ECOTROPICA

INFLUENCE OF HERBIVORE ATTACK PATTERNS ON REPRODUCTIVE SUCCESS OF THE SHRUB *PIPER HISPIDUM* (PIPERACEAE)

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Abstract. Herbivory is defined as the consumption of non-reproductive plant parts, and it can have varying consequences on plant fitness. The aim of the present study was to investigate if the effects of herbivory on the production of inflorescences by the shrub *Piper hispidum* (Piperaceae) depend on how the plant is attacked. I carried out this study at Parque Estadual Intervales, in the montane Atlantic Forest of southeastern Brazil. I tested the relationship between number of inflorescences and plant height, canopy cover, average leaf consumption rates, and variability of this rate between branches. Only the variability of herbivory among branches presented a positive relationship with the variation in number of inflorescences, suggesting that the degree of concentration of herbivore attacks on particular branches may be more important than the overall herbivory intensity. Herbivores that stay longer, consuming leaves on the same branch of a plant, may be more harmful than those that spread damage over several branches. Interspecific differences in defenses against such herbivores may even determine the species diversity of tropical forests. *Accepted 23 February 2007.*

Key words: Atlantic Forest, Brazil, foraging behavior, herbivory, interactions, phenology, Piperaceae, reproduction.

INTRODUCTION

Herbivory is defined as the consumption of non-reproductive plant parts, mainly leaves, by animals or pathogens. It occurs more frequently in tropical than in temperate forests, and represents a strong selective pressure for many plant species (Coley & Barone 1996). Depending on how the plant is attacked, herbivory can affect a plant's competitive abilities (Hambäck & Beckerman 2003). Herbivory may also influence the balance between sexual and vegetative reproduction, among other possible consequences (Olejniczak 2001).

The system formed by plants of the family Piperaceae (Magnoliopsida, Piperales) and their leaf consumers is a good model for studying herbivory, be-

cause it comprises a network of hundreds of plant and thousands of arthropod species that present peculiarities in their interactions, and so provide a wide array of sub-systems in different conditions (Letourneau 2004). This family comprises five genera (*Peperomia*, *Piper*, *Pothomorphe*, *Ottonia*, and *Sarcorhachis*) and more than 1000 species in Brazil (Yuncker 1971). The genus *Piper* Linnaeus 1737 includes shrubs and small trees, with leaves that are alternate, simple, lightly asymmetrical, with pinnate or palmate venation, and whose infructescences are small spike-like drupes that contain tiny fruits and seeds (Trelease 1950). Plants of the genus *Piper* present a strong ecological interaction at different trophic levels with many animals (Letourneau 2004), including seed dispersers like bats of the genus *Carollia* (Fleming 1988), defender ants of the genus *Pheidole* (Letourneau 1998), comensal

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beetles of the family Coccinelidae (Dyer *et al.* 1999), and different orders of herbivorous insects (Letourneau 2004). Species of *Piper* show high variation in life history traits, like investment in different reproductive strategies and preference for particular habitats (Fleming 1985, Greig 1993).

Letourneau (2004) observed no relationship between overall herbivory and inflorescence production in adult *Piper* plants in a field experimental study. However, many studies on *Piper* suggest that effects of herbivory on plant fitness vary widely, and may affect both asexual and sexual reproduction (Dyer *et al.* 2004). Some studies on other plants have shown that herbivores may not use the plant as a whole but mainly new leaves on the outer part (Wilkens *et al.* 2005), and that damage pattern may determine how bad the loss for the plant is (Stinchcombe 2002). Considering that only new branches produce inflorescences in *Piper*, I hypothesized that if herbivores foraged more intensively on some new branches and do not spread their attacks, the plant would produce fewer flowers. This would represent a stronger negative effect on plant fitness, based on herbivore foraging behavior.

MATERIAL AND METHODS

Study area. The study area was the state park "Parque Estadual Intervales", located in the county of Ribeirão Grande, São Paulo state, southeastern Brazil. Intervales covers about 50000 ha, and together with three other reserves forms the largest continuous Atlantic Forest remnant in Brazil (more than 100000 ha). We carried out this study in the region known as "Sede de Pesquisa", approximately 850 m above sea level (24°16'S, 48°24'W). According to Mantovani (2001), the region's climate is classified as Temperate Humid (Cwa in Köppen's System), and its main vegetation is classified as Montane Dense Rainforest.

A previous study listed two *Piper* species in the region, *P. aduncum* and *P. dilatatum*, and also another unidentified species (Passos *et al.* 2003). Mello (2006) identified four additional species in the same area: *P. gaudichaudianum*, *P. hispidum*, *P. mosenii*, and *P. xylosteoides*. As a model for the present study, I chose the species *Piper hispidum* Sw. (Fig. 1), which is apparently the most abundant in the area, presented high individual variability in inflorescence production at the time, and was intensively attacked by herbivores.

FIG. 1. The model species, *Piper hispidum* Sw. (Piperaceae), in Parque Estadual Intervales, southeastern Brazil.
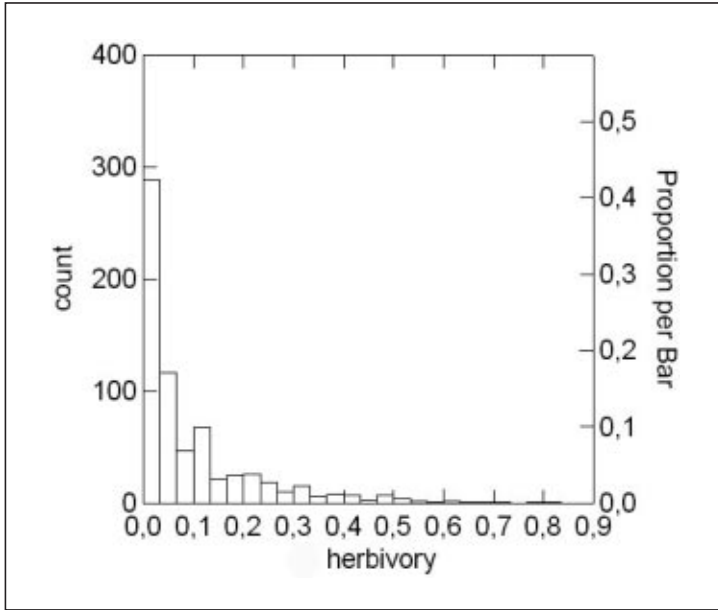
FIG. 2. Frequency distribution of percentage of area consumed by herbivores on 682 leaves collected from 20 individuals of *Piper hispidum*. Percentages are presented as decimals. 'Proportion per bar' represents the proportion of each category in relation to the total number of samples.

This species comprises small shrubs (< 1 m) to trees up to 4 m tall in the area, which grow mostly in shaded areas inside the forest. Leaves of *P. hispidum* usually are 15–17 cm long and 10–12 cm wide.

Time frame and data acquisition. I collected data between 13th and 18th January 2004. In the field, I measured the following variables in 20 individuals of *P. hispidum*: number of inflorescences, height, and canopy openness at that point. I decided to include height and canopy cover in the multiple regression analysis, because those variables may also influence the total number of inflorescences produced by an individual *Piper* (Marquis 1988). I assessed canopy openness by taking digital photographs of the canopy at 2-m height in front of each individual on the trail, and later processing images with the software Gap Light Analyzer, which estimated the percentage of the area not covered by vegetation. This percentage was used as a measure of light availability for the plant. Sampled individuals were at least 20 m apart from each other, to avoid sampling ramets from the same genet.

Additionally, I collected eight apical branches from every individual, four at a lower and four at a greater height. Branches were selected so that they were on different sides of the plant in order to avoid branches subjected to the same conditions. I did not include older branches because each branch produces inflorescences only once, thus only new branches could be used to measure fitness in a given season (Fleming, 1988).

Each branch had three to eight leaves, which I analyzed in the laboratory for herbivore attacks. In order to measure the percentage of the leaf area that had been eaten by herbivores I used a transparency marked with dots, in a 1-cm mesh. I put this transparency on each leaf and used a white paper sheet for contrast. I counted the number of dots on the total leaf surface and the number of dots on the "eaten surface", and calculated herbivory as the ratio eaten/total.

Using these leaf ratios, I calculated the mean herbivory rate for each branch, and for each individual. I also calculated the standard deviation for herbivory among branches of each individual, as a measure of attack dispersion.

For statistical tests I followed Zar (1996), and made calculations using the software Systat 9.0. The relationship between the four independent variables and number of inflorescences was tested according to the multiple linear regression model: number of inflorescences = constant + height + canopy openness + mean herbivory percentage + standard deviation of the herbivory percentage between branches. Variables

3

expressed as ratios were arcsine transformed before being used in the linear model.

RESULTS

I analyzed a total of 160 apical branches from 20 individuals (eight branches from each plant) of *P. hispidum*, which contained 682 leaves.

During the study period I checked several individuals of *P. hispidum* for herbivores. Many kinds of invertebrates were consuming leaves of *P. hispidum*, including snails (Gastropoda), grasshoppers (Orthoptera), stick insects (Phasmatodea), beetles (Coleoptera), and caterpillars (Lepidoptera); all those taxa are tyical *Piper-consumers* in the Neotropics (Letourneau 2004). I also observed many other kinds of invertebrates on leaves, but which were not feeding on them, like spiders (Arachnida: Araneidae and Theridiidae), and many harvestmen (Arachnida: Opiliones) of the genera *Jussara* and *Holcobunus*. I did not find any ant colonies on those plants, only a few solitary individuals.

The average height of the *P. hispidum* individuals was 267 ± 44.0 cm (mean ± SD), varying between 200 and 350 cm. Number of inflorescences per individual was 79.5 ± 52.17, varying between 17 and 207. Percentage of herbivory on each leaf was 9 ± 13%, varying between 0 and 81% (Fig. 2).

The relationships between number of inflorescences and the variables 'height' (standardized partial regression coefficient b' = –0.020, p = 0.937), 'canopy openness' (b' = 0.103, p = 0.706) and 'mean herbivory' (b' = –0.102, p = 0.737) were not significant. However, the variable 'standard deviation of herbivory' was significantly and positively related to the number of inflorescences (b' = 0.550, p = 0.042), suggesting that plants that were attacked with a more scattered pattern produced more inflorescences than plants that suffered attacks concentrated on particular branches. The relationship between the dependent variable and each of the independent variables is presented in Fig. 3.

DISCUSSION

Results obtained in the present study suggest that plants that suffer more concentrated attacks are subjected to a greater reduction in the production of inflorescences. Therefore foraging behavior of herbivores can determine the intensity of negative effects on plant fitness. This interpretation is based on some observations commented in detail below.

I observed many kinds of herbivores consuming *P. hispidum* leaves. Each of those animals has a typical foraging behavior, varying from adult orthopterans that eat leaves from different branches to lepidopteran larvae that remain on the same branch until consuming all leaves (Letourneau 2004). Strauss *et al.* (2002) suggested that the effect of herbivory on sexual reproduction may vary depending on which invertebrate feeds on the plant. Some authors who worked with other plant-herbivore systems observed that consequences of attacks may differ, depending on which parts of the plant were more intensively attacked (e.g., Stinchcombe 2002). Considering both aspects of herbivore foraging behavior, which part of the plant is consumed and how intensively, it is probable that herbivores that stay longer on a particular branch and eat all of its leaves, instead of eating small parts of several different leaves, represent a higher danger for plants. Marquis (1992) also suggested that the consequences of herbivore attacks may vary depending on how leaves are eaten, because old branches, despite being still photosynthetically active, do not produce any flowers (production occurs only where meristems are present). Hochwender *et al.* (2003) also suggest that plants do not invest in flower production equally in all branches, and that herbivore negative impact may be higher if attacks are concentrated on the most productive branches. Therefore if herbivore foraging in *Piper* is concentrated on a few of the new inflorescence-producing branches, the plant may suffer a stronger reduction in its fitness. Those differential effects of attack patterns can have different ecological and evolutionary consequences for plants.

First, if plants that suffer concentrated attacks do not evolve induced defenses against those herbivores, they may invest more in clonal growth than in flower production, possibly reducing genetic variability of the population and thus its resistance to disturbances, and resulting also in more clumped spatial distributions, as suggested by Olejniczak (2001). Alternately, if some plant species evolve specific induced defenses against herbivore species that concentrate attacks, they may be able to invest more in sexual reproduction, which could increase population resistance to disturbances and allow less-clumped and wider spatial distributions (Maron & Crone 2006). Plant species should also have the ability to express induced anti-herbivore defenses at initial stages of ontogeny, because when they are already grown, it may be too late for a defense (Boege & Marquis 2005). Additionally ant-defended species, like some *Piper* of Costa Rica (Letourneau 1998) should have those concentrated
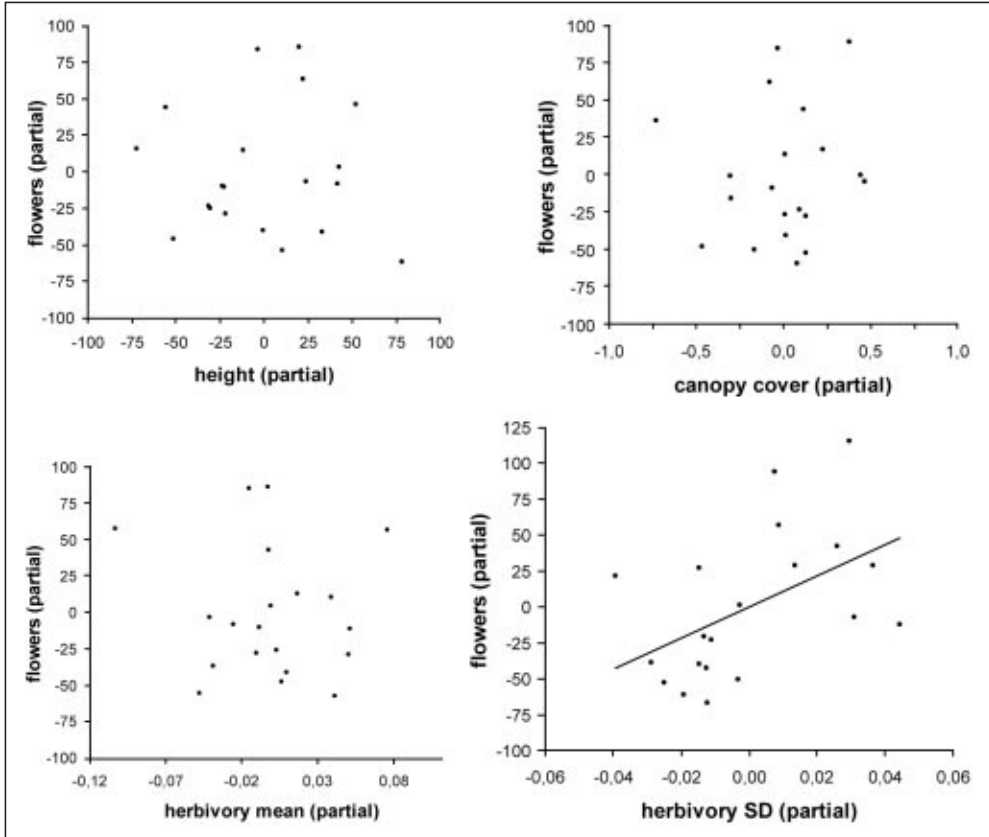
FIG. 3. Relationship between the dependent variable (number of inflorescences) and partial values of the four independent variables (plant height, canopy openness, average herbivory, and standard deviation of herbivory), calculated from the multiple regression analysis by removing the effects of other variables.

attacks and their consequences prevented. Plant species with redundant defenses, like both ants and secondary metabolites (Dyer *et al.* 2001), should be even more protected against concentrated attacks. Effects of herbivory patterns may ultimately influence species diversity patterns in tropical forests, because herbivores can determine which plant species will win competition for space in a particular area (Boege & Marquis 2006).

Finally, I conclude that plant species that are subjected to more concentrated attacks on branches involved in reproduction suffer higher reduction in fitness than plants that are attacked more diffusely. Thus it is likely that species-specific induced defenses evolved by some plant species should be directed towards herbivores that stay longer feeding on the same branch. It would be interesting for future studies to investigate how fitness varies between closely related sympatric plant species that are undefended or that have different kinds of anti-herbivore protection.

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