Patterns of attack by herbivores on the tropical shrub *Bauhinia brevipes* (Leguminosae): Vigour or chance?

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Abstract. The plant vigour hypothesis (PVH) predicts that females of galling insects preferentially oviposit on the most vigorous plants or plant modules, where their offspring's performance is highest. In the years 1995 to 1998, we evaluated the responses of species of two different guilds, two chewing species, *Pantomorus* sp. and *Naupactus* lar (Coleoptera: Curculionidae) and one galling species, *Contarinia* sp. (Diptera: Cecidomyiidae), to the length of shoots that were assumed to show the vigour of the tropical shrub *Bauhinia brevipes* (Leguminosae). The abundance of the chewing herbivores was not influenced by shoot length, since attack rates were randomly distributed among shoot length classes. The abundance of *Contarinia* galls increased with increasing shoot length, as proposed by the PVH. However, when we related the attack rate to unit length of shoot (cm), which denotes the resource availability per unit length, there was no effect of shoot length on *Contarinia* sp. These data corroborate the idea of a continuum of responses to plant quality, even when different herbivores feed on the same host plant.

INTRODUCTION

Animal occurrence and feeding is influenced by plant geographical range and local abundance, their size, structural complexity and nutritional quality, secondary chemistry, and phenology, among other factors (Price et al., 1991). Any or all of these parameters are important in determining the consequences of animal feeding patterns and intensity (Crawley, 1989).

Studies on the effects of plant quality on the attack rates of herbivorous insects have shown opposite results that have been incorporated into two major hypotheses. The plant stress hypothesis (PSH) proposed by White (1984) and Mattson & Haack (1987) argues that herbivore abundance is higher on stressed host plants. The mechanism accounting for this pattern would be a decrease in protein synthesis coupled with an increase in soluble amino acid content in plant tissue. Moreover, stressed plants are less able to produce chemical defenses (Rhoades, 1979), and stress, such as water shortage, hastens senescence of plant tissues, and translocated nutrients benefit insect herbivore nutrition, growth and survival (Prada et al., 1995). The term "stress" usually refers to plant performance, which is reduced below that achieved under optimal conditions (Price, 1991).

The host plant vigour hypothesis (PVH) predicts that insect herbivores, that oviposit close to where their offspring feed, and whose larvae develop best on rapidly growing plant parts, prefer to oviposit on vigorously growing plants and/or plant modules (Price et al., 1990; Price, 1991, 1994). The term "vigour" refers to plant performance, i.e., vigorously growing plants grow rapidly and are highly reproductive compared to others. Vigour is readily measured using such criteria as size of leaves,

length of shoots produced in a particular season, number and size of flowers (Prada et al., 1995).

The PVH is not only an alternative way to explain herbivory patterns, which are not covered by the PSH, but a proposal to broaden the hypothesis: Vigorous and Stressed Plant Hypotheses are at opposite ends of a continuum.

In this study, we evaluated the effect of plant shoot length on insects feeding on *Bauhinia brevipes* Vog. (Leguminosae) in southeastern Brazil. We tested the hypothesis that herbivore attack is higher on more vigorous plant shoots for both chewing and galling herbivores on *B. brevipes*. In addition, the level of response of these guilds – chewing and galling herbivores – to different host plant shoot lengths was determined.

MATERIAL AND METHODS

System

Bauhinia brevipes is a cerrado (savanna) leguminous shrub, up to 3 m tall (Cornelissen et al., 1997), which flowers and fruits from June to August. Several galling and free-feeding insect herbivores attack this plant (Cornelissen et al., 1997). During this study, the chewing herbivores attacking *Bauhinia* were primarily *Naupactus* lar (Coleoptera: Curculionidae) and *Pantomorus* sp. (Coleoptera: Curculionidae) causing damage to leaf edges, and chewing circular holes in the lamina of the leaves. Seven undescribed species gall *B. brevipes*, a new species of *Contarinia* and two other undetermined species of Diptera: Cecidomyiidae, and four species gall the stems: one Cecidomyiidae, one Lepidoptera, and two Curculionidae (see Cornelissen et al., 1997; Fernandes, 1998; Cornelissen & Fernandes, 1998). The undescribed species of *Contarinia* induces leaf galls on the adaxial leaf surface of *B. brevipes*. The spherical galls are covered with long red hairs and enclose a single chamber, containing one larva (Fernandes, 1998).

Study Site

The study site was at the Estação Ecológica de Pirapitinga (IBAMA) in Três Marias-MG, southeastern Brazil. The biological station is a man-made island of 1100 ha in the Três Marias reservoir (18°23'S, 45°20'W), which was built in 1965, at an altitude of 560 m a.s.l. The average annual temperature at the study site varies from 20 to 22°C, and the average annual precipitation is 1,600 mm (Goodland & Ferri, 1979; Eiten, 1993). The vegetation is primarily cerrado (savanna), with three distinct physiognomies: cerrado, cerrado sensu strictu, and campo sujo (Azevedo et al., 1987). The cerrado sensu strictu is the primary vegetation type of the island, consisting of more than a hundred plant species from more than fifty families (Gonçalves-Alvim & Fernandes, 2001). It is composed of trees and shrubs approximately 6 m in height, and an herbaceous layer.

Sampling

Patterns of herbivory were determined over a period of four consecutive years by randomly collecting 25 shoots of *Bauhinia brevipes* from around the canopy of 170 plants. The shoots were placed in plastic bags and taken to the laboratory where their length (to the nearest mm), total number of leaves, number of galled leaves, number of galls, and number of leaves attacked by chewing insects, on each of the 15,116 shoots were determined. The shoot lengths were divided into shoot length classes of 3 cm ($n = 20$ classes) (see Price, 1991). Shoot length was used as an indicator of plant vigour. This measure is consistent with the definition of vigour and applies to any plant or plant module that grows rapidly, and reaches a large size, relative to the mean growth rate and size reached by the population of plants or plant modules (Price, 1991). The attack rates of the chewing and galling herbivores were calculated as the relative number of attacked leaves and number of galls, respectively, per unit of shoot length (cm), in an attempt to correct for the longest shoots having higher probability of being attacked (Gonçalves-Alvim et al., 1999).

RESULTS

More than 15,000 shoots and approximately 17,000 galls were sampled during the four years of study. Long shoots had more leaves than short shoots ($\log y = 0.412 + 0.436 \log x$; $r^2 = 0.64$; $F_{1,163} = 278.98$; $P < 0.0001$; Fig. 1). As predicted by the PVH, most shoots were concentrated in the shorter shoot length classes, and the longer shoots were rare (Fig. 2).

Variation in shoot length did not explain variation in the percentage of attack by chewing herbivores in 1995 ($y = 36.9 - 0.17x$; $r^2 = 0.16$; $F_{1,16} = 1.19$; $P > 0.05$), 1996 ($y = 31.55 - 0.01x$; $r^2 = 0.01$; $F_{1,16} = 0.005$; $P > 0.05$), 1997 ($y = 37.82 + 0.27x$; $r^2 = 0.18$; $F_{1,16} = 3.67$; $P > 0.05$), or 1998 ($y = 19.51 + 0.21x$; $r^2 = 0.16$; $F_{1,16} = 2.92$; $P > 0.05$; Fig 3).

In contrast, variation in shoot length explained approximately 85.0% of the variation in the number of galls per shoot in 1995 ($r^2 = 0.84$; $F_{1,16} = 85.08$; $P < 0.005$), 74.0% in 1996 ($r^2 = 0.74$; $F_{1,16} = 45.53$; $P < 0.005$), 86.0% in 1997 ($r^2 = 0.86$; $F_{1,16} = 104.35$; $P < 0.005$), and 87.0% in 1998 ($r^2 = 0.87$; $F_{1,16} = 105.93$; $P < 0.005$; Fig 3). However, when corrected for the fact that the longer shoots have more leaves, by dividing the number of galls by shoot length (cm), none of the relationships were statistically significant (1995: $r^2 = 0.01$; $P > 0.05$; 1996: $r^2 =$

Fig. 1. Relationship between number of leaves and shoot length in *B. brevipes*. Data were log transformed.

0.13; $P > 0.05$; 1997: $r^2 = 0.001$; $P > 0.05$; 1998: $r^2 = 0.001$; $P > 0.05$; Fig 4).

Fig. 2. Proportion of shoots (thick line) in each shoot length class and the proportion of shoots attacked (dotted line) by two chewing species, *Pantomorus* sp. and *Naupactus* lar and a galling herbivore (narrow line), *Contarinia* sp., from 1995 to 1998.

Fig. 3. The percentage of leaves attacked and number of galls per shoot on shoots of *B. brevipes* of different length classes from 1995 to 1998. The tendency lines indicate the significant statistical relationships. Gall-forming herbivores: open circles, and chewing herbivores: closed circles.

DISCUSSION

The plant vigour hypothesis relates to within-plant-species variation, and the fact that many herbivores attack the most vigorous plant parts or plant individuals in a population is well documented (Price, 1997). Indeed, foresters have long recognized that young vigorous trees are often more susceptible than older plants to attack by herbivores. Kearsley & Whitam (1989) showed that the number of the leaf beetle *Chrysomela confluenta* is 400-fold higher on juvenile narrowleaf cottonwood, *Populus angustifolia*, than on mature leaves. Many studies on other plants demonstrate that gall-forming insects attack long shoots more frequently than short shoots, and younger, vigorous plants more frequently than older, slower-growing plants in temperate regions (e.g., Craig et al., 1986; Price et al., 1987; Price, 1989), and in tropical regions (e.g., Faria et al., 1997; Madeira et al., 1997). Nevertheless, the results of some of these studies are contradictory, and some attempts to test the PVH have failed. Gonçalves-Alvim et al. (1999) tested the PVH using four neotropical species of gall-forming insects and showed that different species responded differentially to shoot length, and just one species of a cecidomyiid galler behaved in

Fig. 4. The relationship between the number of galls per unit shoot length (cm) and shoot length class in *B. brevipes* from 1995 to 1998.

concert with the PVH. Marini-Filho et al. (1997) found that a leaf-miner (Diptera: Agromyzidae) preferred shoot length located around the middle of the continuum between the stressed and vigorous plants.

Faria & Fernandes (2001) suggested that the high attack rates commonly observed on the longest shoots – as proposed by the PVH – were not due to a preference by female herbivores, but due to the greater probability of the longest shoots being attacked. For example, the longer shoots offer more resources – leaves – for gall-forming insects than the shorter shoots. Hence, the resource availability per unit of shoot length should be measured when testing the plant vigour hypothesis.

The two studied curculionid species of chewing herbivores did not prefer a particular shoot length: the attack was randomly distributed among shoot length classes. In addition, the pattern was consistent from year to year over a four year period. This study is in agreement with Cornelissen et al. (1997), which demonstrated that the pattern of attack over a two year period by another chewing herbivore – an undescribed species of Geometridae (Lepi-

doptera) – was also not related to shoot length. In contrast to gall-forming herbivores, the chewing insects – such as *Pantomorus* sp. and *Naupactus* lar in which oviposition is spatially or temporally separated from larval development – typically do not show a preference for vigorously growing plant modules (see Preszler & Price, 1995).

Two conditions of the PVH, however, are satisfied by most species of galling herbivores. They oviposit at the site of gall formation, and gall formation is associated with plant growth processes (Preszler & Price, 1995). Although the longest shoots made a small proportion of the available shoot population, the gall former *Contarinia* sp. attacked them primarily. However, when the attack was related to shoot unit length, the preference for vigorous shoots was not expressed, showing that *Contarinia* sp. did not preferentially select the longer shoots of *B. brevipes*. Therefore, this work is in agreement with the studies of Cornelissen et al. (1997) and Gonçalves-Alvim et al. (1999), and supports the view that the pattern of attack by insect herbivores on shoots of various lengths may be viewed as a consequence of a continuum of responses.

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