



Original Article

Abundance of gall-inducing insects in *Ouratea hexasperma*: response to vigor or escape from hypersensitivity?

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ABSTRACT

The plant vigor hypothesis predicts that more vigorous plants or branches are preferentially selected by female gall-inducing insects for oviposition. The hypersensitivity reaction is a defense mechanism of some plants of Brazilian Cerrado, where morphological and physiological changes cause the death of damaged tissue and the gall-inducing insect. We examine the abundance of Cecidomyiidae galls in *Ouratea hexasperma* in Caldas Novas, Brazil, aiming to answer the following questions: 1) Do gall-inducing insects prefer the more vigorous branches? 2) Is the hypersensitivity reaction more frequent in smaller and less vigorous branches? We sampled 24 individuals from the host plant and collected five branches of each, and measured the length of the branch, the number of leaves, the total number of galls and number of galls with hypersensitivity reaction. Linear regression analysis showed a positive relationship of abundance of galls with the plant's vigor and the number of leaves per branch being the most important variable. The number of galls with a hypersensitivity reaction was influenced both by the length of the module as the number of leaves per branch. As expected, smaller and less vigorous branches had more of a hypersensitivity reaction. Generally, these areas have high concentrations of tannins and phenolic compounds to protect them against attack from herbivores. It is expected that short and young branches have more hypersensitivity reactions of the larger branches. Thus, the preference of gall-inducing by more vigorous branches could be a leak from a hypersensitivity reaction and not simply a response to the vigor.

Key-words: defense mechanism, galls abundance, hypersensitivity, plant vigor.

INTRODUCTION

The plant vigor hypothesis [PVH] is one of the most widely used hypotheses to explain the distribution of insect galls on their host plants [6-26]. This hypothesis refers to the variation in the quality of resources to herbivores within the host plant [21]. PVH predicts that plants or parts thereof more vigorous are preferentially selected by females of galling insects as oviposition sites because they increase the chance of offspring survival [20].

The vigor can be understood as the growth rate of plants or plant modules above the average of a given population [20]. Investigating this, Price [20] compiled data showing that galling repeatedly attack longer branches more frequently than short branches and vigorous and young plants more often than the older ones. In general the abundance of galls [6-9-14], the female preference [13-23] and the larval survival [20-23] seem to be positively correlated with the increase in the size of plant modules. Thus, the size and vigor, between and within plants, is a determining factor for the distribution of galling herbivores [6].

Hypersensitivity reaction is an important type of induced defense in which the plant induces a response to fungi, bacteria, viruses, nematodes or insects [10]. The reaction occurs when the plant responds to the attack with morphological changes, histological and biochemical changes that consequently cause death of the tissue attacked [12]. In some cases, the response occurs at a very high speed, for example, 12 hours after laying eggs [19]. The hypersensitivity reactions are appointed as major and more effective mechanisms of plant resistance to gall-inducing insects [10-25].

In the tropics, the highest rates of herbivory occur in young and expanding branches [5], since they have higher nutritional quality. Therefore, these structures are more heavily protected, for example, by high concentrations of defense compounds in an attempt to mitigate the attack of herbivores [4]. This suggests that hypersensitivity reactions may be more common in smaller branches and less vigorous. In this study we analyzed the pattern of distribution of galls of Cecidomyiidae [Diptera] in *Ouratea hexasperma* [Ochnaceae] to answer the following questions:

1. galling insects prefer the more vigorous branches of *O. hexasperma*?
2. hypersensitivity reactions are more frequent in smaller branches and less vigorous?
3. the distribution pattern of gall-inducing insects in *O. hexasperma* may be a response to the hypersensitivity?

MATERIAL & METHODS

The study was conducted in February 2009 in a fragment of cerrado [savanna] remnant in semi-urban area in the municipality of Caldas Novas, Goiás, Brazil [17°42'39"S e 48°38'27"W]. The area has recently been improved so as to establish a residential subdivision, but also presents some fragments of native vegetation. The regional climate is Aw of Köppen, characterized by rainy summers, October to March, and dry winters, from April to September.

Ouratea hexasperma [Ochnaceae] was chosen for the study because it held a great abundance and frequency of galls of an indeterminate species of Cecidomyiidae, besides presenting galls commonly affected by hypersensitivity. The galls of Cecidomyiidae occur in the leaves; they are discoid and grouped with color ranging from green to brown. The hypersensitivity reaction caused by galling insects can be easily distinguished from other herbivorous insects and pathogens as a aureole of dark brown necrotic tissue around the site of gall induction which confirms the attack of the larva [10]. The galls where the reactions occurred can also be easily differentiated from normal galls.

For the study, we sampled 24 individuals from the host plant and which randomly collected five branches of each one. The length, the leaf number, the total number of galls and the number of galls with hypersensitivity. The structural variables [length of branch and leaf number] were correlated with the variables of abundance [total number of galls and number of galls with hypersensitivity reaction] through the statistical instrument of linear regression Analysis linear regression analysis. To test the effect of the number of leaves per branch in the abundance of galls with hypersensitivity a correction was made, dividing the number of galls with hypersensitivity by the total number of galls. All analysis was made by the program Statistica 7.0 was measured in each branch.

RESULTS & DISCUSSION

The module size did not affect the total abundance of galls [$r^2 = 0.011$, $p = 0.10$]. However, the number of leaves per module was the factor that best explained the abundance of galls [$r^2 = 0.245$, $p < 0.01$, Figure 2]. In general, to each leaf added to the module the abundance increased in 12.4 galls.

The number of galls with hypersensitivity was influenced both by the length of the module and the number of leaves per branch. Smaller and less vigorous modules had the highest number of hypersensitivity reactions [$r^2 = 0.124$, $p < 0.02$, Figure 2]. Our results indicate that to each centimeter increased in size of the module occurs the diminution of 1.7 galls with hypersensitivity. The number of leaves per branch also negatively affected the number of galls with the reaction: branches with fewer leaves had more galls with hypersensitivity [$r^2 = 0.068$, $p < 0.05$, Figure 3].

Araújo et al. [3] found no relationship between the vigor of plants and abundance of galls on *Baccharis pseudomyriocephala* [Asteraceae]. According to them, the plant size can have a positive effect on the insect diversity due to the effect of area [16-24]. Larger plants pose a greater availability of resources [2] and are more apparent for the galling [3-11]. As proposed by Lawton [15], however much greater the structural complexity of the host plant, the more the diversity of the insects associated would be. Thus, larger modules may have a higher number of oviposition sites, showing a positive relationship between gall abundance and plant size [3]. According to [8] the number of leaves per module can be a measure of the number of oviposition sites, justifying a positive correlation between this variable and gall abundance in *O. hexasperma*.

Although the vigor did not explain the abundance of galls of Cecidomyiidae in *O. hexasperma*, interesting results were obtained for the distribution of hypersensitivity reactions: most vigorous branches have a lower frequency of galls with the reaction [Figure 2 and 3]. Although it has not been tested in this study, it seems, that because of this mechanism, the mortality rates are higher in less vigorous branches. Insect herbivores may adjust their distribution pattern before factors that increase mortality, as parasitoids and pathogens [17-18]. This may mean that the frequency of hypersensitivity reactions, also influences the pattern of distribution of insects,

equally or more significantly than the quality of resources, as envisaged in the PVH.

HVP tests were repeatedly made in *Bauhinia brevipes* [Leguminosae], bush typical of the Brazilian savannah, to determine the hypersensitivity as a defense mechanism [7-9-23]. But in none of these studies was found [or simply was not the purpose of research] a direct relationship between the two factors. Santos et al. [23], noted that hypersensitivity is an important mechanism of control and was common in all classes of branch length; however, this was not statistically tested. On the other hand, there was found a strong relationship between the percentage of attack and the size of classes, the most vigorous branches being attacked 10 times more [23]. What we suggest is that when the analysis is done only for the abundance of galls with hypersensitivity reactions, the pattern is reversed: less vigorous branches have a higher frequency of this mechanism.

These branches have a high nutritional quality, and therefore require a greater energy investment of the plants in production [22]. High concentrations of tannins and other phenolic compounds are common in these branches to protect them against attack from herbivores [1-4-5]. For this reason, it is likely that newer and smaller branches have a larger number of hypersensitivity reaction than larger branches. Thus, the preference of galling by more vigorous branches could be a leak from a hypersensitivity reaction to and not simply a response to the vigor.

CONCLUSION

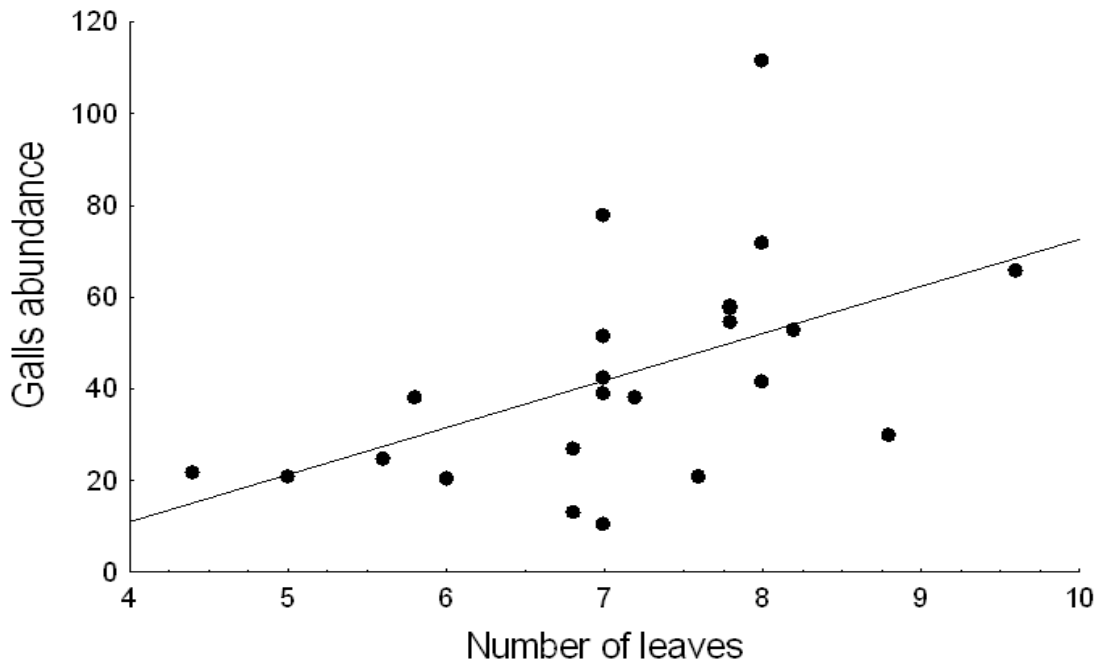
The conclusions reached here are preliminary and based on field observations only. Experimental studies investigating the distribution pattern of insect galls on plants that have this induced defense mechanism are crucial to more definite conclusions. In any case, treating the vigor related with plant defense mechanisms, such as hypersensitivity, appears to be a pathway that will lead to very interesting answers.

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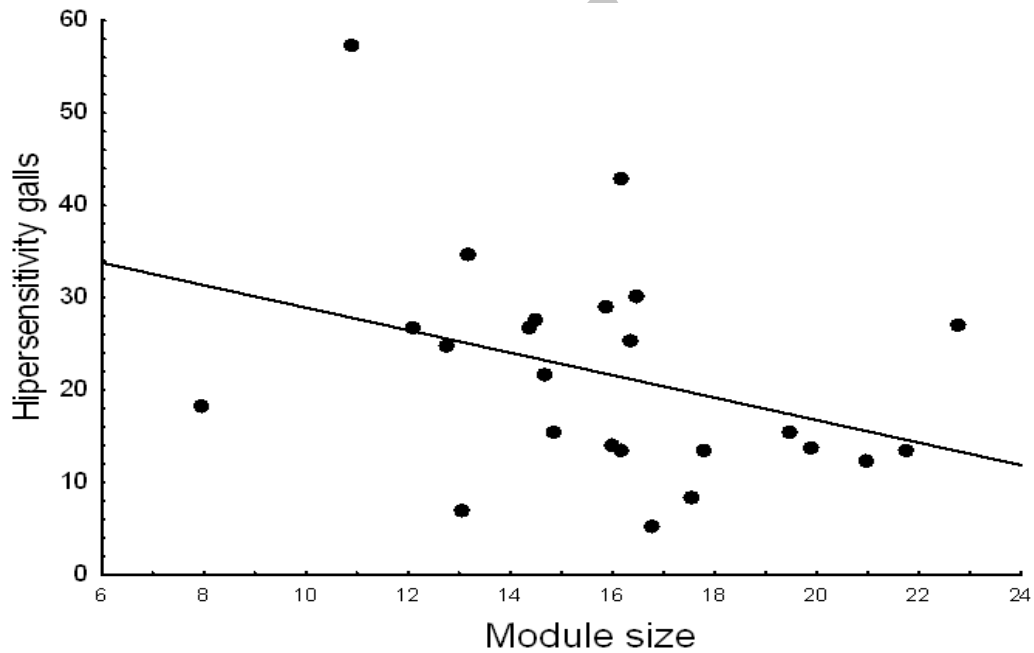
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27.

Fig1. Relationship between the galls abundance of Cecidomyiidae and the number of leaves per branch of the host plant *Ouratea hexasperma* in an area of savanna in Caldas Novas, Goiás, Brazil. (Linear regression: $y = 28.05 + 10.15x$).



28.

Fig 2. Relationship between the number of galls of Cecidomyiidae who presented hypersensitivity reactions and the size of the branch of the host plant *Ouratea hexasperma* in an area of savanna in Caldas Novas, Goiás, Brazil. (Linear regression: $y = 41.07 - 1.21x$).

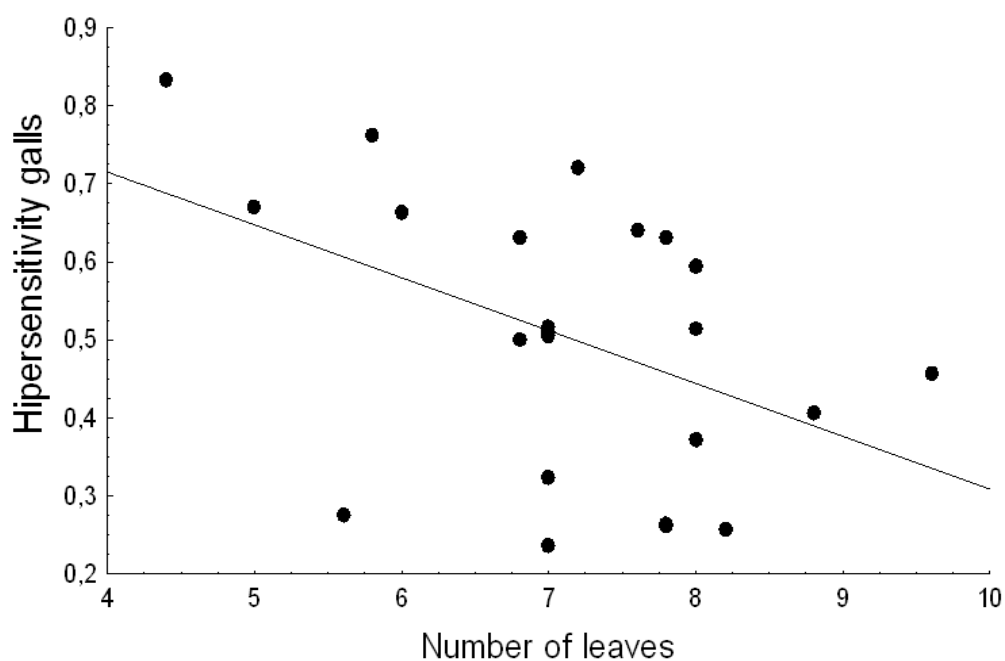


Fig3. Relationship between the number of galls of Cecidomyiidae who presented hypersensitivity reactions and the number of leaves per branch of the host plant *Ouratea hexasperma* in an area of savanna in Caldas Novas, Goiás, Brazil. (Linear regression: $y = 0.98 - 0.06x$).