INSECT FOLIVORY IN *Didymopanax vinosum* (APIACEAE) IN A VEGETATION MOSAIC OF BRAZILIAN CERRADO

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Received September 8, 2004 – Accepted January 14, 2005 – Distributed May 31, 2006

(With 4 figures)

ABSTRACT

Susceptibility of *Didymopanax vinosum* (Apiaceae) to insect herbivores was investigated in three sites of a cerrado mosaic – composed of campo cerrado (a grassland with scattered trees and shrubs), cerradão (a tall woodland) and cerrado *sensu stricto* (intermediate between the two) – situated in Cerrado Pé-de-Gigante, Santa Rita do Passa Quatro, SP, Brazil. We also examined the relationship of folivory with the composition and abundance of the insect herbivore fauna, and with several nutritional and defensive plant characteristics (water, nitrogen, cellulose, lignin, tannin leaf contents, and leaf toughness). We collected insects associated with *D. vinosum* every month, and we measured leaf damage every three months. In general, the annual folivory differed among sites. It reached the highest rates in site 1 and site 3: 7.33 and 8.5 percent, respectively. Only 1.32 percent of annual folivory was observed in site 2. These levels resulted from the higher abundance, in sites 1 and 3, of the thrips *Liothrips didymopanacis* (Phlaeothripidae), the most abundant herbivore sampled, responsible for more than 90 percent of the observed damage. However, no significant relationship was found between insect activity and the chemical and physical composition of the leaves. Our findings suggest that, at least in this species, other chemical compounds or variables related to plant apparency and resource availability to herbivores (*e.g.* plant architecture) might play a more decisive role in the spatial variation of folivory than the nutritional and defensive traits that were analyzed.

Keywords: cerrado, *Didymopanax vinosum*, folivory, herbivory, plant defenses.

RESUMO

Folivoria por insetos em *Didymopanax vinosum* (Apiaceae) em um mosaico de vegetação no cerrado brasileiro

A susceptibilidade de *Didymopanax vinosum* (Apiaceae) a insetos herbívoros foi investigada em três localidades de um mosaico de cerrado – composto de campo cerrado, cerrado *sensu stricto* e cerradão – localizado no Cerrado Pé-de-Gigante, Santa Rita do Passa Quatro, SP, Brasil. Nosso objetivo foi também relacionar a folivoria com a composição e abundância da fauna de insetos herbívoros, e com várias características nutritivas e defensivas da planta (conteúdo foliar de água, nitrogênio, celulose, lignina, taninos e dureza foliar). Para tanto, coletamos mensalmente os insetos associados a *D. vinosum* e a cada três meses medimos as injúrias foliares. De modo geral, a herbivoria anual variou entre as localidades. Os maiores valores foram encontrados em plantas da localidade 1 e localidade 3: 7,33 e 8,5 por cento, aproximadamente, contra apenas 1,32 por cento na localidade 2. Esses níveis são resultado da maior abundância, nas localidades 1 e 3, do trips *Liothrips didymopanacis* (Phlaeothripidae), o principal herbívoro amostrado, responsável por mais de 90% das injúrias observadas. Entretanto, não se encontrou relação entre a atividade desses insetos e a composição química e física das folhas. Nossos resultados indicam que, ao menos para esta espécie, outros compostos químicos ou variáveis relacionadas à aparência e à disponibilidade de recursos aos herbívoros (por exemplo a arquitetura da planta), podem desempenhar um papel mais importante na variação espacial da folivoria que as características nutritivas e as defesas vegetais que foram analisadas.

Palavras-chave: cerrado, defesas vegetais, *Didymopanax vinosum*, folivoria, herbivoria.

INTRODUCTION

Cerrado is a subtropical biome in Central Brazil; it occupies nearly 23 percent of the Brazilian territory (Ratter *et al.*, 1997). Seasonal precipitation, soil fertility and drainage, fire regime, and the climatic fluctuations of the Quaternary are considered important factors in the distribution of cerrado vegetation (Oliveira-Filho & Ratter, 2002). Due to some limiting factors, especially related to soil conditions, plant species in cerrado have some typical scleromorphic characteristics, including thick bark, coriaceous leaves, densely covered by trichomes, and the location of stomata in depressions of the leaf surface (Goodland & Ferri, 1979).

Cerrado *sensu lato* is not a homogeneous type of vegetation. According to Oliveira-Filho & Ratter (2002), it ranges from campo limpo (a dense grassland without shrubs or trees) to cerradão (a tall woodland with a crown cover of 50% to 90%, made up of trees, often of 8-12 m or even taller, casting a considerable shade so that the ground layer is much reduced). Between these two extremes there are intermediate physiognomies, such as campo sujo, a grassland with a scattering of shrubs and small trees; campo cerrado, where there are scattered trees and shrubs and a large proportion of grassland; and cerrado *sensu stricto* (*s.s.*), dominated by trees and shrubs often 3-8 m tall and having more than 30% crown cover but with still a fair amount of herbaceous vegetation between them. The high diversity of physiognomies can be ascribed to geomorphologic, topographical and edaphic factors, fire frequency, and grazing (Coutinho, 1978). According to Goodland (1971), the vegetation gradient from campo limpo to cerradão is basically a gradient of increasing biomass and of decreasing xeromorphism.

The patterns of herbivory found in some cerrado species suggest that herbivore pressure is low in this type of vegetation, probably as a result of the development of both phenological escape (many plants produce new leaves before the increase in abundance of herbivorous insects) and low-quality plant tissues (Fowler & Duarte, 1991; Marquis *et al.*, 2002). According to Coley *et al.* (1985), plant species in environments with low resource availability (such as cerrado) have been selected to have a high investment in quantitative defenses including tannins and lignins, which reduce the digestibility of the plant tissues. Such adaptations are important, since tissue losses to herbivores result in decreased plant fitness (Marquis, 1984; Sagers & Coley, 1995). In addition, herbivory can reduce leaf longevity (Janzen, 1980; Risley & Crossley-Jr, 1988), resulting in a high loss of photosynthetic biomass.

Environmental differences across vegetation can influence the nutritional and defensive qualities of plant species, which in turn can provoke intraspecific variations in herbivory levels (Louda *et al.*, 1987). Moreover, there is great variation in several leaf traits of *Didymopanax vinosum* (Cham. & Schltdl.) Seem. (Apiaceae[1]) in a vegetation mosaic at Cerrado Pé-de-Gigante, Santa Rita do Passa Quatro, SP (Pais & Varanda, 2003).

Thus, the purpose of this study was to examine the susceptibility of *D. vinosum* to insect herbivores in a vegetation mosaic at Cerrado Pé-de-Gigante, examining the relationship between folivory by insects and leaf quality.

MATERIAL AND METHODS

Study area

The study was carried out at Cerrado Pé-de-Gigante (21° 36' - 39' S and 47° 36' - 38' W), one of the vegetation patches that compose the Parque Estadual de Vassununga, a protected state park located in Santa Rita do Passa Quatro SP, Brazil. The following description was extracted from Batalha (1997) and Batalha *et al.* (2001). The patch has typical cerrado *sensu lato* vegetation

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[1] According to Judd *et al.* (1999).

and occupies a 1225,000 ha area at 590 to 740 m altitude. The region, according to Köppen's Cwag climate type classification, has well-defined seasons: a wet season from November to April, with a mean rainfall of more than 1200 mm, and a dry season from May to October with a mean rainfall of 485 mm. Mean temperature ranges from 17 °C in June to 25 °C in January. There are several intermixed physiognomies in this vegetation patch, including mainly campo cerrado, cerrado *s.s.,* and cerradão. Campo cerrado vegetation is open, dominated by herbs, shrubs, and some sparse trees. Cerrado *s.s.* is a more dense vegetation, with an arboreal stratum and a dense stratum composed of herbs and shrubs. Cerradão has few herbs and shrubs under a well-developed arboreal stratum.

The shrub *D. vinosum*, typical of cerrado, grows on all of these sites. Producing composite leaves throughout the year, in cerrado *s.s.* this species occurs in the understory, and in cerradão it is largely limited to small clearings. Sampling was performed in three plots (sites) of about 10,000 m^2 placed at least 50 m far from the border in order to avoid edge effects. Plot or site 1 was positioned in a campo cerrado patch, site 2 in the cerrado *s.s.* matrix, and site 3 in a cerradão patch (Fig. 1).

Analysis of the insect herbivores associated with D. vinosum.

From March 1997 to February 1998 insects were collected every month from three branches of 10 plants per site. Sampled branches were up to 1.5 m tall. We avoided sampling the same plants in subsequent months, although some plants might have been sampled two or more times. Sampling was done by quickly putting the branches into plastic bags and shaking. We also visually inspected branches and leaves for arthropods that may not have been released by the shaking, such as scale insects, leaf miners and gall makers. Some highly mobile or nocturnal insects might be underrepresented by this sampling technique. However, since most insect herbivores are sedentary, this method is the most indicated for measuring the population size of insects associated with particular plants (Majer & Recher, 1988; Schowalter, 1989). The specimens were sorted to morphospecies and tabulated by taxon according to Commonwealth Scientific and Industrial Research Organization classification (1991). We determined the abundance and richness for each site, and two annual similarity indexes among sites: the Sorensen index (C_S) for qualitative, and the Morisita-Horn index (C_{mH}) for quantitative comparisons (Magurran, 1991).

Analysis of folivory

Folivory was estimated from 10 plants/site every three months, using the continuous monitoring method, by which the same leaves are monitored during a given period, without being removed. This method is more efficient than the discrete measurement method, which underestimates folivory by not considering leaves completely eaten

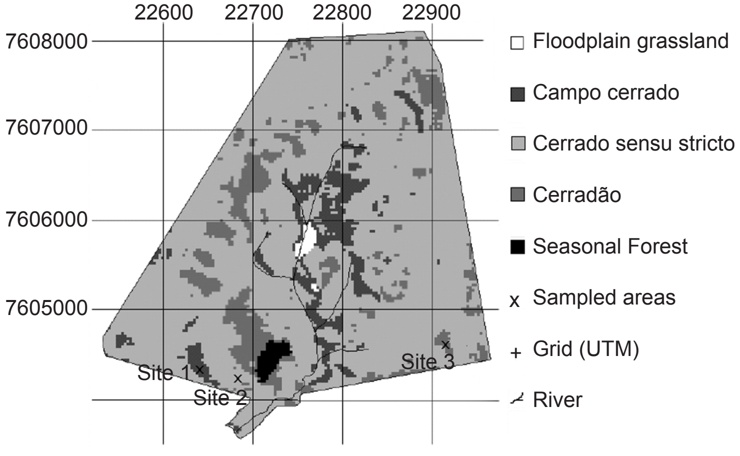

Fig. 1 — Sampling sites in the Cerrado Pé-de-Gigante, Santa Rita do Passa Quatro, SP, Brazil (21° 36 - 39' S and 47° 36 - 38' W). Adapted from Batalha *et al.* (2001).

or abscised due to petiole injury by insects (Aide, 1993; Leoni, 1997). Every sampled plant had three branches marked near the apex, and the leaves developing above the marking were monitored. The leaf shape was outlined on heliographic paper at every sampling; this was then digitized and the area estimated by SIARCS (EMBRAPA), a software for area measurements. We quantified injury caused by chewing insects (Fig. 2a) and sucking insects (Fig. 2b) during the one-year period, based on comparisons among images of the same leaves in different periods.

Leaves that were attacked by sucking insects could be recognized by the necrosis and twisting of leaflet blades. The frequency of leaves attacked by chewers was transformed into a percentage and then compared among physiognomies by the χ^2 test. The Kruskall-Wallis test, a non-parametric test, followed by Dunn's test, was used to carry out a multiple comparison analysis of % leaf loss among attacked leaves. The percentage leaf loss from each site was multiplied by the proportion of attacked leaves to obtain an estimate of % herbivory by chewing insects. We also divided the folivory levels of all sites combined into classes and compared their distribution between young and mature leaves with a χ^2 test. Four folivory classes were created: 1) 0-2.5 percent, excluding non-attacked leaves; 2) 2.6-10 percent; 3) 10.1-50 percent; and 4) > 50 percent.

The frequency of young leaflets that were injured by sucking insects was compared with the frequency of healthy leaflets at the same sites with a χ^2 test. We also estimated the area that attacked leaflets lose by expanding less when they reach a mature phase. This was calculated with the equation: leaf loss (%) = ((An – Aa)/An) x 100, in which An is the area of non-attacked leaflets, and Aa is the area of leaves attacked by sucking insects. The percentage leaf loss at each site was multiplied by the proportion of attacked leaves to obtain an estimate of % folivory by suckers. The Pearson Correlation test was used to evaluate the relationship between the percentage of leaflets attacked by sucking insects and *Liothrips dydimopanacis* (the principal sucking insect of *D. vinosum*) abundance.

Finally, we estimated the total annual folivory for each site by summing annual herbivory by chewing and sucking insects. The correlation (Pearson coefficient) of folivory by sucking and chewing insects with several leaf traits of *D. vinosum*, including water, nitrogen, cellulose, lignin and tannin content, and toughness, was calculated. Leaf trait data had been previously

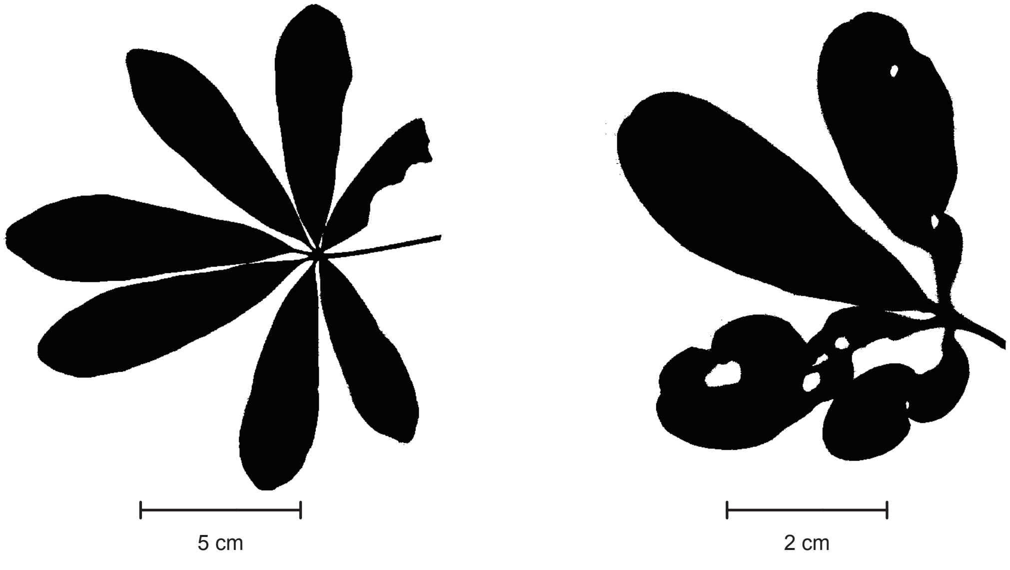

Fig. 2 — Digitalized shape of *D. vinosum* leaves that were attacked by chewing insects (a) and by sucking insects (b).

collected at the same sites sampled in this study (Pais & Varanda, 2003).

RESULTS

Insect herbivores associated with the plants

In general, the species richness in the different sites was fairly similar (60 morphospecies in site 1, 64 in site 2, and 62 in site 3). All sites were populated with herbivores belonging to the same orders (Orthoptera, Coleoptera, Lepidoptera, Hemiptera, and Thysanoptera). However, the similarity of species was low among sites ($C_s \approx 0.4$). Hemiptera and Coleoptera had the greatest number of morphospecies (Fig. 3a) and families, and among families, Cicadellidae, Chrysomelidae, and Curculionidae were the most abundant. No scale insect, leaf miner or leaf galler species was sampled.

A total of 754 insect herbivores were sampled in site 1, 219 in site 2, and 695 in site 3. The only Thysanoptera (Phlaeothripidae family) species, *Liothrips didymopanacis* Del-Claro & Mound (1996), was the main herbivore, especially in site 1 (75.3%), and site 3 (65.8%; Fig. 3b). We found 567 thrips in site 1, 456 in site 3, and 43 in site 2. A large number of *Guayaquila xiphias* (Membracidae) was also sampled in site 1 (*N* = 35) and site 3 *(N* = 63). An undetermined Psyllidae species was abundant in site 2 (*N* = 41) but rare in site 1 (*N* = 2) and site 3 (*N* = 5). Among the chewing insects, Chrysomelidae species were abundant in site 1 (*N* = 15), site 2 (*N* = 32), and site 3 (*N* = 21). Site 2 had a large number of Curculionidae (*N* = 29), however many species in this family normally do not feed on leaves, but rather on fruits and seeds. In site 3, besides Curculionidae (*N* = 17), we sampled a large number of Lepidoptera larvae (*N* = 28).

Adults of *L. didymopanacis* were found throughout the year, mainly in the dry season, and in greater numbers than larvae. *Liothrips didymopanacis* was abundant during the entire dry season in site 1, mainly from June to October, and in the late dry season in site 3, from September to October (Fig. 4).

The most similar environments, considering quantitative data related to the herbivorous fauna, were site 1 and site 3, with a C_{mH} of 0.980. The C_{mH} between site 2 and site 1 was 0.463 and between site 2 and site 3 it was 0.512.

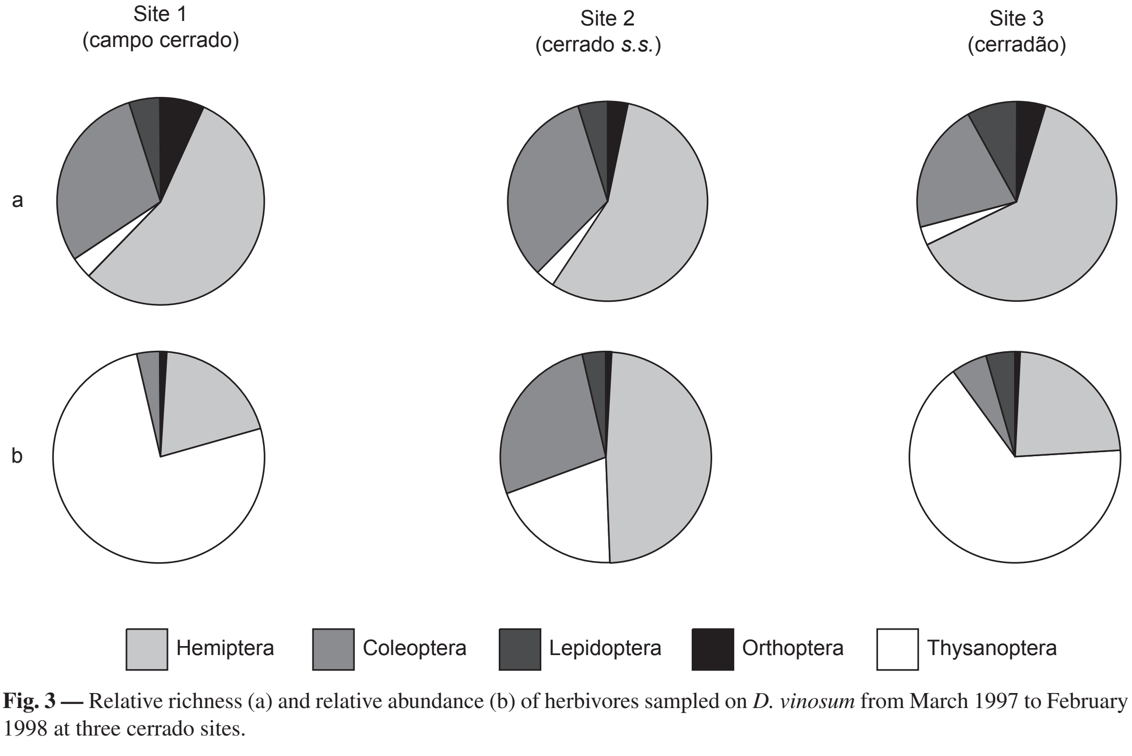

Fig. 3 — Relative richness (a) and relative abundance (b) of herbivores sampled on *D. vinosum* from March 1997 to February 1998 at three cerrado sites.

Folivory

The frequency of leaves attacked by chewing herbivores differed in the three sites (Table 1). Only 5.35 percent of the leaves had been attacked in site 1. In site 2 it amounted to 11.65 percent, and in site 3 it reached 34.5 percent. The area lost by attacked leaves (Table 1) was greater in site 1 (3.64%) and site 3 (2.16%). There was no significant relationship between folivory levels by chewers and leaf age (χ^2, $P = 0.2247$). The distribution of folivory levels by chewers followed the same pattern on young and mature leaves: more than 50 percent of the injured leaves had less than 2.5 percent leaf loss. Losses above 50 percent were encountered in less than 10 percent of the attacked leaves (Table 2). In general, if we take into account the relationship between the proportion of attacked leaves and the herbivory levels, annual folivory on *D. vinosum* leaves by chewers was very low in all sites, although a little higher in site 3 (Table 1).

Leaf injury by sucking insects, basically the thrips *L. didymopanacis*, occurred when leaves were still young. By scraping and sucking from the leaf surface, these insects cause necrosis and twisting of the leaf. The intensity of the attack was affected by plant location (Table 1), since more leaflets were

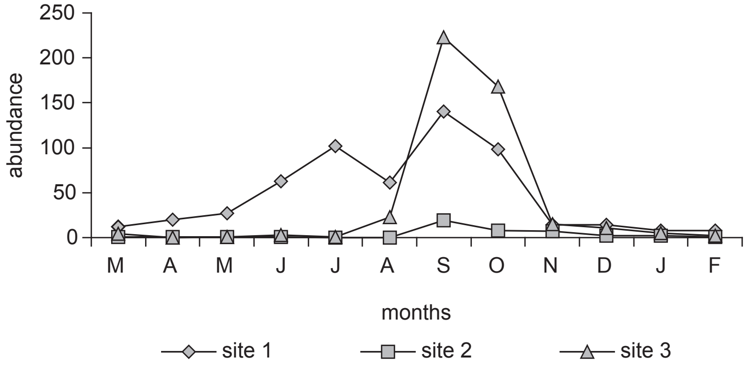

Fig. 4 — *Liotrhips didymopanacis* abundance in *D. vinosum* from March 1997 to February 1998 at three cerrado sites.

TABLE 1
Annual folivory on *D. vinosum* leaves in three sites at Cerrado Pé-de-Gigante.

	site 1 (campo cerrado)	**site 2 (cerrado *s.s.*)**	**site 3 (cerradão)**	**statistical analysis**
by chewing insects:				
Attacked leaves (%)	5.35 (*N* = 467)	11.65 (*N* = 266)	34.50 (*N* = 440)	Chi-square (*P* < 0.0001)
Leaf loss (%)*	3.64^{a} (0.46; 14,3)** (*N* = 25)	0.32^{b} (0.13; 1,68) (*N* = 31)	2.16^{a} (1.07; 7,43) (*N* = 153)	Kruskal-Wallis (*P* < 0.0001) Dunn's Method (*P* < 0.05)
Folivory (%)	0.19	0.04	0.74	-
by sucking insects:				
Attacked leaves (%)	32.3 (*N* = 1163)	8.08 (*N* = 903)	28.3 (*N* = 1532)	Chi-square (*P* < 0.0001)
Leaf loss (%)*	22.1 (- 8.20; 56,1)** (*N* = 194)	15.8 (- 14.15; 57,00) (*N* = 57)	27.4 (-2.06; 48.8) (*N* = 146)	Kruskal-Wallis (*P* = 0.862)
Folivory (%)	7.1	1.28	7.75	-
Total folivory (%)	7.33	1.32	8.49	-

*values denote only attacked leaves; intact leaves were excluded. **median (lower quartile; upper quartile). Different letters ("a" and "b") denote significant differences among sites accordind to Dunn's Method.

TABLE 2
Relative frequency of *D. vinosum* leaves into four classes of folivory by chewing insects.

Folivory classes	Young leaves	Mature leaves
0-2.5%*	63.1	55.8
2.6-10.0%	21.4	25.9
10.1-50.0%	08.3	15.0
> 50.0%	07.1	03.4

*Non-attacked leaves were not included.

injured in site 1 (32.3%) and site 3 (28.3%) than in site 2 (8.08%). Periods of higher injury levels coincided with higher thrips abundance. From August to October, infestation was higher than 70 percent of the total sampled leaflets in site 3, and it was more than 40 percent in site 1 at the same time. In general, injured leaflets attained a smaller mature size than the healthy leaflets did (Mann-Whitney Rank Sum test; $P < 0.0001$; $N > 190$). The area lost from attacked leaflets varied between 15.8 percent and 27.4 percent (Table 1). We found a significant positive relationship between the percentage attacked leaflets and thrips abundance (Pearson correlation: $r = 0.794$, $N = 12$, $P < 0.05$). Based on the relationship between annual infestation and area loss suffered by injured leaflets, we found that annual folivory levels by sucking insects in *D. vinosum* were higher in site 1 and site 3 than in site 2.

When we grouped the two herbivory types, we found that *D. vinosum* annual folivory reached the greatest intensity in site 3 (8.49%) and site 1 (7.32%), while it is only 1.32 percent in site 2 (Table 1).

None of the leaf traits were significantly correlated with folivory levels by sucking or chewing insects (Table 3).

DISCUSSION

Shrubs of *D. vinosum* are infested mainly by sucking insects, especially the thrips *L. didymopanacis* and the treehopper *G. xiphias*, as already related by other studies (Del-Claro & Mound, 1996; Del-Claro & Oliveira, 1999; Oliveira & Del-Claro, 2005). However, as *G. xiphias* aggregations prefer plants located in sunny places (Del-Claro & Oliveira, 1999), they were found in few plants because we avoided the edge vegetation. Patterns we found concerning infestation levels by the thrips *L. didymopanacis* on *D. vinosum* shrubs over time are very similar to the patterns observed in the absence of ant-*G. xiphias* association on the plant (Oliveira & Del-Claro, 2005). These authors concluded that abundance of thrips is negatively affected by ant-treehopper interactions.

Total annual herbivory on *D. vinosum* leaves was lower than the 10.9 percent level reported by Coley & Aide (1991) in their study of tropical forests. If we take into account only folivory by chewing insects, the levels are even lower, less than one percent. Tannins and lignins might defend this plant against these insects. Indeed, no abundant chewing species were detected. On the other hand, sucking insects, which are responsible for more than 90 percent of the observed injury, would hardly be deterred by compounds such as lignins and condensed tannins. Lignins are components of cellular walls, especially of sclerenchyma and xylem. Condensed tannins are accumulated in the cell wall as well (Zucker, 1983), and therefore sucking herbivores do not ingest them.

The different folivory levels found could be explained by the abundance variation of important herbivores. The higher folivory by chewers in site 3 is probably due to the activity of Lepidoptera larvae, which are more abundant at this site. However, most of the folivory suffered by *D. vinosum* in all sites is due to suckers, mainly *L. didymopanacis*, which is responsible for more than 90 percent of the injury. The higher incidence of *L. didymopanacis* in site 1 and site 3 is the reason for the higher quantitative faunistic similarity between these sites, since the Morisita-Horn index considers both composition and abundance similarity. The higher *L. didymopanacis* abundance in site 1 and site 3 also justifies the higher level of folivory in both sites, mainly from August to October, when the population abundance peaks.

TABLE 3
Pearson correlation coefficients of *D. vinosum* leaf traits against folivory by sucking and chewing insects. P values in brackets.

	Folivory by chewers	Folivory by suckers
Young leaves		
Water	- 0.161 (0.897)	- 0.795 (0.415)
Nitrogen	0.647 (0.552)	- 0.054 (0.966)
Cellulose	0.640 (0.558)	0.992 (0.076)
Lignin	0.298 (0.808)	0.872 (0.326)
Tannins	0.446 (0.706)	- 0.291 (0.812)
Toughness	- 0.984 (0.114)	- 0.593 (0.596)
Mature leaves		
Water	0.195 (0.875)	-
Nitrogen	0.643 (0.532)	-
Cellulose	0.766 (0.445)	-
Lignin	- 0.007 (0.995)	-
Tannins	0.152 (0.903)	-
Toughness	- 0.388 (0.746)	-

However, in our study, the variation in thrips abundance and therefore in the folivory levels was not explained by nutritional and defensive plant traits. Basset (1991) also could not find a relationship between folivory and local variation in the nutritional quality of *Argyrodendron actinophyllum* (Sterculiaceae) leaves in an Australian forest.

What then determines the higher thrips abundance and folivory levels in site 1 and site 3? One hypothesis would be the differential concentrations of other plant metabolites that were not analyzed in this study. Plants of the Apiaceae family usually have terpenes, another important chemical group involved in plant-insect interactions. Terpenes, together with moisture, nitrogen, phenolics and toughness have a significant role in the relationships between two leguminous genera (*Copaifera* and *Hymenaea*) and their main lepidopteran herbivores in a cerrado region (Langenheim *et al.*, 1986a, 1986b; Macedo & Langenheim, 1989a, 1989b).

Secondly, as stated by the resource-concentration hypothesis (Root, 1973), there is a higher probability of herbivores finding, remaining on, and consequently becoming more abundant on hosts growing at a high density or abundance. According to Batalha (1997), the relative density of *D. vinosum* at Cerrado Pé-de-Gigante is about 0.32 percent in campo cerrado, 0.25 percent in cerrado *s.s.*, and 0.99 percent in cerradão, where we have distributed plots (sites) 1, 2 and 3, respectively. *Didymopanax vinosum* density could therefore justify the higher thrips abundance in site 3, but not in site 1. Strong *et al.* (1984) reported several studies suggesting that the effect of plant density varies according to the insect species. Marquis (1991), for example, in a study of curculionids and geometrids grazing on *Piper* (Piperaceae) leaves, discovered that the abundance of a given herbivorous species does not correlate with host abundance.

As a third hypothesis, we could then consider the importance of plant architecture (Lawton, 1983). *Didymopanax vinosum* plants growing in site 1 and site 3 are larger and have more branches, leaves, and inflorescences than plants from site 2 (data not shown). The probable reason for this difference is the variation in luminosity. Plants growing in site 1 are totally exposed to light due to low tree density, and in site 3 they mainly grow in small clearings, where luminosity is also intense. In site 2, in contrast, trees compose a continuous stratum, followed by a dense stratum of shrubs and vines, where *D. vinosum* competes for light with other plant species. Larger plants provide two types of benefits for herbivores: higher apparency (Feeny, 1976; Karban, 1993), which renders then more easily located by insects, and higher resource availability. Loyola-Júnior & Fernandes (1993) found a positive correlation between the number of insects (and of attacked leaves) and number of *Kielmeyera coriacea* leaves. Similarly, Alonso & Herrera (1996) found that the abundance of Noctuidae larvae was directly related to the number of *Daphne laureola* (Thymelaeaceae) branches, their host plant. The coincidental peak of thrips abundance with the period of higher leaf production by *D. vinosum* (Del-Claro & Mound, 1996) is an indicator of the importance of resource availability for the life cycle of the insect. Future research to test this hypothesis would contribute to the comprehension of the principal factors affecting folivory.

Although several theories emphasize the importance of defensive compounds and nutritional quality in plant–herbivory interactions at the interspecific level (Feeny, 1975; Coley, 1983; Coley *et al.*, 1985), we suggest that spatial variation in *D. vinosum* folivory among the sampled sites is not influenced by the plant traits that were analyzed, but probably by other compounds or factors related to apparency and resource availability for herbivores.

Acknowledgments — This study was supported by CAPES, FAPESP (Proc. 96/8148-0) and CNPq. We are grateful to K. Del-Claro for helpful suggestions and the identification of the sucking insects, to S. A. P. Godoy, J. R. Barosela and B. A. O. Silva for discussions and to W. Mantovani for help with the recognition of the plant physiognomies. We thank the Instituto Florestal for permission to work in the park.

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