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Growth, defense and herbivory on young leaves of *Qualea parviflora* (Vochysiaceae) in three different Cerrado habitats

Crescimento, defesas e herbivoria em folhas jovens de *Qualea parviflora* (Vochysiaceae) em três diferentes habitats de Cerrado

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Abstract

Insect herbivory is strongly influenced by the properties of their host leaves. Otherwise, such influence may be mediated by the environment in which the host plant is found. We examined three characteristics that may influence insect herbivory on young leaves of *Qualea parviflora* Mart. (Vochysiaceae), a widespread tree of the Brazilian Cerrado: leaf expansion rate, sclerophylly (leaf toughness), and tannin concentration during four consecutive months. Herbivory rates were measured on four marked intact leaves in five trees in three different physiognomies of the Cerrado biome: *campo sujo* (grassland), *cerrado sensu stricto* (savanna), and *cerradão* (woodland). Sclerophylly was higher in February while the highest concentration of tannins occurred in November but no variation in the rates of herbivory among months and physiognomies was found. A tendency of higher mean leaf growth rates was observed in the "cerradão" (1.03%) and "cerrado" (1.04%) in comparison with the campo sujo trees (0.86%). Higher sclerophylly and lower expansion rates and leaf size were observed in trees of the *campo sujo*. There was a tendency for higher herbivory rates in *cerrado* (10.5%), where the leaves showed lower concentration of tannins (1.5%) than in *cerradão* (2.1%). New leaves of *Q. parviflora* showed higher tannins concentration and lower damage than fully expanded leaves. Final leaf area explained 24% of the variation in total herbivory. Leaf size and associated nutritional factors exerted stronger influence on herbivory than defensive compounds on young leaves of *Q. parviflora*.

Key words: Cerrado, leaf age, leaf growth, Neotropical savanna, plant defenses, sclerophylly.

Resumo

A herbivoria por insetos é fortemente influenciada pelas propriedades das folhas hospedeiras. No entanto, esta influência pode ser mediada por condições ambientais do habitat da planta. Neste estudo foram examinadas três características que podem influenciar a herbivoria por insetos em folhas jovens de *Qualea parviflora* Mart. (Vochysiaceae), uma árvore comum do Cerrado brasileiro: taxa de expansão foliar, esclerofilia (rigidez foliar) e concentração de taninos. As taxas de herbivoria foram medidas em quatro folhas intactas de cinco árvores em três diferentes fitofisionomias do bioma Cerrado: "campo sujo", "cerrado *sensu stricto*" e "cerradão". A esclerofilia foi maior em Fevereiro enquanto altas concentrações de taninos ocorreram em Novembro. No entanto, não foi observada variação nas taxas de herbivoria entre os meses e entre fisionomias. Uma tendência em maiores taxas de crescimento foliar foi observada em árvores ocorrentes no "cerradão" (1,03%) e no "cerrado" (1,04%) em comparação com as ocorrentes no "campo sujo" (0,86%). Maiores valores de esclerofilia, baixas taxas de expansão foliar e menor tamanho foliar foram observadas no "campo sujo". Houve uma tendência em altas taxas de herbivoria no "cerrado" (10,5%), onde as folhas

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apresentaram concentrações de taninos mais baixas (1,5%) que no "cerradão" (2,1%). As folhas jovens de *Q. parviflora* apresentaram maiores concentrações de taninos e menor dano por herbivoria que folhas maduras. A área foliar final explicou 24% da variação da herbivoria total. O tamanho das folhas e fatores nutricionais associados exerceram influências mais fortes na herbivoria que a concentração de compostos de defesa em folhas jovens de *Q. parviflora.*

Palavras-chave: Cerrado, crescimento foliar, defesa de plantas, esclerofilia, idade foliar, savana neotropical.

Introduction

Through their lifetime leaves are subjected to herbivory by an enormous diversity of organisms, of which insects and pathogens comprise the most important ones. The loss of photosynthetic area may lead to reduced growth, reproduction, longevity, and translocation of energy from the main metabolic pathways to the production of defensive compounds (e.g., Nascimento *et al.*, 1990). In addition, the combined effects of herbivory, leaf loss and reduction in photosynthetic rates both limit plant productivity (Franco, 1998).

In tropical forests, approximately 11% of the annual leaf area produced is consumed by herbivores and pathogens (Coley and Aide, 1991). In the Cerrado biome, the percentage of herbivore damage ranges from 6% to 20% in some tree species (Nascimento and Hay, 1993; Franco, 1998; Marquis *et al.*, 2001; Gonçalves-Alvim *et al.*, 2006). Young expanding leaves are the most vulnerable stage during the life of a leaf and 70% of the lifetime damage can occur during this small window of vulnerability (Woodman and Fernandes, 1991; Coley and Kursar, 1996). Therefore, many developmental traits, such as rapid expansion, higher secondary compounds and synchronous leaf production may be the result of selection by herbivore and pathogens (Coley and Kursar, 1996; Dyer and Coley, 2002).

Young leaves tend to be more pubescent (Woodman and Fernandes, 1991) and contain higher tannin concentrations and other secondary metabolites (Coley, 1983b) than older ones. High leaf expansion rates may reduce the period of vulnerability before leaves have fully expanded, toughened, and become better defended against herbivores (Kursar and Coley, 1991). Also, synchronous production of young leaves has been shown to satiate herbivore and, thus, reduce leaf damage (Coley and Kursar, 1996).

Notwithstanding these defenses, young leaves generally experience higher rates of herbivory than mature leaves (Kursar and Coley, 1991; Woodman and Fernandes, 1991). Expanding leaves are generally less sclerophyllous, easier to chew and digest, and have higher water and nutrient contents than mature leaves of the same species (Coley, 1983a; Coley and Kursar, 1996; Moles and Westoby, 2000). Many herbivorous insects grow better and attain higher fecundity levels when feeding on higher nutritional value young leaves as compared to those feeding on mature or senescent leaves of the same plant (Schoonhoven *et al.*, 1998).

The *lato sensu* Cerrado is the second most important biome in Brazil covering about 20% of its territory (Felfili and Silva Jr., 1993). Three physiognomic types are commonly seen in the *lato sensu* Cerrado: *campo sujo*, a grassland with widely scattered tree and shrub with a canopy cover of less 2%; *stricto sensu* Cerrado, a savannic woodland with total woody cover about 20%; and *cerradão*, a xeromorphic forest woodland type with a fairly continuous tree strata with canopy cover of about 85% (Oliveira-Filho and Ratter, 2002).

Qualea parviflora Mart. (Vochysiaceae) is a widespread brevidecidous tree of tropical savannas, commonly observed in the three Cerrado physiognomies. *Q. parviflora* stay leafless throughout one month at the end of dry season (Oliveira and Gibbs, 1994), but when leaves are present it is intensively attacked by folivorous insects commonly belonging to Blattodea, Coleoptera, Hemiptera, and Lepidoptera orders along all the year (Morais *et al.*, 1995; Gonçalves-Alvim *et al.*, 2006).

In the present study we examined three leaf traits of *Q. parviflora* that may influence insect herbivory: rate of leaf expansion, sclerophylly (leaf toughness) and tannin concentration. Also, we aimed to answer the following questions: (i) is there variation in leaf growth, herbivory rates, and defenses in young leaves of *Q. parviflora* among three different physiognomies of the Cerrado biome?; and (ii) are young leaves better defended, and still, more attacked by herbivores than fully expanded leaves?

Material and methods

The study was conducted in the Pirapitinga Ecological Station (PES), an island of approximately 1,000 ha area that varies with the level of the artificial reservoir of Três Marias dam (PES). The PES is located in southeastern Brazil (18º20'S to 18º23'S and 45º17'W to 45º20'W) at an altitude from 590 to 630 m above sea level (Azevedo *et al.*, 1987; Gonçalves-Alvim and Fernandes, 2001). The vegetation is formed by *lato sensu* Cerrado with the three physiognomic formations:

"campo sujo", *stricto sensu* Cerrado and "cerradão". The climate is tropical wet and hot (Aw type of Köppen, 1931), with a long dry season of 5 to 8 months (Figure 1). The mean annual temperature ranges from 20º to 26°C, and the mean annual precipitation is above 1,600 mm (Azevedo *et al.*, 1987). The study was initiated in November 2000, soon after *Q. parviflora* has produced its first new leaves in the beginning of rainy season until the complete leaf expansion, in February 2001. Five trees with 1.80 up to 3.50 m height were marked in each one of the physiognomies of Cerrado (n = 15). To determine herbivore damage, four new and intact leaves were marked with plastic labels below the bud on each tree. Every month, the contour of the marked leaves was drawn in a transparency film. The drawings were scanned and the total leaf area (cm^2) and removed leaf area (cm^2) were obtained using the computer program Scion-Image. Herbivore damage (%) was calculated by the following formula: $[(X_{Final} - X_{Initial})*100]$/total leaf area, where X = leaf area lost in each month. Cumulative herbivory (%) was obtained using the sum of the total lost leaf area and final leaf area. Only herbivore damage that resulted in lamina loss (leaf removal, chewing, or mining) was measured (see Moles and Westoby, 2000).

To quantify leaf sclerophylly and tannin concentration (%), four adjacent leaves with same age and size were harvested. After leaves were drawn and scanned to obtain the leaf area, they were dried in an oven for a period of 72 hours (or until reaching constant weight) at 45ºC, and then weight to estimate leaf specific mass (g/cm^2), which indicates sclerophylly. Condensed and hydrolysable tannins were obtained by the method of radial diffusion (Hagerman 1987; Cornelissen and Fernandes, 2001), in which fresh leaves were used with three replicates for each plant. Only at the end of the experiment, the tagged leaves were collected for tannin analyses and to quantify sclerophylly. All variables used in the statistical analyses were initially submitted to the Ryan-Joiner test for normality and to the Bartlett test for homogeneity of variances ($\alpha = 0.05$). In some cases, decimal logarithm(x) or arc-sin transformations were used for normalization of data. Significant differences among the averages of the leaf traits and insect herbivory among physiognomies were analyzed by one-way ANOVA (one way analysis of variance) or Kruskall Wallis, while differences among months were tested by Friedman and Wilcoxon tests for multiple variables (Zar, 1996). Paired-sample T-test or Wilcoxon test were also used to compare leaf traits and herbivory between young and fully expanded leaves. Correlation and regression analyses were also used to obtain the relationships between herbivory and leaf traits (Zar, 1996).

Results and discussion

Leaf flush occurred between the dry-wet season transition in September and the onset of the rainy season in October (Figure 1). The period of leaf expansion of *Q. parviflora* lasted two months and complete expansion of leaves was reached in December ($\bar{x} = 19.61 \pm 11.14$ cm^2; $P < 0.05$, Figure 2). However, most of the sampled plants presented mature leaves only in January (Figure 1). Gonçalves-Alvim *et al.* (2006) found a mean leaf area of 22.10 cm^2 and a sclerophylly index of 0.0146 g/cm^2 in mature leaves of *Q. parviflora* in January 2000 during a study in the same site.

Leaf area of fully expanded leaves of *Q. parviflora* was three times larger than the initial leaf area (Figure 3). Plants in the *stricto sensu* Cerrado had the largest leaf area, while the smallest leaf area was found in trees of the *campo sujo* physiognomy (Table 1; Figure 3A). Higher growth rate values were observed in December in comparison with the other studied months (Friedman = 12.4, P =0.002, df = 2; Figure 3B). Although the *campo sujo* trees had smaller leaf growth/day (0.86%), there were no significant differences in this variable among the three physiognomies (Table 1, Figure 3B).

The leaf expansion rate of *Q. parviflora* was similar to the growth pattern observed in other plant species of the Cerrado, such as *Byrsonima crassifolia* (L.) H.B.

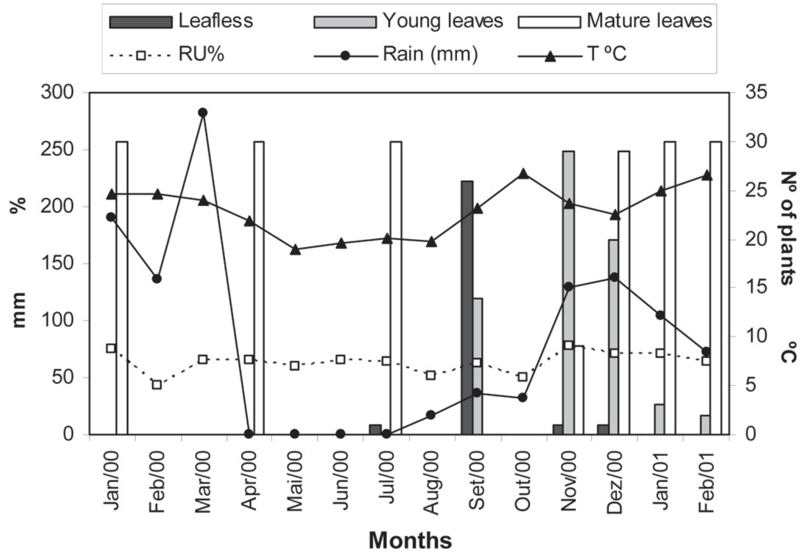

Figure 1. Climate data and leaf phenology (n= 30 trees) of *Q. parviflora* from January/2000 to February/2001, in PES, southeastern Brazil.

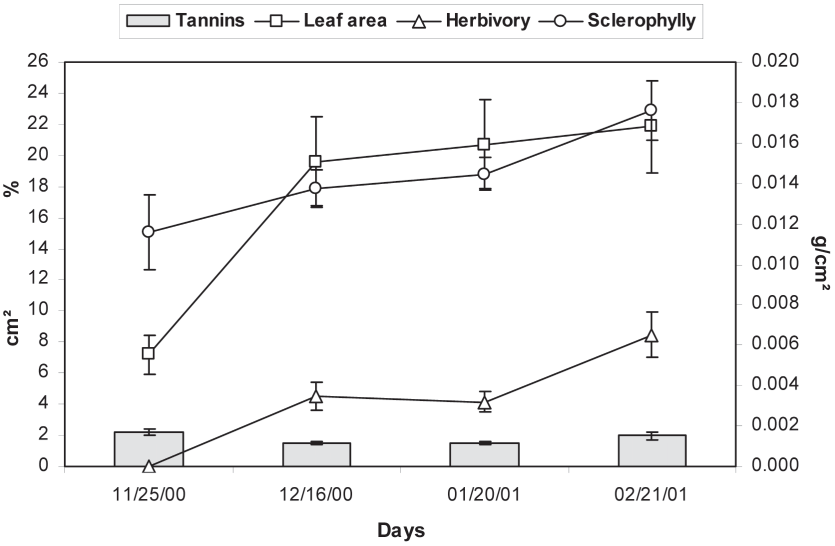

Figure 2. Leaf growth, sclerophylly, concentration of tannins, and herbivory rate during leaf expansion of *Q. parviflora* in the three physiognomies of Cerrado in PES, southeastern Brazil.

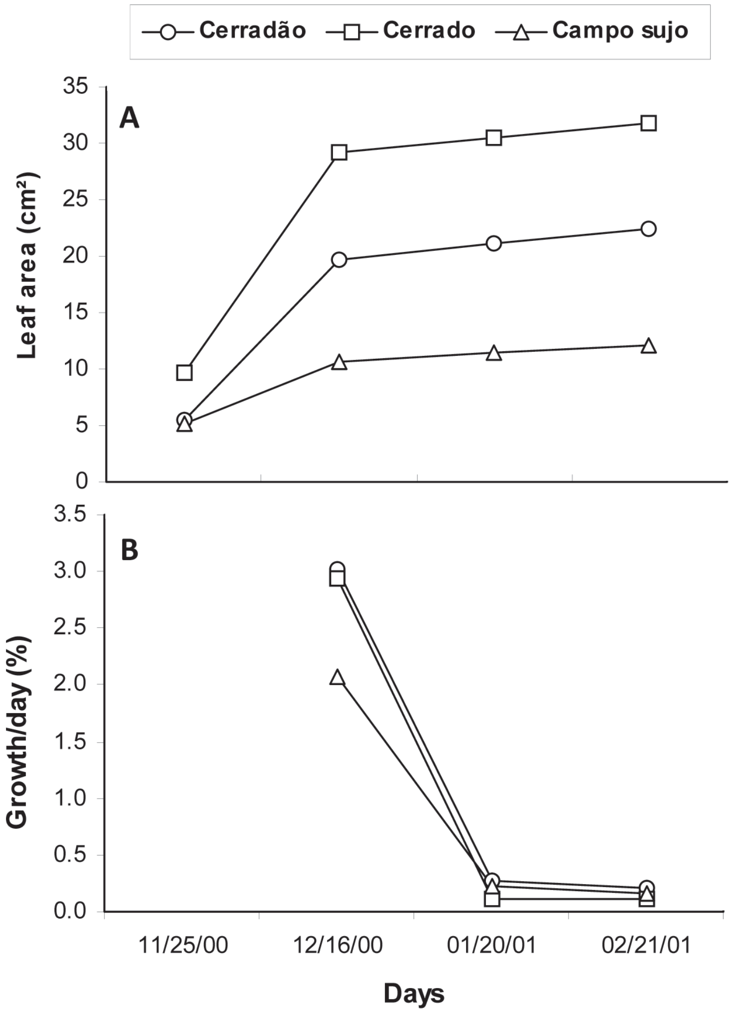

Figure 3. (A) Leaf area and (B) Leaf growth of *Q. parviflora* from November/2000 to February/2001, in the three physiognomies of cerrado in PES, southeastern Brazil.

and K. (Malpighiaceae), *Curatella americana* L. (Dilleniaceae), and *Vochysia rufa* Mart.(Vochysiaceae) (Montes and Medina, 1977; Nascimento *et al.*, 1990). The strategy of production and development of leaves before or at the beginning of the rainy period is quite common in plants of tropical savannas (Paulilo and Felipe, 1992; Ribeiro *et al.,* 1994). This provides plants with the photosynthetic apparatus to operate in the rainy season, when the stock of nutrients will be restored through absorption by roots, and translocation from the old leaves (Paulilo and Felipe, 1992). Some authors (e.g., Janzen and Shoener, 1968; Coley and Aide, 1991; Nascimento *et al.*, 1990) proposed that the flushing and fast leaf growth at the end of dry season/ beginning of rainy season could be an anti-herbivory strategy since herbivores are rarer in this period.

The nitrogen concentration, the content of water and fibers, and concentration of defensive compounds vary as much either between plants of the same species and within the same organ of the plant. These variations strongly influence the patterns of herbivory (e.g., Ernest, 1989; Raupp and Denno, 1983; Woodman and Fernandes, 1991). Leaves of *Q. parviflora* were more sclerophyllous in February, while in December and January no significant differences were observed (Friedman =28.44, P =0.000, df = 3; Figure 3). The concentration of tannins varied along the experiment, with higher concentrations in November (Friedman = 27.59, P = 0.000, df = 3; Figure 3). However, no variation in tannins was observed between plants of the three physiognomies (Table 1). The rate of leaf herbivory on *Q. parviflora* did not vary between physiognomies (Table 1), but temporal variation was observed during the study (Friedman =13.23, P =0.001, df = 2; Figure 2), indicating that herbivory increases with leaf age. Moles and Westoby (2000) found that

Table 1. Means (±SE) of leaf growth, sclerophylly, concentration of tannins, and herbivory rate during leaf expansion of *Q. parviflora* in three physiognomies of Cerrado in PES, southeastern Brazil (F= One way-ANOVA, H = Kruskall Wallis test). Different letters represent statistical differences at α = 0.05 (Tukey test).

Traits	Vegetation Physiognomies					
	Cerradão	Cerrado	Campo sujo	F	H	P
Leaf area (cm²)^{L}	16.36±2.13^{b}	25.78±2.90^{a}	9.90±0.89^{c}	31.09		< 0.001
Leaf growth/day (%)*	1.03±0.37	1.04±0.41	0.86±0.31		1.49	> 0.05
Sclerophylly (g/cm²)	0.0117 ± 0.001^{b}	0.0143± 0.001^{ab}	0.0171 ± 0.001^{a}		19.41	< 0.001
Herbivory (%)^{A}	4.76±075	7.22±1.51	5.16±1.01	1.31		> 0.05
Tannins (%)	2.06±0.24	1.51±0.10	1.84±0.18		3.09	> 0.05

^{L}Log$_{10}$ and ^{A}Arc-sin transformations; *was calculated by the formula $X_{Final} – X_{Initial}$/days.

species with short leaf expansion time and small leaf size had lower levels of leaf area loss. On the other hand, we did not find any relationship between percentage of damage and growth rate of *Q. parviflora* leaves ($r^2 = 0.00$, n=15, F = 0.69, P = 0.17).

Younger leaves of *Q. parviflora* tended to show higher concentration of tannins than fully expanded leaves (Table 2). Some authors (Feeny, 1976; Cornelissen and Fernandes, 2001) have pointed out that compounds acting as digestibility-reducing factors (e.g., tannins and resins) reduce the nutritional plant quality by binding with digestive proteins increase in concentration with leaf age, rendering young leaves more suitable for herbivores. Other studies found opposite patterns (e.g., Coley, 1987; Woodman and Fernandes, 1991) in which defenses are deployed according to the value of the organ, structure, or tissue being defended. From this point of view, young leaves and other growing plant parts could be better protected by secondary compounds than mature tissues (Cates, 1980; Schoonhoven *et al.*, 1998).

No significant relationship was observed between herbivory and tannins in *Q. parviflora* leaves (r = -0.14, P= 0.87). Similar results were found in other studies (e.g., Nascimento, 1989; Ribeiro *et al.*, 1994). Madeira *et al.* (1998) did not find any correlation between herbivory with either sclerophylly or tannin concentration in *Chamaecrista linearifolia* Barneby (Fabaceae) in the mountainous grasslands in Brazil. In addition, no relationship between tannin concentration and percentage of leaf area damaged in *Bauhinia brevipes* Vog. (Fabaceae) was found by Cornelissen and Fernandes (2001). These authors suggested that other aspects of foliar chemistry, including leaf water content, sugar concentration, toughness, and nitrogen content could influence herbivory in those species.

We found a positive relationship between final leaf size and percentage of accumulated damage during the study (r^2 = 24.3, P = 0.03, Figure 4), indicating that herbivore feeding decision could be influenced by leaf size. In addition, although young tannin-richer leaves of *Q. parviflora* are better protected against herbivorous damage, fully expanded leaves are more attacked by herbivores (Table 2). Other authors (e.g., Mopper *et al.*, 1984; Whitham, 1978; Cooke *et al.*, 1984; Ribeiro *et al.*, 1994) reported similar results. Nascimento and Hay (1993) reported that some insect species prefer attacking young leaves of *Metrodorea pubescens* St. Hill and Tull (Rutaceae)

Table 2. Means (±SD) of leaf traits and herbivory in young (Nov/2000) and fully expanded leaves (FE) (February/2001) of *Q. parviflora* and statistical results (n = 15, T-paired or Wilcoxon test, α = 0.05).

Traits	Young	FE	T	W	P
Leaf area (cm²)^{L}	7.2 ± 4.89	21.86 ± 11.51	-7.21		0.000
Leaf growth/day (%)*	2.56 ± 1.38	0.17 ± 0.11		-3.11	0.002
Sclerophylly (g/cm²)	0.0116 ± 0.0072	0.0176 ± 0.0056		2.56	0.011
Herbivory (%)**^{A}	4.54 ± 3.53	8.48 ± 5.51	-5.80		0.000
Tannins (%)	2.23 ± 0.84	1.97±1.13		-1.25	0.211

^{L}Log$_{10}$ and ^{A}arc-sin transformations; *was calculated by the formula $X_{Final} – X_{Initial}$/days; **in young leaves is correspondent to herbivory found between November-December

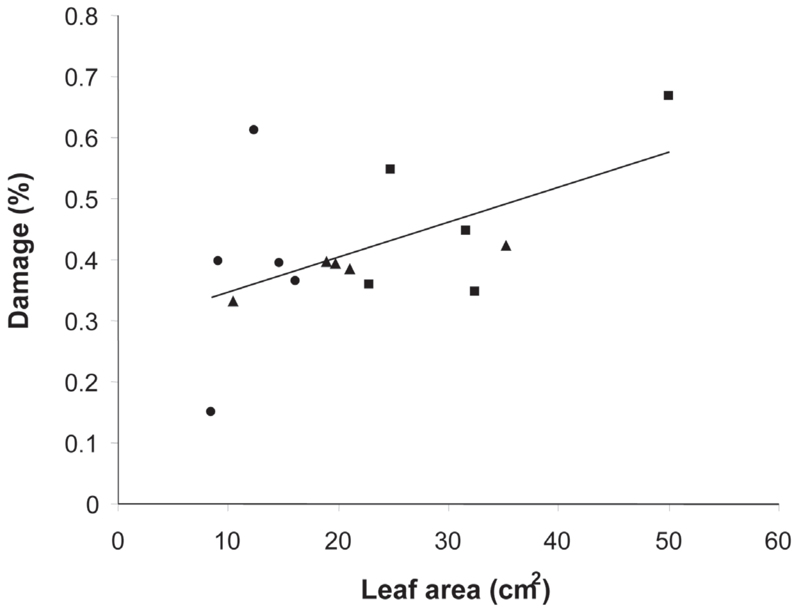

Figure 4. Relationship between final leaf area (cm^2) and accumulated herbivory (arc-sin transformed) on *Q. parviflora* (y = 0.288 + 0.00582x; $r^2 = 24.3$, $F_{1,14} = 5.49$, $P < 0.05$) from November/2000 to February/2001 in ESP, southeastern Brazil. ▲ Cerradão; ■ *stricto sensu* Cerrado ; ● campo sujo.

while others prefer mature ones. Young, fully-expanded leaves that operate at a maximum photosynthetic rate are probably more nutritionally rewarding for some herbivores (Zangerl and Bazzaz, 1992). These leaves are richer in nitrogen and water which are important resources for herbivore growth. Water and nitrogen contents are positively correlated with food choice for some species of chewing and sucking insects (e.g., Mattson, 1980; Basset, 1991; Kursar and Coley, 1996). Thus, leaf size and associated nutritional factors can exert more influence on herbivore behavior than defensive compounds on young leaves of *Q. parviflora*. Otherwise, future studies should be performed to evaluate the role of plant quality on herbivory during leaf lifetime.

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