

PLANT RESPONSE TO HERBIVORY: TWO EXAMPLES FROM THE NEOTROPICS

RESPUESTA DE LAS PLANTAS A LA HERBIVORIA: DOS EJEMPLOS DEL NEOTRÓPICO

G. Wilson Fernandes^{1,2} and Sérgio P. Ribeiro²

¹Department of Biological Sciences, Box 5640, Northern Arizona University, Flagstaff, AZ
86011 - U.S.A.

²Present Address: Departamento de Biologia Geral, Caixa Postal 2486, Instituto de Ciencias
Biologicas, Universidade Federal de Minas Gerais, 30.161 - Belo Horizonte, MG - BRAZIL

ABSTRACT

The responses of two neotropical plant species to herbivory and frost were studied. Within-plant comparisons indicated that *Brickellia pinnifolia* (Compositae) branches responded to herbivory by a stem galling tephritid species and frost by producing larger and more shoots than unaffected branches. Damage-response (measured in terms of number of shoots and shoot length) was significantly higher on frost affected than on galled branches, which was higher than on unaffected branches. Herbivory by a buprestid insect on the flower stalk of *Paepalanthus speciosus* (Eriocaulaceae) significantly increased production of compound umbels and individual inflorescences. However, fewer individual inflorescences developed to fruit stage on eaten plants compared to uneaten plants. No clear influence of herbivore attack was observed on host plant final height, or on overall compound umbel diameter. A second wave of herbivory followed after plants responded to the first one. In this second wave, 72% of the compound umbels were destroyed and no further plant response was observed. It appears that resource manipulation by the herbivore may be involved in this case. The adaptive nature of plant response to damages caused by frost and herbivory is discussed.

KEY WORDS: *Brickellia pinnifolia*, herbivory, Neotropics, *Paepalanthus speciosus*, plant compensatory responses.

RESUMEN

Se estudió el efecto de los herbívoros y la formación de escarcha en dos especies de plantas neotropicales. La comparación entre las plantas indicó que las ramas de *Brickellia pinnifolia* responden tanto a la formación de escarcha como a la herbivoría por parte de un tefritido que induce agallas en el tallo, produciendo retoños más largos y más numerosos que en las ramas no afectadas. La respuesta al daño (medida en términos de número y longitud de retoños) fué significativamente mayor en las ramas afectadas por la formación de escarcha que en las que tenían agallas, las cuales a su vez sufrieron un daño mayor que aquellas que no fueron atacadas. El impacto de un insecto buprestido en el tallo de las flores de *Paepalanthus speciosus* (Eriocaulaceae), incrementó significativamente la producción de umbelas e inflorescencias individuales. Sin embargo, en estas plantas muy pocas inflorescencias individuales llegaron a fruto en comparación con las plantas que no sufrieron este ataque. No se observó una clara influencia del ataque del herbívoro sobre el peso final de la planta ni sobre el

diámetro completo de la umbela. Una segunda ola de herbívoros le sigue a la primera una vez que las plantas han respondido al ataque. En este segundo ataque, 72% de las umbelas fueron destruidas y no se observaron más respuestas de la planta. Al parecer, en éste ataque existe una manipulación del recurso por parte de los herbívoros. Se discute la naturaleza adaptativa de las plantas a daños ocasionados por la formación de escarcha y por la herbivoría.

PALABRAS CLAVE: *Brickellia pinnifolia*, herbivoría, Neotrópico, *Paepalanthus speciosus*, respuestas compensatorias de plantas.

INTRODUCTION

After examining numerous studies on the beneficial effects of herbivory, Belsky (1986) concluded that there is as yet no convincing evidence that herbivory is beneficial to plants under natural conditions. However, Paige and Whitham (1987) experimentally demonstrated that under natural field conditions plants can benefit from being eaten. They found that after the removal of 95% or more of the above ground biomass of the biennial scarlet gilia, *Ipomopsis aggregata*, seed production and seedling survival were 2.8 times greater than that of uneaten controls. Unbrowsed plants produced only single inflorescences, whereas browsed plants produced multiple inflorescences. Despite Paige and Whitham's (1987) clear demonstrations of the beneficial impact of browsing herbivores on plants, more studies on the effects of herbivores on plants in both temperate and tropical regions are needed. We present preliminary evidence on how two tropical plant species respond to insect herbivory. The morphology of *Brickellia pinnifolia* A. Gray (Compositae) is modified by gall formers and frost. A tephritid insect gall on stems of *B. pinnifolia* is very common in Serra do Cipó, MG, Brazil. Galled branches exhibit modified morphology because gall formation interferes with normal growth

patterns. Galled branches resembled "witch-brooms", with many shoots growing from the proximal and distal portions of the gall. Gall formation is frequently cited as a factor interfering with host plant plp-morphology and fitness (e.g., Dennill 1985, 1988; Fernandes 1987 and references therein). Frost also damages terminal shoots and alters branch morphology, causing branches to depart from their normal growth pattern, and the death of terminal shoots. Frost affected branches also resembled "witch-brooms", but only the terminal portion of the branches were affected.

We also censused a second plant species, the monocot *Paepalanthus speciosus* (Bong) Kolin (Eriocaulaceae), that is attacked by an unidentified species of buprestid beetle. Adults of the beetle chew the single flower stalk produced by the host plant; they chew through it until the terminal compound umbel falls off the plant. Casual field observations suggested that chewed plants produced more compound umbels, and individual inflorescences than unchewed plants (Fig. 1). It appears that *P. speciosus* is an annual (T.S.M. Grandi, personal communication). In the *B. pinnifolia* system we asked: 1) Does herbivory and/or frost influence shoot production and shoot length? In the *P. speciosus* system we asked the following questions: 1) Does herbivory influence plant

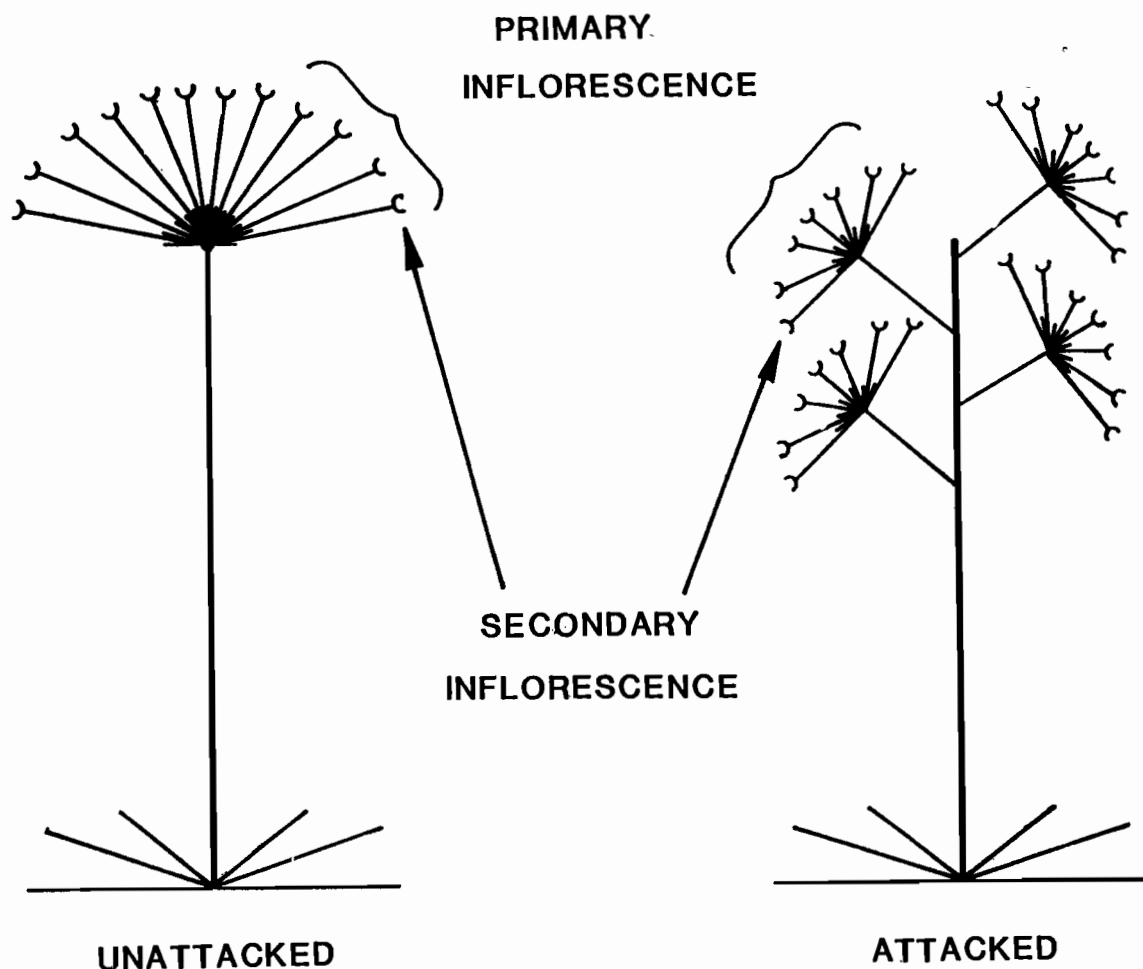


FIGURE 1. Schematic representation of *P. speciosus* plants. Only one terminal compound umbel is produced by uneaten plants. Eaten individuals produce many more terminal compound umbels. Nevertheless, these are significantly smaller than the terminal compound umbels of uneaten plants.

final height? 2) Do eaten plants produce more compound umbels than uneaten plants? 3) What is the effect of herbivory on inflorescence quality?

MATERIALS AND METHODS

The plants we studied are located in Serra do Cipó, Minas Gerais State, Brazil, which is characterized by rocky, nutrient-poor soil and low-nutrient status plants (see Silveira 1908, Hoene 1927, Hutchinson

1943, 1945, Joly 1970, Goodland and Ferri 1979). We sampled *B. pinnifolia* in February 1988, and *P. speciosus* in April 1988. Flower buds in the distal portion of the branches of *B. pinnifolia* break dormancy after a vegetative growth phase, thus starting the flowering season. Many flower heads are produced at the terminal portion of the branches. Many dormant buds are also present along the branches. These buds may become active after the dominant buds are damaged or destroyed.

We counted the number of new shoots and measured the length of galled, frost affected, and uneaten branches. After a vegetative rosette stage, *P. speciosus* produces a leafy stalk terminating with one large compound umbel (Fig. 1). Thus, a compound umbel, and several individual inflorescences are produced. Dormant buds are present along the plant's leafy stalk. There is no study available on the floral biology of *P. speciosus* (A.M. Giulietti, personal communication). We measured plant final height, number of primary inflorescences, number of flower heads, quality of inflorescences (here measured as developed or atrophied), and inflorescence diameter, as the plant variables affected by the flower stalk herbivore.

Because the number of shoots and their lengths are not independent

measurements, we multiplied the number of shoots by their lengths for each treatment in order to have what we called a "damage response index". A non-parametric test to analyze the *B. pinnifolia* data was used because of unequal variances among the treatments (Quade test, Conover 1980, Zar 1984).

RESULTS

Frost and gall effects on *B. pinnifolia*

Frost affected and galled branches produced significantly more shoots and longer shoots than unaffected branches of *B. pinnifolia* (Quade test, $p < 0.0001$, Fig. 2a). Frost affected ($N = 41$) and galled branches ($N = 41$) produced an average of 9.37 ($SE \pm 0.62$), and 5.56

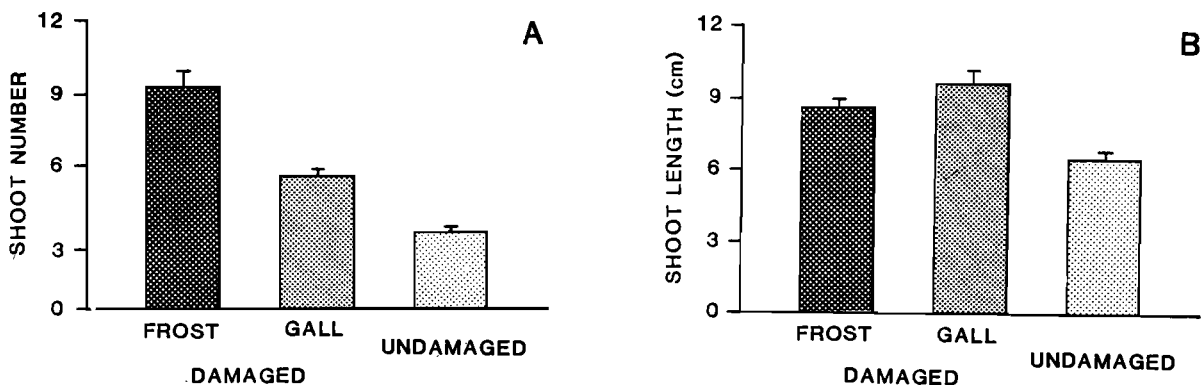


FIGURE 2. *Brickelia pinnifolia* response to frost, and herbivory by a tephritid stem galling insect. A) Shoot number produced by frost affected, galled, and unaffected *B. pinnifolia* stems. There were statistically significant differences in the number of shoots produced by frost, and galled stems compared with unaffected stems (Quade test, $F_{2,80} = 3.15$, $p < 0.0001$). B) Length of shoots produced by frost affected, galled, and unaffected branches of *B. pinnifolia*. There were statistically significant differences between all treatment means (see Table 1 and text for results).

(SE \pm 0.24) shoots, respectively. On the other hand, unaffected branches produced an average of only 3.15 (SE \pm 0.15) shoots. Branches hit by frost, and by the gall herbivore produced the longest shoots. Frost affected branches produced shoots averaging 8.72 cm (SE \pm 0.36 cm), and galled branches produced shoots averaging

9.62 cm (SE \pm 0.63); while unaffected branches produced shoots averaging 6.5 cm (SE \pm 0.23, N = 41, Fig. 2b). Multiple comparisons of treatment means (see Conover 1980: 297) indicated significant differences between all treatments (Table 1).

TABLE 1. Multiple comparisons of treatment means among effects of damage on *B. pinnifolia* (see Conover 1980: 297). The treatments were considered different from each other if the difference between their sums $|S_i - S_j|$ exceeded:

$$|S_i - S_j| > t_{1-\alpha/2} \frac{2b(A_1 - B_1)^{1/2}}{(b-1)(k-1)}$$

All treatments were significantly different among them.

| TREATMENT COMPARISON DIFFERENCE | $ S_i - S_j $ |
|---|---------------|
| $ S_{\text{unaffected}} - S_{\text{frost}} $ | 1534.0 |
| $ S_{\text{unaffected}} - S_{\text{galled}} $ | 911.0 |
| $ S_{\text{frost}} - S_{\text{galled}} $ | 623.0 |

Herbivore Effects on *P. speciosus*

Plant final height was not influenced by the umbel stalk herbivore (Anova, $p > 0.05$, Fig. 3a). Eaten plants had an average height of 113.33 cm (SE \pm 6.33 cm, N = 15), and uneaten plants averaged 129.21 cm (SE \pm 8.28, N = 24).

Eaten individuals produced significantly more compound umbels than uneaten individuals (Anova, $p < 0.0001$, Fig. 1, and 3b). Eaten individual produced an average of 5.8 (SE \pm 1.32, N = 15) compound umbels, while uneaten produced

only one compound umbel per plant (N = 24). In addition, eaten plants produced significantly more individual inflorescences than uneaten plants (Anova, $p < 0.05$, Fig. 3c). Eaten plants produced an average of 178.0 (SE \pm 28.3, N = 15) individual inflorescences while uneaten plants only produced 128.2 (SE \pm 14.6, N = 24) individual inflorescences. Both compound umbels and individual inflorescences produced by eaten plants were significantly smaller than those produced by uneaten plants. However, the overall size (total diameter) of the compound umbel of eaten

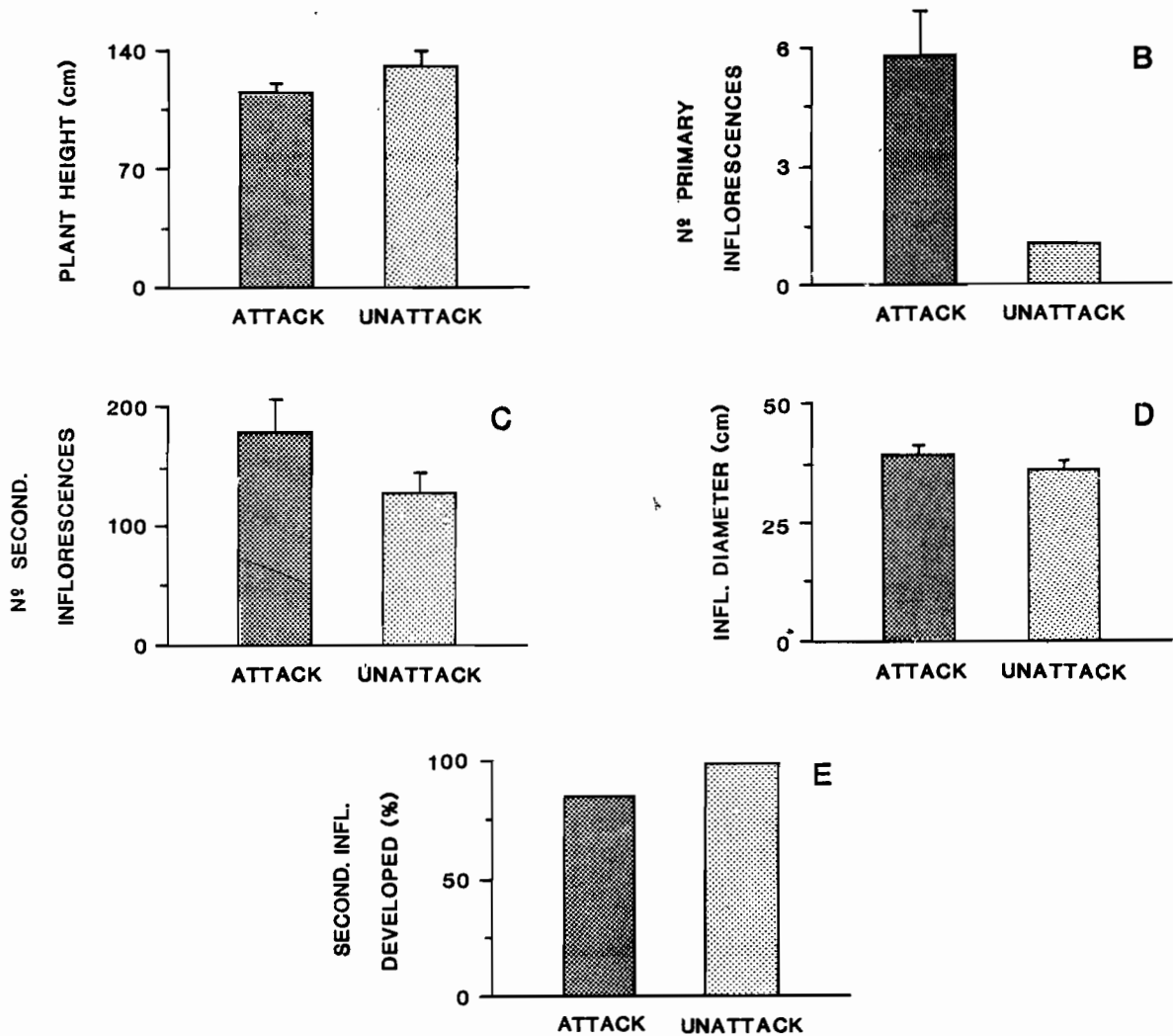


FIGURE 3. *Paepalanthus speciosus* response to a buprestid beetle herbivory. A) Final plant height was not influenced by the inflorescence stalk herbivore (Anova, $F_{1,37} = 1.87$, $p > 0.05$). B) Eaten individuals produced significantly more primary inflorescences than uneaten individuals (Anova, $F_{1,37} = 21.59$, $p < 0.0001$). C) Eaten individuals produced significantly more secondary inflorescences than uneaten individuals (Anova, $F_{1,37} = 2.96$, $p < 0.05$). D) Inflorescence size of eaten individuals was not significantly different from that of uneaten individuals (Anova, $F_{1,37} = 0.099$, $p > 0.05$). E) Significantly fewer secondary inflorescences developed on eaten plants compared to uneaten plants (Anova, $F_{1,37} = 9.60$, $p < 0.002$). (see text for results).

plants was not significantly different from that of uneaten individuals [Anova, $p > 0.33$, Fig. 3d; eaten 39.60 cm diameter ($SE \pm 2.34$, $N = 15$), uneaten 36.58 cm diameter ($SE \pm 1.91$, $N = 24$)].

Although significantly more compound umbels and individual inflorescences were produced on eaten plants compared to uneaten plants (Figs. 3b and 3c), significantly fewer flowers on individual inflorescences developed to fruit stage on eaten plants compared with uneaten plants (Anova, $p < 0.002$, Fig. 3e). Eighty five percent of the flowers on individual inflorescences of eaten plants developed completely to the fruit stage (85.44%, $SE \pm 0.05$, $N = 15$) as opposed to 97% that developed completely to the next stage on uneaten plants (97.34%, $SE \pm 0.01\%$, $N = 24$).

Failure to develop was due primarily to atrophy of the individual inflorescences. Undeveloped (atrophied) individual inflorescences were smaller and blackish compared to developed ones.

Of the fifteen plants that were attacked by the flower herbivore, 5 (33%) suffered a second attack which was responsible for the loss of 72% of the newly produced compound umbels.

DISCUSSION

Brickellia pinnifolia branches responded to herbivory by producing larger and more shoots than unaffected branches. Furthermore, the number of shoots, and shoot length were significantly higher on frost affected than on galled branches which were higher than on unaffected branches. The higher number of shoots, as well as longer shoots, produced by frost affected branches compared with galled branches

is intriguing. There are at least four alternative but not mutually exclusive hypotheses that may be responsible for this plant response pattern.

The first hypothesis predicts that apical buds grow more vigorously than lateral buds, and plant energy is canalized to the apical meristems thus enabling more buds to break dormancy (see Longman 1978, Tomlinson 1978). In fact, frost affected only apical meristems whereas the stem gall tephritid destroyed only lateral buds.

The second hypothesis predicts that fewer buds were damaged by frost than by the gall tephritid, thus resulting in the higher numbers and larger shoots found on frost-affected branches compared with galled branches. Only terminal buds were hit by frost whereas galling may have affected more buds that were perhaps less active and less dominant lateral buds, thus reflecting in fewer, and smaller branches.

The third hypothesis predicts that the gall competes for energy with the adjacent buds thus making them shorter, and suppressing bud break in some dormant buds. Insect galls induce dramatic metabolic changes in their host plants during gall formation and growth (e.g. Rohfritsch and Shorthouse 1982, Fernandes 1986 and references therein) that could be associated with the *B. pinnifolia*'s observed response patterns. Furthermore, galls are nutrient sinks within host plants (see Jankiewicz et al. 1970, Stinner and Abrahamson 1979), so that portion of the nutrients available for plant growth is diverted to gall maintenance. On the other hand, in frost damaged branches, all the energy would be directed to the growth of new shoots because a branch would not have part of its energy diverted to a different structure.

The fourth hypothesis predicts that frost response is more predictable than gall response and that plants have evolved to respond to frost damage with longer and more numerous shoots. Frost is a phenomenon of high predictability in the high elevations of the Serra do Cipó that affects all *B. pinnifolia*'s unhardened buds, whereas galling is phenomenon dependent on highly variable factors such as host plant defense, host plant quality, herbivore abundance, and herbivore host finding behavior, for instance. Frost would then be more predictable both in space and time than galling. However, more work is called to unravel the mechanisms and processes behind the trends found.

Each stem of *B. pinnifolia* terminates in many flower heads. We speculate that more branching will lead to more flowers and fruits being produced. We do not know, however, how many viable seeds the new branches produce, and whether the replacement of damaged shoots affects timing of seed dispersal and seedling establishment. Another important unanswered question is how this extra expenditure of resources affects survivorship and life time seed production.

Herbivory by a buprestid beetle on the flower stalk of *P. speciosus* significantly increased production of compound umbels and individual inflorescences. However, fewer flowers in the individual inflorescences developed into fruits on eaten plants compared with uneaten plants. The "atrophy" and consequent fruit failure observed on eaten individual inflorescences might be the result of herbivory. Flowers in this family are generally unisexual and male and female flowers occur in the same flower heads (Dahlgreen et al. 1985) and herbivore

attack may also have altered the sex ratios among flowers within individual inflorescences. Herbivory may delay flowering such that the newly produced flowers on eaten plants are not pollinated or are more likely to be adversely affected by temperature or weather condition (e.g. Schemske 1977). No clear influence of herbivory was observed on host plant final height, or on overall compound umbel diameter. Inflorescence size is an important factor for pollinator attraction (e.g. Willson and Price 1977, Zimmerman 1980, Wyatt 1982, Schmid-Hempel and Speiser 1988, but see Willson and Rathcke 1974). Inflorescence display and competition for pollinators may also be adaptive (e.g. Campbell 1985, Campbell and Motten 1985). They may be even more important in annuals and in habitats such as the Serra do Cipó in which there is a marked flower season. Furthermore, the adaptive value of inflorescence display and size might be amplified in tropical habitats where plants are, in general, far away from a conspecific, and thus hard to find for the pollinator species.

The significance of compensatory production of compound umbels and individual inflorescences in *P. speciosus* is not clear. A second wave of herbivory follows after plants respond to the first herbivore attack. In this second wave of attack 72% of the compound umbels were destroyed and no plant growth response was observed. There are at least two, not necessarily mutually exclusive, mechanisms or hypotheses that may be involved here. The first hypothesis is one of meristem limitation in which axillary buds located in the compound umbel stalk had already developed into secondary inflorescences prior to the first wave of attack. The

second hypothesis is one of resource limitation in which the plant could not respond to the second attack because there were no resources left. These plants live in nutrient-poor soil habitats. Thus, plants may be constrained in their response to herbivory after the "limited" energy backup supply is used. The differential response of nutrient-stressed and healthy plants to herbivory remains to be fully evaluated. In similar systems, Paige and Whitham (1987), and Hendrix (1979, 1984) did not observe a second wave of attack by the herbivore on their study plants. A second wave of attack by the herbivore would jeopardized the compensatory growth response of the host plant. The argument that plant overcompensation is adaptive to the plant (see Paige and Whitham 1987) was only partially supported in this study.

An herbivore's view of these findings indicates that the *P. speciosus* flower herbivore may be manipulating its resources. The plant response to the first attack would cause many more resources to be produced which would then be used by the herbivore. If the herbivore is a specialist on this plant species and/or this plant family, this strategy would be adaptive for the herbivore. In fact, we observed similar damage on other closely related *Paepalanthus* species. A resource manipulation strategy would be important to the herbivore for adjusting phenologically to *P. speciosus* if plant populations present asynchronous flowering seasons in the altitudinal gradient of Serra do Cipó, and/or *Paepalanthus* species present different flowering phenologies. Nevertheless, more studies are called to unravel the mechanisms and processes involved in this system.

In summary, plants may respond to abiotic or frost damage, and herbivory in many different ways. Many historic and ecological factors may influence these responses, such as the type of damage, plant phenology, plant nutritional status, plant phylogenetic constraints, as well as the kind of interactions plants have with their herbivores (see Maschinsky & Whitham 1989, Whitham et al. 1990). Generalizations about whether a plant's compensatory responses to herbivory, as well as physical damage, are adaptive for the plant can be made only after the whole spectrum of responses of both plant and herbivore are fully explored and more studies are performed in both tropical and temperate systems.

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