Plant Vigor Hypothesis refuted: preference-performance linkage of a gall-inducing weevil on small-sized host plant resources

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(With 5 figures)

Abstract

The Plant Vigor Hypothesis (PVH) predicts an oviposition preference of females and higher offspring performance for insect herbivores on longer and fast-growing plant modules. We tested the PVH predictions by investigating the effects of leaf size of *Miconia prasina* (Sw.) DC. (Melastomataceae) on the oviposition preference and on the offspring survival of the gall-inducing weevil *Prospoliata bicolorata* (Coleoptera: Curculionidae). Additionally, we analysed the effects of top-down mortality force on this system. Approximately 83% of the developed galls resulted in adults of *P. bicolorata*, whereas 17% of the galls successfully induced were killed by natural enemies (top-down effect). Leaves of intermediate size were more abundant while smaller and longer leaves were rare. Nevertheless, the percentage of *P. bicolorata* galls was higher on the smallest leaves of *M. prasina*, refuting the preference prediction of the PVH. Our results also refuted the performance prediction: the ratio of survival per leaf was negatively related to the leaf length. Thus, we found a link between female preference and larval performance of *P. bicolorata* on small-sized leaves of *M. prasina*. The next goal is to understand the mechanisms involved in the selection of gall-inducing weevil on short leaves of its host plant.

Keywords: herbivory, host plant selection, insect galls, mortality factors.

Hipótese do Vigor de Plantas refutada: ligação entre preferência e performance de um gorgulho galhador sobre recursos vegetais de tamanhos pequenos

Resumo

A Hipótese do Vigor de Plantas (HVP) propõe oviposição preferencial e maior performance da prole de insetos herbívoros sobre módulos de plantas maiores e mais vigorosas. Testamos as previsões da HVP investigando o efeito do tamanho da folha de *Miconia prasina* (Sw.) DC. (Melastomataceae) sobre a oviposição preferencial e a sobrevivência da prole de um gorgulho indutor de galha *Prospoliata bicolorata* (Coleoptera: Curculionidae). Além disso, analisamos os efeitos da força de mortalidade topo/base sobre este sistema. Aproximadamente 83% das galhas desenvolvidas resultaram em adultos de *P. bicolorata*, enquanto 17% das galhas induzidas com sucesso foram mortas por inimigos naturais (efeito topo/base). Folhas de tamanho intermediário foram sempre mais abundantes, enquanto folhas menores e longas foram raras. No entanto, a porcentagem do número de galhas de *P. bicolorata* foi maior sobre folhas pequenas de *M. prasina*, refutando a predição de preferência da HVP. Nossos resultados também refutaram a predição de performance: a taxa de sobrevivência por folha foi negativamente relacionada com o comprimento da folha. Assim, encontramos uma relação entre preferência de fêmeas e a performance larval de *P. bicolorata* sobre as folhas de tamanho pequeno de *M. prasina*. O próximo objetivo é entender os mecanismos envolvidos na seleção de galhas induzidas por besouros sobre folhas pequenas da planta hospedeira.

Palavras-chave: herbivoria, seleção de planta hospedeira, insetos galhadores, fatores de mortalidade.

1. Introduction

Over recent decades, the Plant Vigor Hypothesis (PVH; sensu Price, 1991) has gained strength among the many hypotheses raised to explain the patterns of host plant selection by herbivores. The PVH predicts that insect herbivores will preferentially choose large, more vigorously growing plants or plant modules because offspring performance will be greater on them (Price, 1991). Several studies have addressed the relationship between female oviposition preference and offspring performance in an attempt to shed light on the PVH.

Recently, Cornelissen et al. (2008) conducted a meta-analytical review of the literature on the effects of plant vigor on insect herbivore abundance and survivorship by reviewing 71 published articles regarding PVH. In general,

their results showed that: a) the preference prediction was corroborated and insect herbivores were significantly more abundant on more vigorous plants; b) the performance prediction was refuted and no effect was detected on herbivore survivorship; c) the studies did not support a preference-performance linkage; and d) effects of plant vigor on abundance were different among feeding guilds, being stronger for sap-suckers, leaf-miners and gall-formers (see Cornelissen et al. 2008). This meta-analytical review was extremely important as it highlighted the main advances regarding insect preference for host plants, as well as setting a framework for PVH.

In this study, we tested the Plant Vigor Hypothesis in a neotropical system comprised of the beetle gall maker *Prospoliata bicolorata* (Coleoptera, Curculionidae, Baridinae) and their host plant *Miconia prasina* (Sw.) DC. (Melastomataceae). We used leaf size as a measure of plant vigor (e.g., Clancy et al., 1993) because *P. bicolorata* induced an elliptical, green and one-chambered gall on the petiole of leaves. We expected that the females of *P. bicolorata* would prefer and achieve higher performance on larger leaves compared to smaller leaves of *M. prasina.* Therefore, we addressed the following questions: 1) what is the effect of leaf size of *M. prasina* on the oviposition preference and *P. bicolorata* larval survival?; and 2) what are the effects of top-down mortality factors on the survivorship of *P. bicolorata*?

2. Material and Methods

2.1. Study site and species

This study was conducted at the Refúgio Ecológico Charles Darwin, a remnant of the Atlantic forest preserved during the last 40 years and comprised of a 60 ha fragment of the highly-threatened Atlantic forest, in Igarassu, Pernambuco, northeastern Brazil (07° 48' 37'' - 07° 49' 2'' S and 34° 27' 25" - 34° 56' 52" W). The Refúgio Ecológico Charles Darwin is at an altitude of between 10-100 m a.s.l., with a wet season from March to August and a dry season from September to February, and an average annual temperature of 27 °C and relative humidity around 80%. The forest is formed by a herb-shrub stratum and by a tree layer varying between 8 and 15 m in height. A floristic survey of the pteridophytes registered 21 species (Santiago and Barros, 2003).

Miconia prasina (Sw.) DC. (Melastomataceae) "camasey blanco" is a shrub or a small tree reaching up to 12 m high, commonly found in Central and South America. This species is a shade intolerant pioneer species that grows in secondary and remnant forests, as well as disturbed areas (e.g., Pascarella et al., 2007). Several organisms within different trophic levels attack *M. prasina.* It is attacked by at least five species of gall inducing insects: three unidentified species of leaf gall midges (Diptera: Cecidomyiidae), one unidentified species of a bud gall (Lepidoptera) and the one coleopteran species *Prospoliata* cf. *bicolorata* (Curculionidae) (Almeida-Cortez et al., 2006; Silva and Almeida-Cortez, 2006). Moreover, *M. prasina* is also attacked by a diversity of free-feeding herbivores (Braga et al., 2007) and an unidentified species of galling nematode (Santos J.C., personal communication).

2.2. Sampling and statistical analysis

Patterns of insect attack were determined in 2007 by randomly collecting 10 old leaves around the canopy of 73 haphazardly selected *M. prasina* individuals (five leaves lost). Leaf collection was performed early in September, on a single day, when most leaves were mature. All leaves were bagged, numbered and taken to the laboratory where their length, weight, number of galls, and galled leaves were recorded. Leaf length was then divided into 15 size classes of 2 cm based upon previous studies (e.g., Santos et al., 2008), with leaf length classes ranging from 1.5 cm (lowest class) to 29.5 cm (highest class). We used the following definitions of preference and performance: a) preference - defined as non-random oviposition on plant resources offered simultaneously; and b) performance - defined as a measurement of offspring survival (egg, larval or pupal), growth, or reproduction (see Singer, 1986; Thompson, 1988). In this study, preference was estimated by quantifying the number of galled leaves, while performance was estimated by counting the number of larvae which survived.

The relationship between preference - performance with shoot length classes was tested by simple linear regressions (Zar, 1996) using the program STATISTICA 6.0 (StatSoft, 2001). The number of galled leaves, survival, and mortality factor rates were divided by the number of leaves in each size class in an attempt to eliminate the effects of differential resource abundance and to eliminate the effects of longest leaves having higher probability of being attacked (Cornelissen and Fernandes, 2001). 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 (top-down) acting upon the galling larva were grouped in the following categories: parasitoidism, predation, pathogens, and unidentified factors (for details see Fernandes and Price, 1992). To understand how effects of mortality factors were influenced by leaf length, all factors were also divided into 2 cm leaf length classes (see Fernandes, 1998) and compared with preference and performance distributions.

3. Results

We recorded 233 *Prospoliata* cf. *bicolorata* galls found on 725 leaves, and only one gall was found on each leaf sampled. Of the 233 galls recorded on these leaves during the studied period, around 83% (n = 194) survived, resulting in adults of the galling insect, whereas 17% (n = 39) of the galls successfully induced were killed by predators, pathogens, parasitoids and unknowns mortality factors (Figure 1).

Intermediate leaf length classes were always more abundant, whereas smaller and longer leaves were rare

(Figure 2). However, the percentage of galled leaves by the females of *P. bicolorata* was negatively related to leaf size ($r^2 = 0.89$; $p < 0.00001$; Figure 2). The percentage of galled leaves was also negatively related to an increase in the mean leaf area ($r^2 = 0.795$; $p = 0.0001$; Figure 3a) and an increase in the mean weight of leaves ($r^2 = 0.70$; $p = 0.0007$; Figure 3b). Hence, these results refuted the preference prediction of the PVH.

Percentage of survivorship on each leaf length class showed a similar pattern to that observed for leaf distribution, higher survivorship was related to higher leaf (Figure 4). However, when we eliminated the effects of leaf abundance in each leaf length classes, the ratio of survivorship per leaf was negatively related with leaf length ($r^2 = 0.74$; $p = 0.0003$; Figure 5) indicating that the performance prediction of the PVH was also refuted. The percentage of top-down mortality and mortality per leaf on each class of leaf length did not show any relationship with leaf length (Figure 4).

4. Discussion

The size of plant modules is an important feature that influences the preference (oviposition choice), and performance (survival, and pupal or adult biomass) of many guilds of endophagous insect herbivores, such as gall formers, because plant size represents a quantity-quality indicator of resources (e.g., Price, 1991; Clancy et al., 1993; Cornelissen et al., 2008). The Plant Vigor Hypothesis (Price, 1991) is very important for the attempts to understand the patterns of host selection by the insect herbivores. Although a strong corroboration of the PVH was recently found by a meta-analytical review of the literature (see Cornelissen et al., 2008), our study did not support this hypothesis. *Prospoliata bicolorata* oviposited and survived preferentially on small-sized leaves of *Miconia prasina*, and we also found evidence to support the linkage between preference and performance. Therefore, 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).

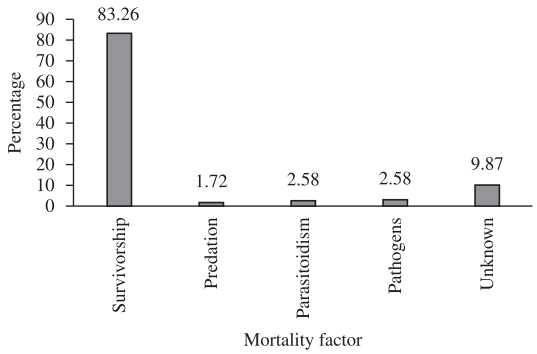

Figure 1. Percentage of survivorship and mortality factors of *Prospoliata cf. bicolorata* (Coleoptera: Curculionidae) galls on the host plant *Miconia prasina* (Melastomataceae).

Some studies have also refuted the predictions of the PVH. In *Bauhinia brevipes* (Fabaceae), a leaf gall midge *Asphondylia microcapillata* (Cecidomyiidae: Diptera) oviposited and survived preferentially on medium-sized shoots (9.6-24.5 cm) (Santos et al., 2008). McKinnon et al. (1999) found that the abundance of galls of *Adelges abietis* (L.) (Homoptera: Adelgidae) was higher on intermediate-

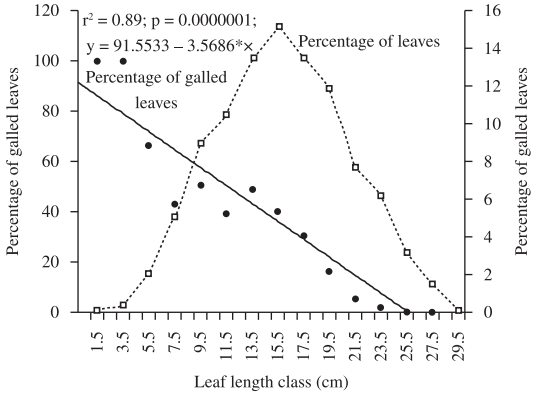

Figure 2. Percentage of galled leaves by *Prospoliata cf. bicolorata* (Coleoptera: Curculionidae) on different leaf length classes and the percentage of available leaves in each class of leaf length of *Miconia prasina* (Melastomataceae).

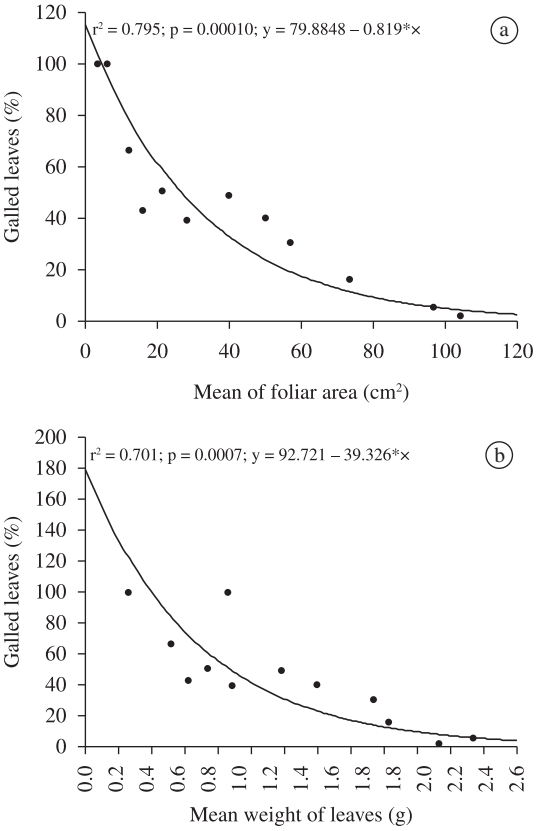

Figure 3. a) Relationship between mean leaf area of *Miconia prasina* (Melastomataceae) and percentage of galled leaves by *Prospoliata bicolorata* (Coleoptera: Curculionidae); and b) relationship between mean leaf weight and percentage of galled leaves.

sized trees and shoots of the white spruce *Picea glauca* (Moench) Voss (Pinaceae). Finally, Gonçalves-Alvim et al. (1999) found a negative relationship between the number of galls induced by the psyliid *Neopelma baccharidis* (Homoptera) per shoot and the shoot size of *Baccharis dracunculifolia* (Asteraceae). However, these three examples of insect gall-host plant interactions represent only a small proportion compared with all the studies that corroborate the PVH (see Cornelissen et al., 2008). Given the great biological diversity of interactions between insects and plants, the exceptions to the PVH are important to define under what circumstances and to which ecological groups of organisms this hypothesis might be refuted.

The Plant Stress Hypothesis (PSH) states that environmental stresses cause physiological changes on host plants that can be measured as an increased availability of nutrients and/or a decreased concentration of defensive compounds to insect herbivores (White, 1984). Many studies have erroneously corroborated the PSH based on the simple exclusion of the PVH (see White, 2009), especially when herbivore attack decreased with an increase in size of plant modules. A strong link between female preference

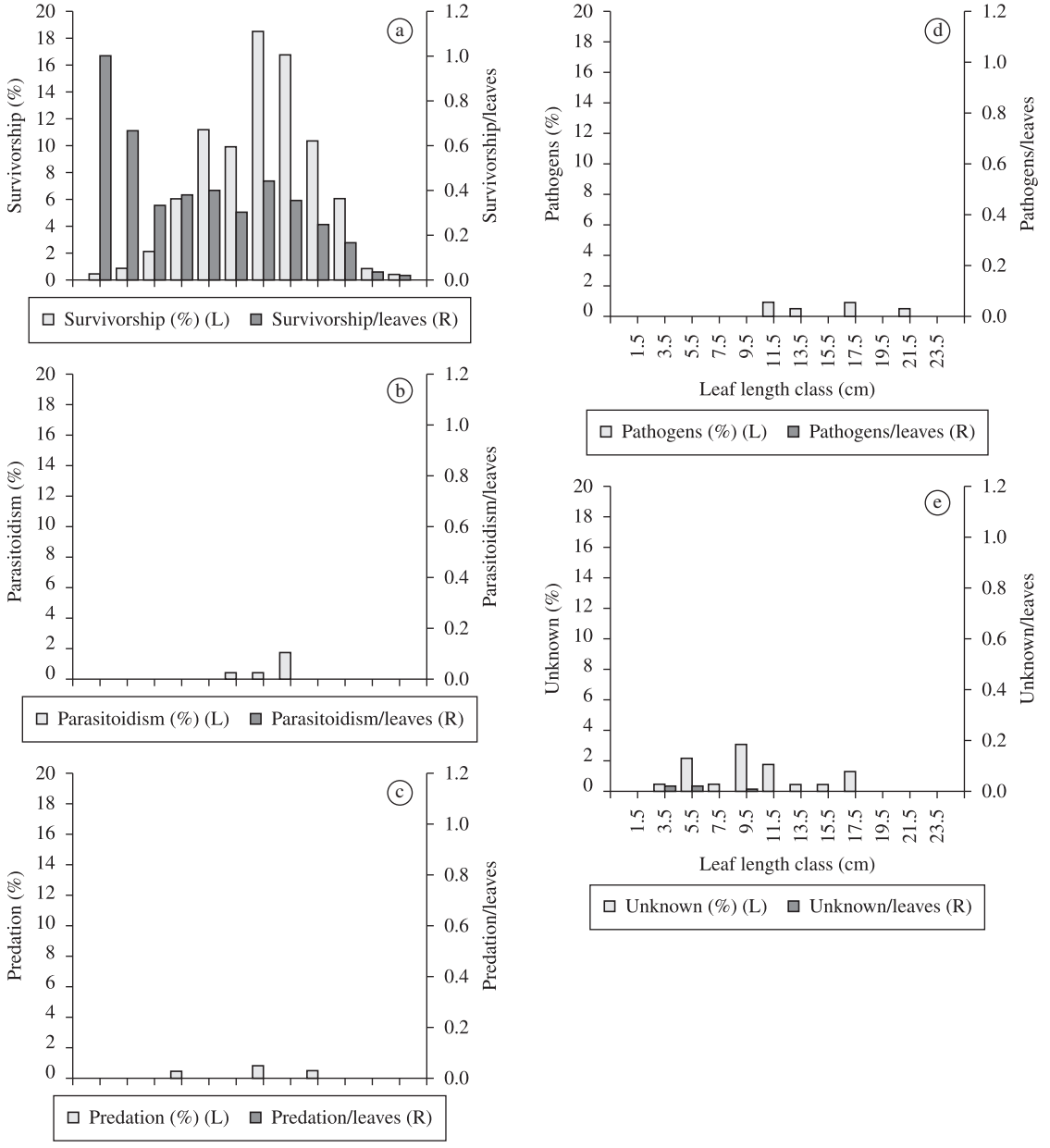

Figure 4. a) Percentage of survivorship and the ratio survivorship/leaves, and percentage of mortality and the ratio mortality/leaves (b) parasitoidism; c) predation; d) pathogens; and e) unknown) of *Prospoliata* cf. *bicolorata* across the classes of leaf length of *Miconia prasina* (Melastomataceae).

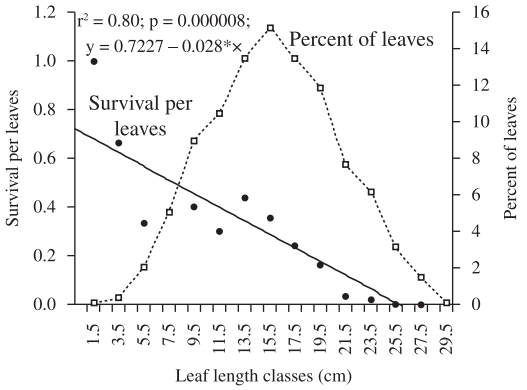

Figure 5. Ratio of survivorship of *Prospoliata bicolorata* per leaf of *Miconia prasina* (Melastomataceae) on different classes of leaf length and the percentage of leaves available in each leaf length class.

and larval performance of *P. bicolorata* was found on small-sized leaves of *M. prasina*. However, in this study, we cannot support the PSH based on our results of plant module size, although the PSH is an alternative hypothesis to be tested in future for the *P. bicolorata - M. prasina* system. We argue that smaller leaves should possess higher rates of resource quality essential for larval development; nevertheless, only detailed field and experimental studies on this system will shed light onto this question.

5. Conclusion

The Plant Vigor Hypothesis (PVH) predicts oviposition preference and higher offspring performance on longer and fast-growing plant modules, and although several studies have tested its predictions, studies concerning the patterns of host selection by galling species are still lacking. A decrease in preference and performance rates of *P.* bicolorata was coupled with an increase in the leaf length classes of *M. prasina*. These findings do not support the PVH and show that *P. bicolorata* can maximize the female preference and larval performance on small-sized leaves of *M. prasina*, resulting in more than 83% survival rate.

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