

CROP PROTECTION**Relationships between Four Neotropical Species of Gall-ing Insects and Shoot Vigor**

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Relações entre Quatro Espécies de Insetos Galhadores Neotropicais e o Vigor de Ramos

RESUMO - A hipótese do vigor de plantas (HVP) prediz que plantas ou módulos de plantas mais vigorosos são preferencialmente selecionados por fêmeas de insetos galhadores como sítios de oviposição, pois aumentam a chance de sobrevivência da prole. A HVP foi testada para *Neopelma baccharidis* Buckhardt (Homoptera: Psyllidae) e *Rhoasphondylia friburgensis* Tavares (Diptera: Cecidomyiidae) que causam galhas em *Baccharis dracunculifolia* D.C. (Asteraceae), e para duas espécies diferentes de Cecidomyiidae (Diptera) que provocam galhas em *Maytenus salicifolia* Reiss. (Celastraceae) e *Vernonia polyanthes* Less (Asteraceae). A abundância de galhas aumentou com o aumento do comprimento do ramo nas quatro espécies, como previsto pela HVP. Entretanto, ao considerarmos a taxa de ataque por unidade de ramo (cm), que inclui nas análises o efeito da disponibilidade de recursos por unidade de comprimento, o padrão de resposta dos quatro galhadores desapareceu. *R. friburgensis* e o cecidomídeo que induz galhas em *M. salicifolia* não responderam ao vigor do ramo ($P > 0,05$), enquanto as outras espécies responderam diferencialmente. A abundância de galhas de *N. baccharidis* correlacionou-se negativamente com o aumento do comprimento do ramo ($y = 0,185 - 0,007x$; $r^2 = 0,21$; $F = 6,013$, $P < 0,05$), enquanto o número de galhas provocadas pelo cecidomídeo em *V. polyanthes* correlacionou-se positivamente com o vigor do ramo ($y = 0,09 + 0,002x$; $r^2 = 0,34$; $F = 6,157$; $P < 0,05$). Portanto, apenas o padrão de ataque do cecidomídeo galhador em *V. polyanthes* suportou a HVP.

PALAVRAS-CHAVE: Insecta, Diptera, Homoptera, galhas, interações inseto-planta.

ABSTRACT - The plant-vigor hypothesis (PVH) predicts that females of gall-ing insects preferentially oviposit on the most vigorous plant or plant modules, where their offspring performance is highest. We tested the PVH on *Neopelma baccharidis* Buckhardt (Homoptera: Psyllidae) and *Rhoasphondylia friburgensis* Tavares (Diptera: Cecidomyiidae) which induce galls on *Baccharis dracunculifolia* D.C. (Asteraceae), and on two different Cecidomyiidae (Diptera)

species that induce galls on *Maytenus salicifolia* Reiss. (Celastraceae) and *Vernonia polyanthes* Less (Asteraceae), respectively. The abundance of galls induced by the four galling species increased with increasing shoot length, as predicted by the PVH. However, when we considered the rate of attack per shoot unit length (cm), which includes in the analyses the effect of availability of resource per unit length, the response patterns of the four gallers disappeared. *R. friburgensis* and Cecidomyiidae species which cause galls on *M. salicifolia* did not respond to shoot vigor ($P > 0.05$) while the other species responded differentially. The abundance of *N. baccharidis* galls correlated negatively with shoot length ($y = 0.185 - 0.007x$, $r^2 = 0.21$, $F = 6.013$, $P < 0.05$) while the number of galls caused by Cecidomyiidae on *V. polyanthes* showed a positive relationship with shoot vigor ($y = 0.09 + 0.002x$, $r^2 = 0.34$, $F = 6.157$, $P < 0.05$). Hence, only the attack pattern of the cecidomyiid galler on *V. polyanthes* corroborated the PVH.

KEY WORDS: Insecta, Diptera, Homoptera, galls, insect-plant interactions.

Studies on the effects of plant quality on the attack rates by herbivorous insects have shown contradictory results that have led to two major hypotheses. Many species show high preference and improved larval performance on stressed hosts, which have resulted in the formulation of the "plant stress hypothesis" (PSH) (e.g., White 1969, 1976). It predicts that plants under abiotic stress become more suitable as food to herbivores due to an increase in the availability of nutrients. In addition, stressed plants may synthesize less chemical defenses (Rhoades 1979, White 1984). Some studies support White's hypothesis (e.g., Waring & Cobb 1992, Bruyn 1995, Cobb *et al.* 1997). On the other hand, other studies have shown that several species of herbivorous insects respond positively to vigorously growing plants or plant parts (e.g., Price *et al.* 1990, Hunter & Price 1992, Preszler & Price 1995), which have resulted in the "plant vigor hypothesis" (PHV) (Price 1991). Vigor is defined as any plant or plant module that grows rapidly and reaches a larger size in relation to the mean growth rate. Price (1991) postulated that insect herbivores, whose larval development is associated with their host-plant growth processes, should prefer to attack the most vigorous plants or plant modules where subsequent larval performance

is highest. The archetype herbivores with these characteristics are galling insects, whose association with host-plant vigor have important implications on their population dynamics (Preszler & Price 1995).

Price (1991) also suggested a solution for the divergence in the results of these two hypotheses, proposing an alternative view in which there is a continuum of strategies. This approach predicts that insect herbivores more specialized and intimately related with the growth processes of plants (latent species) tend to select shoots at one extreme of the continuum, hence characterizing the PVH. Other herbivores, notably those with oviposition and larval development spatially and temporally separated (eruptive species) tend to select modules at the other end of this continuum, characterizing the PSH.

Several studies on the role of plant vigor on insect herbivores have now been done in tropical region (e.g., Prada *et al.* 1995, Vieira *et al.* 1996, Cornellissen *et al.* 1997, Madeira *et al.* 1997, Faria *et al.* 1997). Some of these studies corroborate the PVH, such as the work by Prada *et al.* (1997) in which they observed that fire induced higher production of flowers, resulting in a positive relationship between the number of herbivore insects per plant and the number of capitula per plant.

Faria *et al.* (1997) also verified a positive relationship between attack by a Scarabaeidae beetle and shoot length in *Erythroxyllum suberosum* Turcz. (Erythroxyllaceae). Nevertheless, other studies have shown different results. Madeira *et al.* (1997) did not find any support for female preference for longer shoots, while Cornelissen *et al.* (1997) suggested idiosyncratic responses of the herbivores that attack shoots of *Bauhinia brevipes* Vog. (Leguminosae).

In this study, we evaluate the pattern of attack by four galling insects on three species of host plants, *Maytenus salicifolia* Reiss. (Celastraceae), *Baccharis dracunculifolia* D.C. (Asteraceae) and *Vernonia polyanthes* Less (Asteraceae). The study aims to answer the following questions: Are the longest shoots in the available shoot population of the three plant species most attacked by the gallers? Do the four galling species respond similarly to plant vigor?

Material and Methods

Study Area. This study was done in the Campus of the Federal University of Minas Gerais (19°52' S, 43°58' W), Belo Horizonte (MG) in southeastern Brazil. The campus is at 800 m above sea level and has a heterogeneous vegetation with native, introduced and ornamental species (Fernandes *et al.* 1988). The studied area has a marked dry period of 3 to 4 months with an average monthly precipitation of 50 mm and average temperature between 19°C and 21°C. The rainy season lasts eight to nine months and the average monthly precipitation is 300 mm with an average temperature of 23.9°C.

Host Plants and Galling Insects. An unidentified species of Cecidomyiidae (Diptera) induces galls on the central leaf vein of *M. salicifolia*. Galls are spheroid, brownish, glabrous, one-chambered and have one larva per chamber. These galls are frequently observed on the host plant throughout the year.

V. polyanthes is a weed species of cultivated and disturbed areas (Leitão Filho *et al.*

1972). Spheroid galls are formed on the central vein of its leaves by an unidentified species of Cecidomyiidae (Diptera). Galls are green, glabrous, one-chambered with one or two larvae per chamber. They occur on the abaxial leaf surface and are very common in studied area.

Approximately 17 species of galling insects attack *B. dracunculifolia* (Fernandes *et al.* 1996). The host plant is a dioecious shrub which is widespread in Brazil. Two species of gallers were studied: *Neopelma baccharidis* Buckhardt (Homoptera: Psyllidae) is the most common galling insect on *B. dracunculifolia* which causes an elongated globular leaf gall (Lara & Fernandes 1994) and *Rhoasphondylia friburgensis* Tavares (Diptera: Cecidomyiidae) which produces globular, green and glabrous galls on the stems of the plant (Gagné 1994).

Sampling and Statistical Analyses. Random samples of 20 shoots were taken around the canopy of 10 individuals of each plant species between January and February of 1994. Shoots were placed in plastic bags and taken to the laboratory for measurements of shoot length (cm) and counts of the total number of galls. To answer how galling insects respond to plant vigor, shoots were grouped into size classes at 1 cm intervals (Price 1991). The attack rates of the galling insects were obtained by two methods: the number of galls was divided by the number of shoots in each size class, which resulted in an estimate of the number of galls per shoot; and the number of galls was divided by shoot length in each size class, which resulted in number of galls per shoot unit (cm). The attack rates were also calculated as the number of galls per unit of shoot length (cm) in an attempt to eliminate the effect of the longest shoots having higher probability of being attacked. The data was analyzed by simple linear regressions to test for the relationship between shoot length and number of galls per shoot and between shoot length and the number of galls per centimeter of the shoot.

Results

Longer shoots were less abundant than shorter shoots on the three plant species. However, high rates of attack by galling insects were always observed on the longest shoots (Fig. 1). The highest density of galls occurred

on *M. salicifolia* with 10,090 galls per 1,000 shoots. *N. baccharidis* induced 570 galls/1,000 shoots, *R. friburgensis* induced 215 galls/1,000 shoots, while the unidentified species of cecidomyiid induced 2,695 galls/1,000 shoots on *V. polyanthes*.

Galling insects showed divergent re-

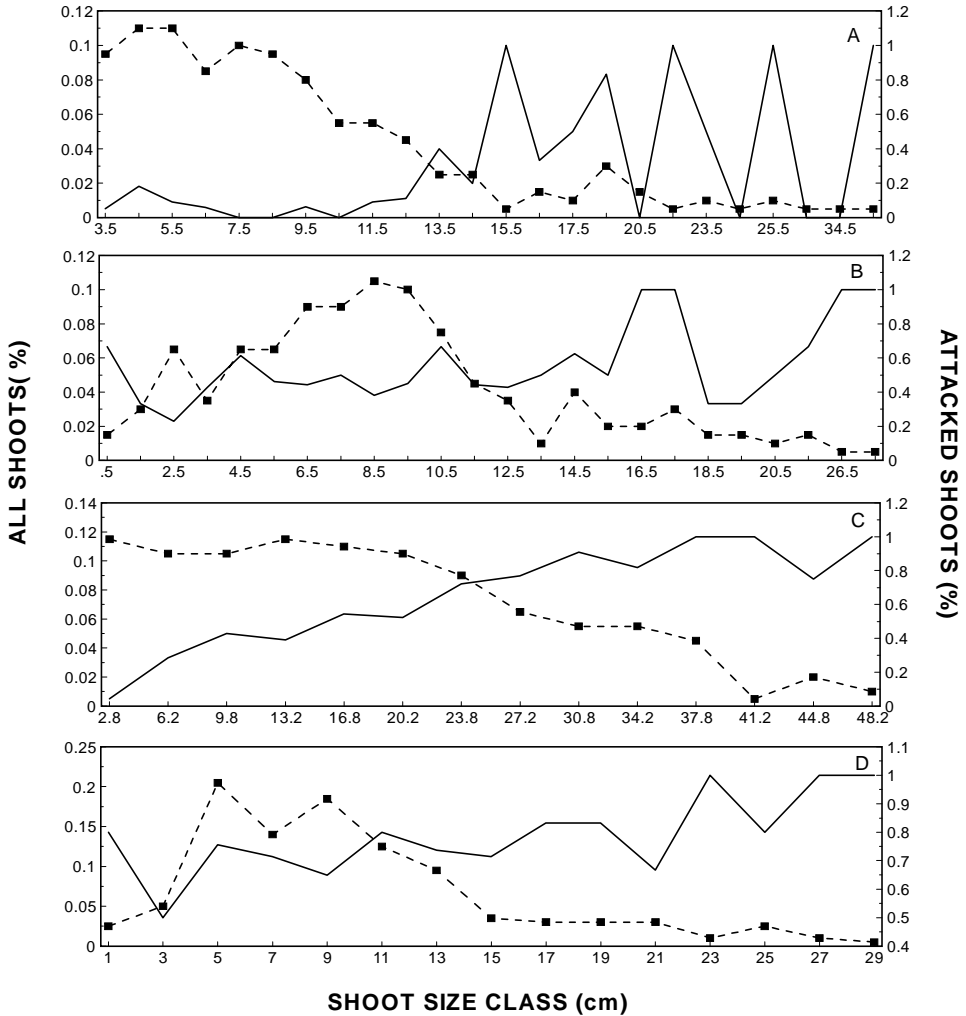


Figure 1. Frequency distribution expressed as the percentage of total shoots (—) and percentage of shoots galled (◆ --- ◆) in each shoot length class on A) *B. dracunculifolia* (Asteraceae) galled by *R. friburgensis* (Diptera: Cecidomyiidae); B) *B. dracunculifolia* (Asteraceae) galled by *N. baccharidis* (Homoptera: Psyllidae); C) *V. polyanthes* (Asteraceae) galled by Cecidomyiidae (Diptera) and D) *M. salicifolia* (Celastraceae) galled by Cecidomyiidae (Diptera).

sponses to shoot length classes. The attack by *R. friburgensis* did not correlate with shoot length ($y = 0.082 + 0.021x$, $r^2 = 0.12$, $F = 2.934$, $P > 0.05$). On the other hand, the number of galls per shoot positively correlated with shoot length in the other three gall-ing species: *N. baccharidis* ($y = 0.183 + 0.043x$,

$r^2 = 0.52$, $F = 23.923$, $P < 0.05$), cecidomyiid on *V. polyanthes* ($y = -0.77 + 0.19x$, $r^2 = 0.86$, $F = 71.617$, $P < 0.05$), and cecidomyiid on *M. salicifolia* ($y = 2.42 + 0.67x$, $r^2 = 0.30$, $F = 5.059$, $P < 0.05$) (Fig. 2). These results cor-roborate the plant vigor hypothesis.

However, when the attack rates were re-

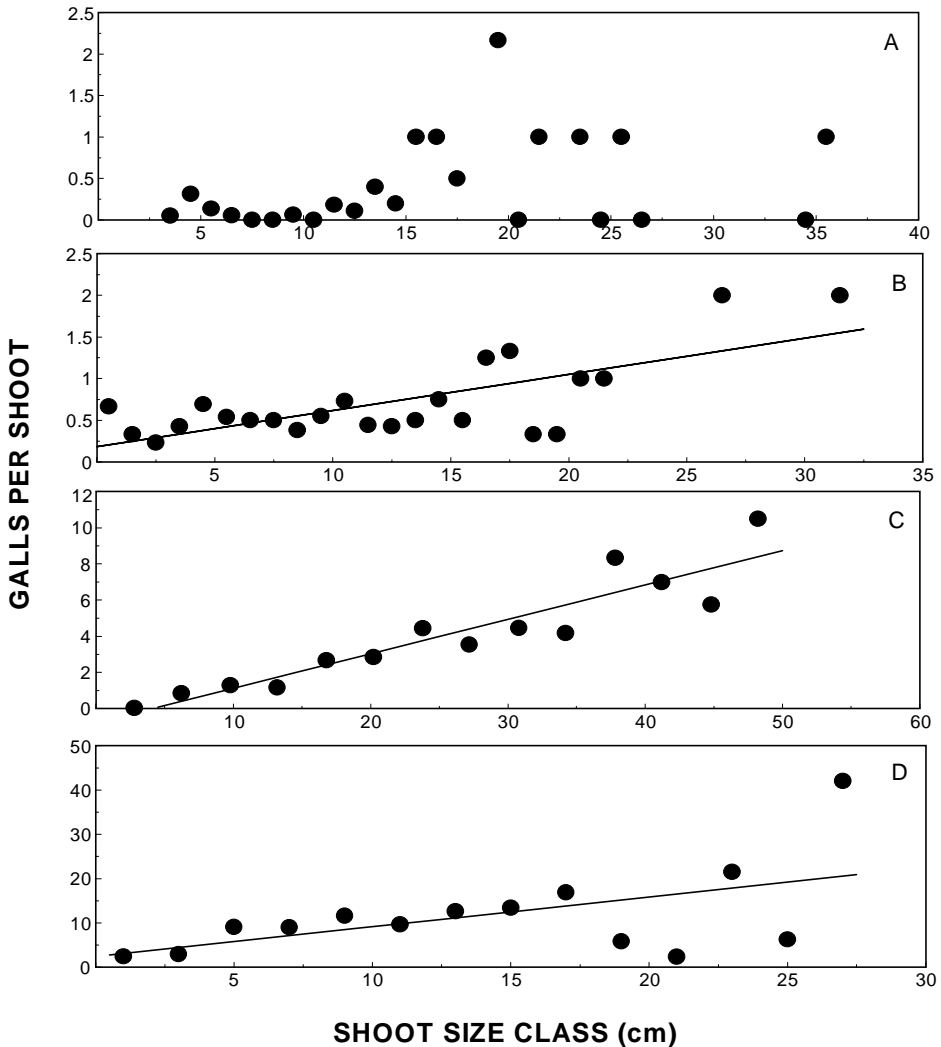


Figure 2. Observed distribution of the number of galls per shoot on A) *B. dracunculifolia* (Asteraceae) galled by *R. friburgensis* (Diptera: Cecidomyiidae); B) *B. dracunculifolia* (Asteraceae) galled by *N. baccharidis* (Homoptera: Psyllidae); C) *V. polyanthes* (Asteraceae) galled by Cecidomyiidae (Diptera) and D) *M. salicifolia* (Celastraceae) galled by Cecidomyiidae (Diptera).

calculated as the number of galls per shoot unit length (cm), the patterns previously reported were modified (Fig. 3). The attack by *N. baccharidis* became negatively correlated with shoot length ($y = 0.185 - 0.007x$, $r^2 = 0.21$, $F = 6.013$, $P < 0.05$). The attack by the

cecidiomyiid on *V. polyanthes* became positively correlated with shoot length ($y = 0.09 + 0.002x$, $r^2 = 0.34$, $F = 6.157$, $P < 0.05$). The patterns of attack of *R. friburgensis* ($y = 0.023$, $r^2 = 0.01$, $F = 0.038$, $P > 0.05$) and that of the cecidiomyiid on *M. salicifolia* ($y = 1.13$

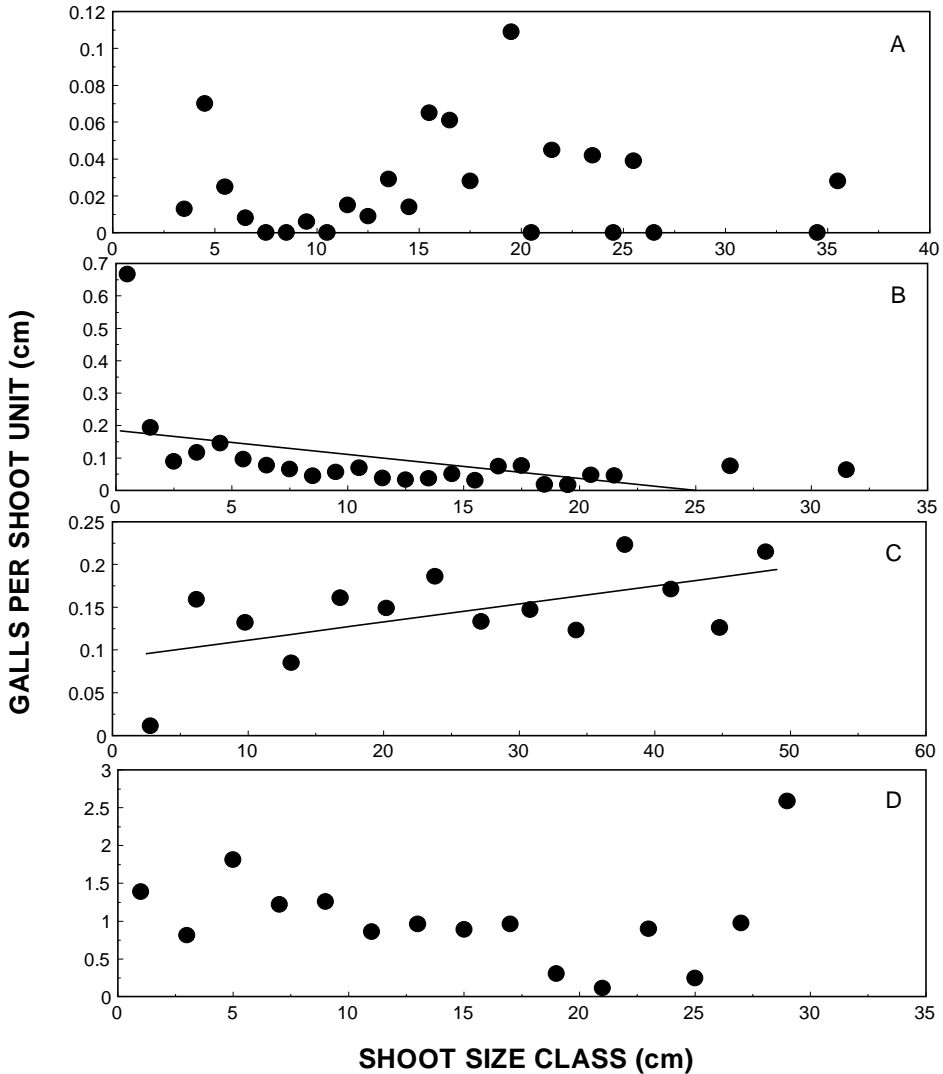


Figure 3. Observed distribution of the number of galls per shoot unit length (cm) on A) *B. dracunculifolia* (Asteraceae) galled by *R. friburgensis* (Diptera: Cecidiomyiidae); B) *B. dracunculifolia* (Asteraceae) galled by *N. baccharidis* (Homoptera: Psyllidae); C) *V. polyanthes* (Asteraceae) galled by Cecidiomyiidae (Diptera) and D) *M. salicifolia* (Celastraceae) galled by Cecidiomyiidae (Diptera).

- $0.008x$, $r^2 = 0.01$, $P > 0.05$) did not show any relationship with shoot length. These results indicate that the plant vigor hypothesis was not supported for most insect species when we considered the attack rate per shoot unit length.

Discussion

The distribution patterns of shoot sizes in the three species of plants corroborate with many other studies (e.g., Craig *et al.* 1986, Craig *et al.* 1989), including tropical species (e.g., Cornellissen *et al.* 1997, Madeira *et al.* 1997) where the longest shoots are always rare in the population of shoots. The longest shoots also tend to be more attacked by gall-ing insects than the shortest shoots. In the tropics, Madeira *et al.* (1997) studied galling insect preference on *Baccharis concinna* Barroso (Asteraceae) and observed that the herbivores preferred the most vigorous shoots.

However, the longest shoots have a greater probability of being attacked than the smaller shoots even if no selection is at work. Longer shoots offer more leaves and buds to be used by gallers than shorter shoots (Madeira *et al.* 1997). Furthermore, other variables such as the availability of sites for colonization and shoot age tend to produce greater attack frequencies in longer shoots (Karban 1987). Therefore, we argue that resource availability per shoot unit length should be incorporated when testing the plant vigor hypothesis to avoid repetition in the results of galling insect attacks. The grouping of shoot length into size classes may force the relationship where the longest shoots are always attacked due to chance alone (Cornellissen *et al.* 1997).

When we considered attack rate per shoot unit length (cm), the four galling species did not respond similarly to plant vigor. Instead, each species responded differentially or did not respond at all to shoot vigor. Thus, the observed pattern which supported the vigor hypothesis disappeared after applying a correcting method. This work corroborates the study of Cornellissen *et al.* (1997) where the authors observed the existence of a continuum

of responses by herbivores to plants and that herbivores may have idiosyncratic responses to plant quality even when feeding on the same host.

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