposition by *S. macrocapillata* takes place. Shoot collection was performed early in December, on a single day, when most shoots were mature. Shoots were bagged, numbered and taken to the laboratory where their length, total number of leaves, number of galls, and galled leaves were recorded. The lengths of shoots were divided in size classes of 3 cm based in previous studies (see Cornelissen and Fernandes 2001c and references therein), with shoot length classes ranging from 0.2 cm (lowest class) to 45.2 cm (highest class) and with usually 10–16 incremental classes of 3 cm each. 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). In this study, preference was estimated by quantifying gall abundance and number of galled shoots, while performance was estimated by counting the number of larvae that survived.

The relationship between preference or performance with shoot length classes was tested by simple linear regressions (Zar 1996; STATISTICA 6.0 StatSoft 2001). Number of galls, galled shoots, survival, and mortality factor rates were divided by the number of shoots in each size class in an attempt to eliminate the effects of abundance of shoots and to eliminate the effects of longest shoots having higher probability of being attacked (Gonçalves-Alvim et al. 1999; Cornelissen and Fernandes 2001c).

To test the differences between observed and expected distribution of female preference or larval performance of the galling insect, shoot length was considered as an indicator of plant vigor and their distribution was used to find the estimated distribution. Let P be the probability of any particular shoot and leaf being galled, where:

$$P = \frac{\text{Sum total of } G \text{ in the sample}}{\text{Sum total of shoots in the sample}}$$

G could be defined as number of galled shoots, galls or larvae survived. If a size class i is made of M shoots, then MR shoots will be galled, for instance. Thus, the ratio between G and total of shoots in a sample is taken as a measure of the probability of attack or survivorship (see Faria and Fernandes 2001). Afterward, the preference and performance was tested by comparing the expected and observed distribution along shoot length classes using the non-parametric Chi-square test (see Faria and Fernandes 2001; STATISTICA 6.0 StatSoft 2001). Less well-represented shoot length classes were combined to form classes containing at least five shoots per class, in the expected distribution (Zar 1996).

Data on larval survival and mortality factors were compared with data on female preference to test for a linkage between female preference and larval performance. Mortality factors, both top-down and bottom-up, acting upon the galling larva were grouped in the following categories: parasitoidism, predation, pathogens, hypersensitivity and unidentified factors (for details see Fernandes and Price 1992). To understand the effect of mortality factors by shoot length, all factors were also divided into 3 cm shoot length classes (see Fernandes 1998) and compared with preference and performance distributions.

Results

Resource distribution and percent of attack

During the six consecutive years we recorded the attack by *Schizomyia macrocapillata* on 106,019 leaves found on 15,202 shoots. Of the 29,874 galls by *S. macrocapillata* recorded on these leaves during the studied period, 1,302 developed galls resulted in adults of the galling insect. The elicitation of hypersensitivity by the host plant killed 27,634 larvae before gall formation while 938 galls successfully induced were killed by predators, pathogens and parasitoids. Nearly 54% of shoots were galled, while approximately 15% of leaves were galled (Table 1). Among the leaves attacked, a mean of three galls was found per leaf (2.91 ± 3.16 , $\bar{x} \pm SE$; range: 1–27 galls per leaf; $n = 447$). Gall abundance, number of galled shoots and galled leaves were higher in 1999 and decreased along the observation period. At 2004 the number of galled shoots had decreased by almost 3-fold, while the number of galled leaves and number of galls decreased almost 4-fold compared with 1999 (Table 1).

Table 1 Number total of shoots and leaves, and their respective abundance and percent of galled shoot and leaves induced by *Schizomyia macrocapillata* on *Bauhinia brevipes* during six consecutive years. Attacked leaves represent the abundance and percent of leaves attacked by free-feeding insect species

Year	Shoots	Galled shoots	Leaves	Galled leaves	Attacked leaves
1999	2,893	2,170 (75.01%)	21,869	4,822 (22.05%)	9,359 (42.80%)
2000	2,180	1,316 (60.37%)	14,926	2,563 (17.17%)	4,686 (31.39%)
2001	2,720	1,875 (68.93%)	17,228	3,583 (20.80%)	7,107 (41.25%)
2002	2,599	1,254 (48.25%)	18,623	2,103 (11.29%)	4,018 (21.58%)
2003	2,409	871 (36.16%)	15,949	1,332 (8.35%)	2,570 (16.11%)
2004	2,401	793 (33.03%)	17,424	1,157 (6.64%)	2,134 (12.25%)
Total	15,202	8,279 (54.46%)	106,019	15,560 (14.68%)	29,874 (28.18%)

Attacked leaves by free-feeding insect species represent approximately a third of the total amount of leaves (Table 1).

As it is generally observed in woody plants, smaller shoots were always more abundant while longer shoots were rare (Fig. 1). However, the percent of galled shoot by *S. macrocapillata* female was positively correlated with increasing shoot length (Fig. 1). The percent of attack on the largest shoot length classes was 2–10 times greater than that on the smaller shoot length classes (1999— $r^2 = 0.64$; $df = 1,10$, $F = 17.959$, $P < 0.01$; 2000— $r^2 = 0.61$, $df = 1,11$, $F = 17.307$, $P < 0.01$; 2001— $r^2 = 0.65$, $df = 1,8$, $F = 15.069$, $P < 0.01$; 2002— $r^2 = 0.81$, $df = 1,11$,

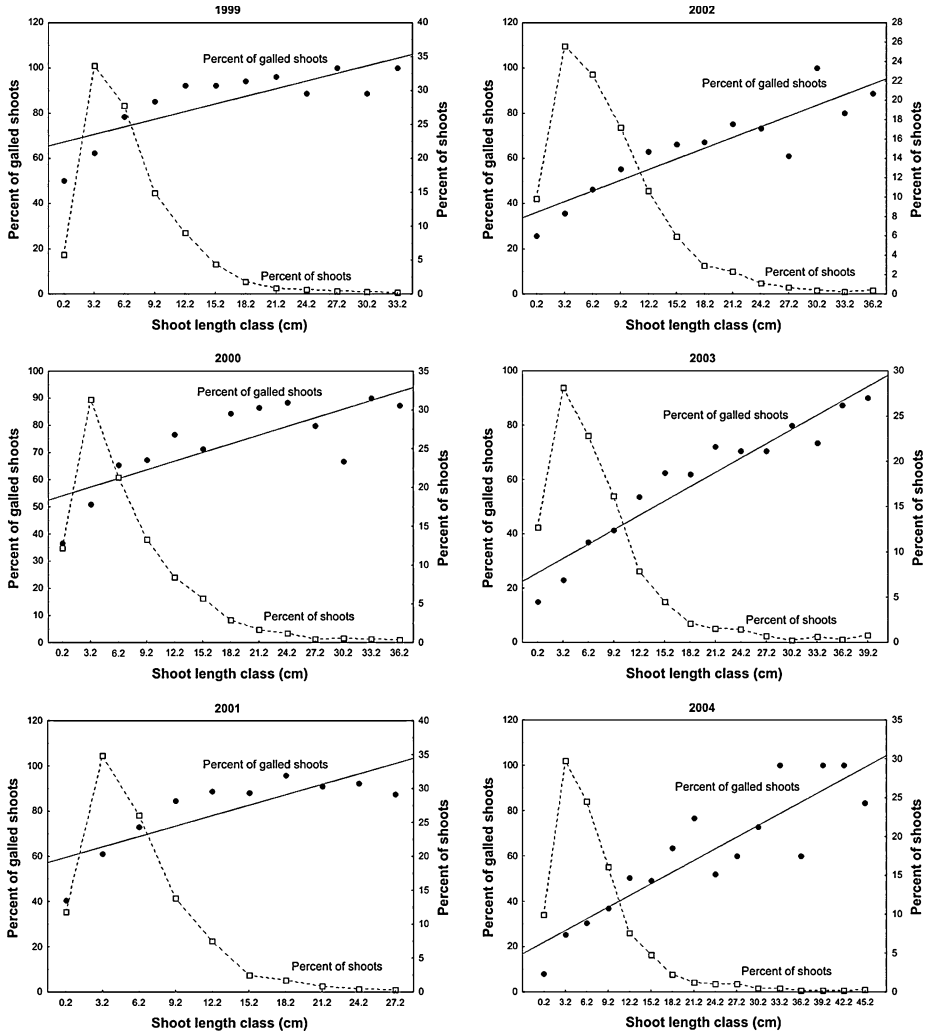


Fig. 1 Percent of galled shoots by *Schizomyia macrocapillata* on different shoot length classes and the percent of shoots available in each shoot length class of *Bauhinia brevipes* during six consecutive years (1999–2004). The regression equations between percentage of galled shoots and shoot length class were: 1999— $y = -273.939 + 3.378 * x$; 2000— $y = -268.679 + 3.195 * x$; 2001— $y = -406.356 + 4.613 * x$; 2002— $y = -441.717 + 4.731 * x$; 2003— $y = -507.005 + 5.274 * x$ and 2004— $y = -498.235 + 5.150 * x$

$F = 45.887$, $P < 0.0001$; 2003— $r^2 = 0.92$, $df = 1,12$ $F = 129.178$, $P < 0.0001$ and 2004— $r^2 = 0.79$, $df = 1,14$, $F = 53.618$, $P < 0.0001$, Fig. 1). Therefore, the oviposition preference by *S. macrocapillata* for larger shoots was corroborated in this long term tropical study as predict by the PVH.

Observed versus expected female preference and larval survival distribution

The analysis of oviposition preference showed that the number of galls in each shoot length class differed significantly from the expected value in the six consecutive years (Fig. 2). The same trend was observed for the number of galled shoots (Fig. 3). The larval performance in each shoot length class also differed significantly from the expected value in the six consecutive years (Fig. 4). These results indicate that the observed number of galls, galled shoots and surviving larvae were always smaller than expected on smaller shoot classes. On the other hand, usually from 9-cm shoot length class upward there was an inversion of the tendency, and the observed gall abundance and galled shoots were always greater than expected in these classes (9.2–45.2 cm). These results suggest an over-preference and over-performance on larger shoots.

Bottom-up and top-down mortality factors

Only 3–9% of *S. macrocapillata* oviposition events successfully resulted in mature galls ($5.22 \pm 2.73\%$; $\bar{x} \pm SD$; range 2.71–9.47%; Fig. 5). Hypersensitivity was the most important mortality factor acting upon *S. macrocapillata* larvae. This bottom-up induced mechanism killed more than 90% of the larvae ($90.61 \pm 6.37\%$; $\bar{x} \pm SD$; range 78.02–94.45%; Fig. 5). Otherwise, an increase in the survivorship rate was observed through the study period, coinciding with a decrease in the hypersensitivity rate. Among the top-down mortality factors, predation was the most important ($2.94 \pm 3.75\%$; $\bar{x} \pm SD$; range 0.90–10.54%; Fig. 5); followed by parasitism ($0.48 \pm 0.48\%$; $\bar{x} \pm SD$; range 0.12–1.41%; Fig. 5), while few pathogenic fungus hyphae were found inside the galls ($0.21 \pm 0.19\%$; $\bar{x} \pm SD$; range 0–0.40%). Mortality due to unknown factors represented nearly 0.5% of the galls killed ($0.53 \pm 0.27\%$; $\bar{x} \pm SD$; range 0.19–0.85%; Fig. 5). Survivorship and mortality percent on each shoot length class apparently showed an inconsistent pattern for each shoot length class in all years (Fig. 6). Hypersensitivity percent on each shoot length class apparently showed a similar pattern to that observed for shoot and leaf distribution; i.e., mortality decreased with increasing shoot length in all years (Fig. 6).

Number of galls, survivorship and mortality per abundance of shoots

Linear regressions showed that shoot length class and attack per shoots were positively related. Variation in shoot length explained 59–94% of the variation in the number of galls per shoot length class (Table 2). Hence, these results corroborate the predictions of the PVH. The ratio of survival per shoot was positively related with shoot length in 2 years. Variation in shoot length explained 48 and 66% of survival per shoot (Table 2, Fig. 6). These results indicate that the performance prediction of the PVH was partially supported as it varied during the study period. Top-down mortality per shoot length classes in shoot length classes did not show any

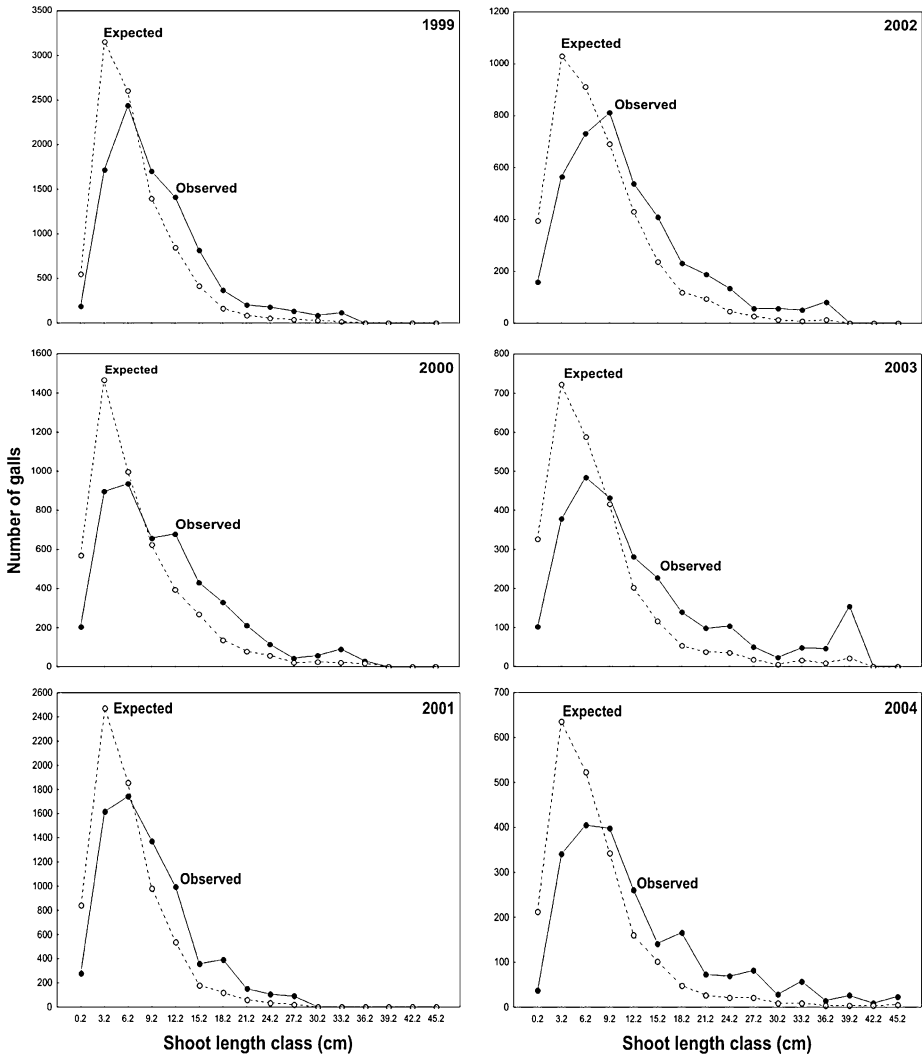


Fig. 2 Observed and expected distributions of total number of *Schizomyia macrocapillata* galls on *Bauhinia brevipes* during six consecutive years (1999— $\chi^2 = 3,210.88$, $df = 11$, $P < 0.0001$; 2000— $\chi^2 = 1,618.33$, $df = 12$, $P < 0.0001$; 2001— $\chi^2 = 2,531.22$, $df = 9$, $P < 0.0001$; 2002— $\chi^2 = 1,668.99$, $df = 12$, $P < 0.0001$; 2003— $\chi^2 = 2,016.98$, $df = 13$, $P < 0.0001$ and 2004— $\chi^2 = 1,451.55$, $df = 12$, $P < 0.0001$)

relationship with shoot length. On the other hand, the number of hypersensitivity reactions per shoot was strongly related with shoot length class (range 43–94% of the variation) for all years (Table 3, Fig. 6).

Discussion

Offspring survival of galling insects depends on the ability of the adult females to find suitable sites for larval growth and survival. Presumably, natural selection

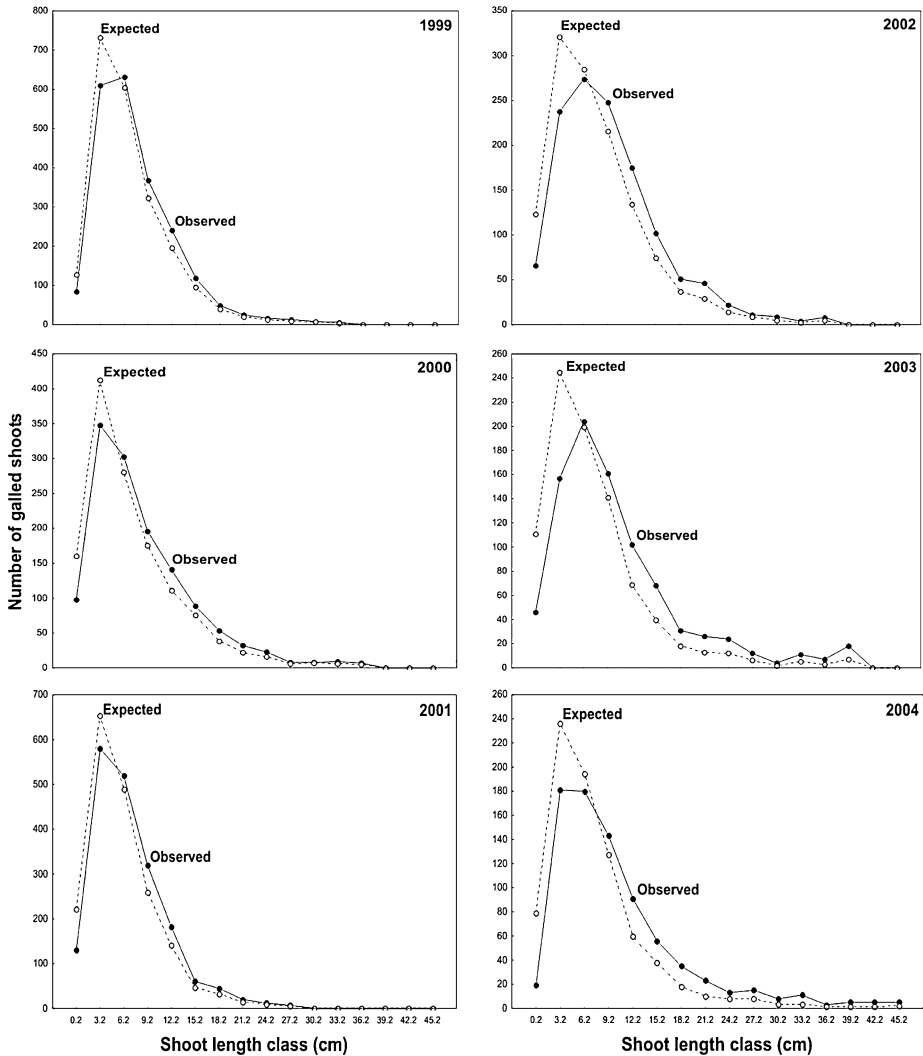


Fig. 3 Observed and expected distributions of number of galled shoots of *Schizomyia macrocapillata* on *Bauhinia brevipes* during six consecutive years (1999— $\chi^2 = 63.11$, $df = 10$, $P < 0.0001$; 2000— $\chi^2 = 65.97$, $df = 11$, $P < 0.0001$; 2001— $\chi^2 = 84.04$, $df = 9$, $P < 0.0001$; 2002— $\chi^2 = 104.71$, $df = 10$, $P < 0.0001$; 2003— $\chi^2 = 177.75$, $df = 10$, $P < 0.0001$ and 2004— $\chi^2 = 164.29$, $df = 10$, $P < 0.0001$)

should act to create some kind of correlation between female oviposition preference and performance of offspring on plants (Thompson 1988). The PVH proposes that natural selection on female oviposition choice results from higher fitness of larvae on larger modules (see Price 1991). Our results showed that the percent of shoots and leaves galled by *S. macrocapillata* increased with shoot length classes as predicted by PVH [also observed in previous studies of this system (Fernandes 1998; Cornelissen et al. 1997; Cornelissen and Fernandes 2001c)].

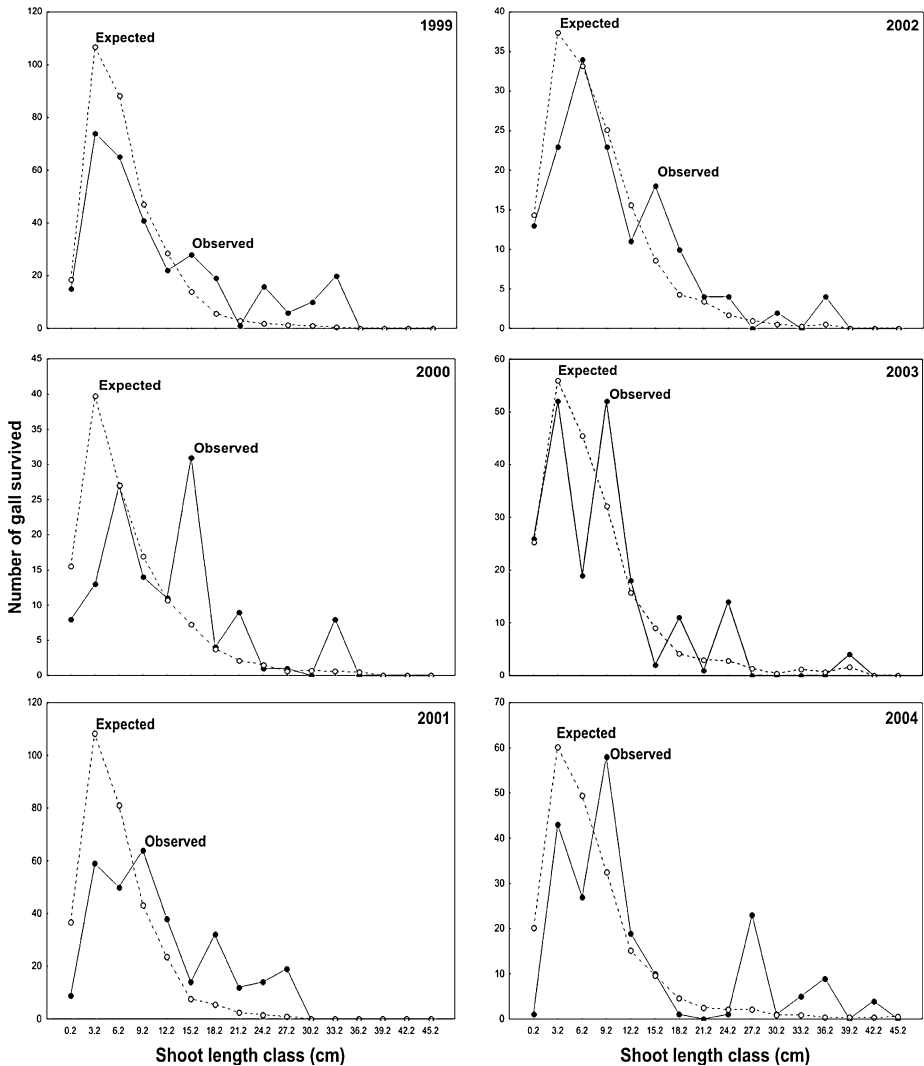


Fig. 4 Observed and expected distribution of total number of *Schizomyia macrocapillata* galls that survived on *Bauhinia brevipes* during six consecutive years (1999— $\chi^2 = 322.13$, $df = 7$, $P < 0.0001$; 2000— $\chi^2 = 117.54$, $df = 6$, $P < 0.0001$; 2001— $\chi^2 = 512.11$, $df = 6$, $P < 0.0001$; 2002— $\chi^2 = 30.33$, $df = 6$, $P < 0.0001$; 2003— $\chi^2 = 47.86$, $df = 6$, $P < 0.0001$ and 2004— $\chi^2 = 110.52$, $df = 6$, $P < 0.0001$)

The observed female preference and larval performance were always greater than expected on larger shoot classes. We suggest that *S. macrocapillata* over-attacks the larger shoots that maximize the preference for, and consequently increase the performance on long shoots. Linear regression analyses also support the predictions of higher attack and partially support the predictions for higher rates of survivorship on longer shoots. Longer shoots offered more leaves to be used by gallers than shorter shoots, but the percent of shoots was distributed un-proportionally along shoot length classes. For this reason the rates of attack and survival per abundance of shoots in each shoot length class must be considered in order to have an exact and

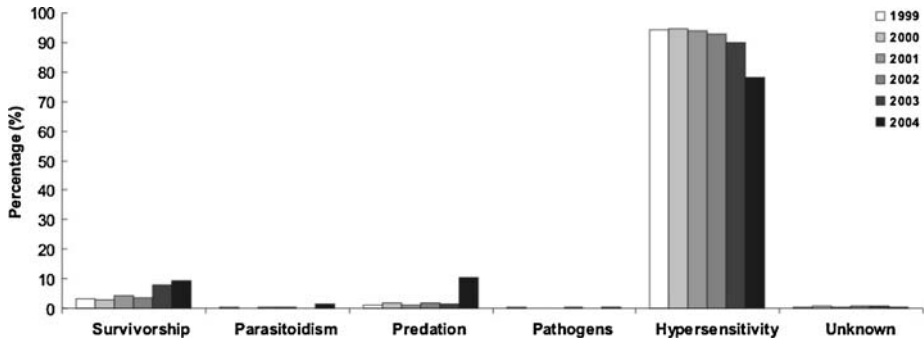


Fig. 5 Temporal variation in the percent survivorship and mortality of *Schizomyia macrocapillata* on *Bauhinia brevipes* during six consecutive years (1999–2004)

comparative measure among shoot length classes (Gonçalves-Alvim et al. 1999; Cornelissen and Fernandes 2001a, b). Our results showed that females of *S. macrocapillata* preferentially selected the longer shoot classes of *B. brevipes* where performance was higher in two out of 6 years. Thus, we found a link between female preference and larval performance on large-sized shoots, at least in some years. Although we found some variation, higher survival rates as a result of female preferential attack on large-sized shoots should provide an evolutionary mechanism for the maintenance of preference on large shoots.

Our results indicate the importance of temporal variability of plant resistance and natural enemies on the performance of *S. macrocapillata* on *B. brevipes*. Several studies have demonstrated the importance of bottom-up effects on population regulation of herbivores (e.g., Fernandes 1990, 1998; Wratten 1992; Fernandes et al. 2000; Price and Hunter 2005). The impact of bottom-up factors in controlling the *S. macrocapillata* populations was demonstrated by the high levels of plant resistance. Regardless, of the studied year, the hypersensitive reaction accounted for more than 90% larval mortality, making available few galls to be killed by natural enemies (top-down effect) (Fernandes et al. 2000). Moreover, hypersensitivity was common in all classes of shoot-length suggesting that hypersensitivity strongly influenced the performance of the galling larvae. Top-down forces do not appear to be selective factors favoring preference and/or performance in this system, as comparatively fewer galls are formed to be killed by natural enemies. Although mortality driven by natural enemies did not show any relationship with shoot length classes, larval predation represented the strongest top-down mortality factor acting upon larvae across shoot-length classes. The consumption of the *S. macrocapillata* gall tissue by lepidopteran larvae, adult coleopterans and orthopterans may kill the galling larvae or lead to a desiccation process (see Fernandes and Price 1992; Fernandes 1998). The attack by natural enemies on galling insects is variable, ranging from relatively low levels to as high as 99% (Abrahamson and Weis 1987) and, therefore, the data on *S. macrocapillata* mortality is in agreement with that found in many other systems. Natural enemies did not play a role in the correlation between preference and performance of *Nematus oligospilus* (Tenthredinidae) (Carr et al. 1998).

In conclusion, this study provides additional support for the importance of how plant traits determine the distribution and abundance of herbivores and how bottom-up and top-down forces drive preference and performance of an herbivore. Our

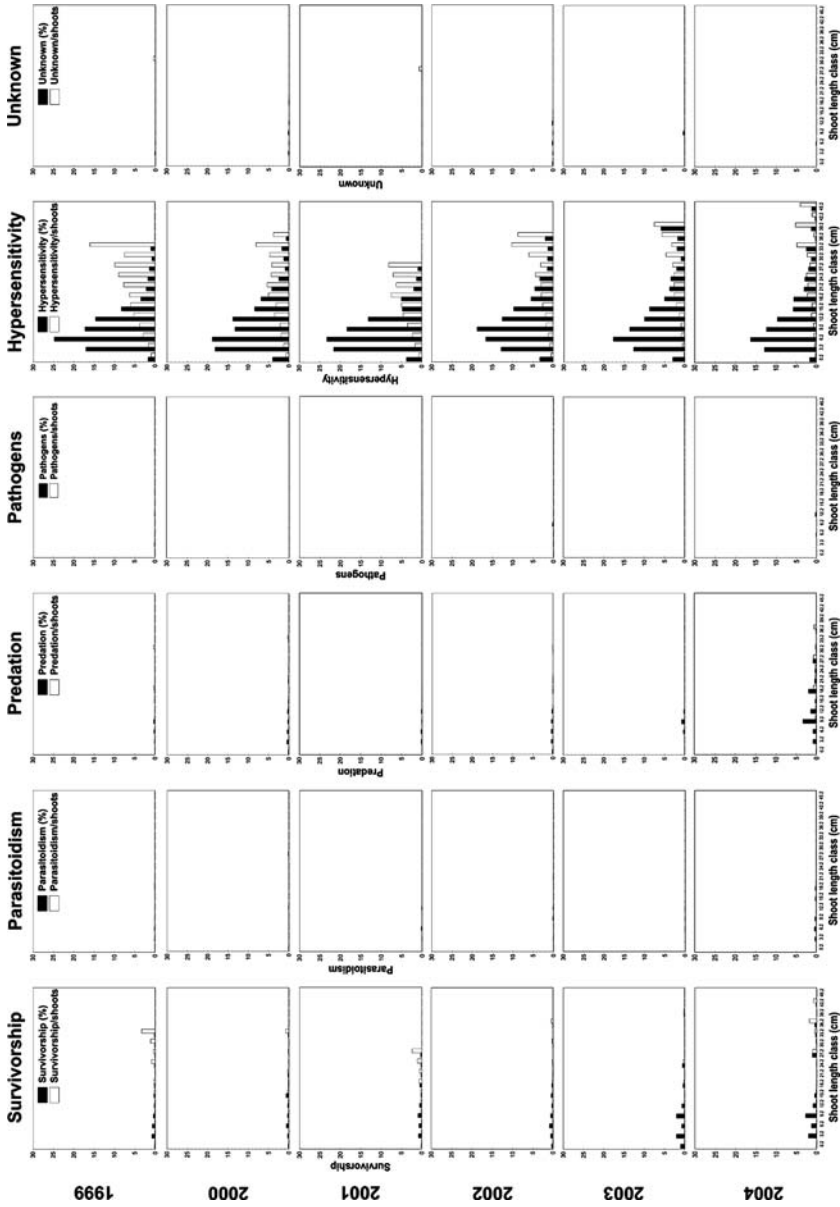


Fig. 6 Temporal variation of the percent survivorship and the ratio survivorship/shoots, and mortality and the ratio mortality/shoots of *Schizomyia macrocapitata* across shoot length classes of *Bauhinia brevipes* during six consecutive years (1999–2004)

Table 2 Linear regressions between shoot length class (X) and number of galls per shoot, and survival per shoot (Y) between 1999 and 2004

Dependent variable	Year	r^2	df	F	P	Regression equation
Number of galls per shoot	1999	0.85	10	54.54	<0.0001	$y = -127.3991 + 1.2635 * x$
	2000	0.59	11	15.99	<0.01	$y = -41.9103 + 0.4282 * x$
	2001	0.94	8	124.87	<0.0001	$y = -106.63 + 1.0613 * x$
	2002	0.80	11	44.00	<0.0001	$y = -71.1948 + 0.7002 * x$
	2003	0.85	12	68.02	<0.0001	$y = -46.6447 + 0.46 * x$
	2004	0.63	14	23.75	<0.001	$y = -25.7889 + 0.2598 * x$
Survival per shoot	1999	0.48	10	9.32	<0.05	$y = -18.6634 + 0.1806 * x$
	2000	0.13	11	1.59	n.s.	
	2001	0.66	8	15.40	<0.01	$y = -20.0199 + 0.1949 * x$
	2002	0.26	11	3.80	n.s.	
	2003	0.00	12	0.00	n.s.	
	2004	0.17	14	2.85	n.s.	

n.s. = no significant

Table 3 Linear regressions between shoot length class (X) and top-down mortality per shoot, and hypersensitivity per shoots (Y) between 1999 and 2004

Dependent variable	Year	r^2	df	F	P	Regression equation
Top-down mortality per shoot	1999	0.05	10	0.54	n.s.	
	2000	0.05	11	0.61	n.s.	
	2001	0.01	8	0.04	n.s.	
	2002	0.04	11	0.45	n.s.	
	2003	0.03	12	0.34	n.s.	
	2004	0.00	14	0.02	n.s.	
Hypersensitivity per shoot	1999	0.85	10	56.69	<0.0001	$y = -106.1327 + 1.0569 * x$
	2000	0.65	11	20.04	<0.001	$y = -39.8129 + 0.4067 * x$
	2001	0.94	8	129.68	<0.0001	$y = -82.1189 + 0.8226 * x$
	2002	0.80	11	42.97	<0.0001	$y = -70.0536 + 0.6882 * x$
	2003	0.86	12	70.88	<0.0001	$y = -46.6381 + 0.4589 * x$
	2004	0.43	14	10.44	<0.01	$y = -21.4348 + 0.2149 * x$

n.s. = no significant

findings showed that the observed preference was higher than expected for larger shoot classes and that the performance prediction of the Plant Vigor Hypothesis was partially supported. Finally, our results indicate the strong effect of plant resistance (bottom-up effect) on survivorship of *S. macrocapitata* on *B. brevipes*.

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