Climate and host plant characteristics effects on lepidopteran caterpillar abundance on *Miconia ferruginata* DC. and *Miconia pohliana* Cogn (Melastomataceae)

Scherrer, S.[a]*, *Diniz, IR.*[b]* *and Morais, HC.*[c]*

[a]Programa de Pós Graduação em Ecologia, Instituto de Ciências Biológicas, Universidade de Brasília – UnB, Brasília, DF, Brazil

[b]Departamento de Zoologia Instituto de Ciências Biológicas, Universidade de Brasília – UnB, CEP 70910-900, Brasília, DF, Brazil

[c]Departamento de Ecologia, Instituto de Ciências Biológicas, Universidade de Brasília – UnB, CEP 70910-900, Brasília, DF, Brasil

*e-mail: sscherrer@uol.com.br, irdiniz@unb.br, morais@unb.br

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Abstract

Folivore cerrado caterpillars are found on their host species in low frequencies, which vary between plants and throughout the year. We analysed the effects of climatic variation and of the characteristics of two host species (*Miconia*, Melastomataceae) on caterpillar abundance. The work was carried out in a cerrado sensu stricto area in Brasília, Federal District, Brazil, from May 1998 to September 1999. One hundred plants of each species were inspected monthly. All caterpillars found were collected and raised in the laboratory with *Miconia* leaves as food sources. Climatic data for the study area and plant characteristics such as local density, spatial distribution, foliar phenology, leaf pilosity and nutritional content were used to test the effects on caterpillar abundance. Less than 10% of the plants had larvae. Caterpillars were more frequent and abundant in *M. pohliana*, which was also present at higher densities than *M. ferruginata*. Low caterpillar frequency in host plants and an abundance peak during the dry season are consistent patterns for different cerrado Lepidoptera larvae. This abundance peak, however, is not coincident with higher leaf production in host species. We suggest that *M. pohliana*'s higher local density and better leaf digestibility can account for the higher abundance of caterpillars in this species.

Keywords: cerrado, foliar nutritional content, host plant, leaf phenology, leaf pilosity

Efeitos do clima e das características das plantas hospedeiras na abundância de lagartas de Lepidoptera em *Miconia ferruginata* e *Miconia pohliana*

Resumo

No cerrado, as lagartas de Lepidoptera, folívoras externas, são encontradas em baixas frequências e variam entre plantas e ao longo do ano. Este trabalho teve como objetivo analisar os efeitos das variações climáticas e das características das plantas (*Miconia*, Melastomataceae) na abundância das lagartas. O estudo foi feito no cerrado sensu stricto, Brasília, DF, de maio de 1998 a setembro de 1999. Mensalmente, 100 plantas de cada espécie foram vistoriadas. Todas as lagartas foram coletadas e criadas. Foram correlacionados com os resultados obtidos da abundância de lagartas, os dados climáticos e as seguintes características das plantas: densidade local, distribuição espacial, fenologia, pilosidade e conteúdo nutricional foliar. Menos de 10% das plantas tinham lagartas. As lagartas foram mais frequentes e abundantes em *M. pohliana* que também foi a espécie de planta com maior densidade na área. A frequência baixa de lagartas em plantas do cerrado é um padrão bastante consistente, assim como o pico de abundância desses imaturos na estação seca. Entretanto, esse pico de abundância não coincide com a produção de folhas em nenhuma das espécies de plantas. A maior densidade local e digestibilidade das folhas de *M. pohliana* são os fatores que mais explicam a abundância de lagartas nessa espécie.

Palavras-chave: cerrado, conteúdo nutricional foliar, fenologia foliar, pilosidade foliar, planta hospedeira.

1. Introduction

Herbivorous insect abundance and richness are influenced by several factors such as climate, presence of parasitoids and/or predators, and a multitude of host plant characteristics such as size, density, spatial distribution, phenology, nutritional content, and chemical composition (Lawton, 1983; Basset, 1991; Stamp and Casey, 1993; Bernays and Chapman, 1994; Kursar and Coley, 2003; Stiling and Moon, 2005). Pilose leaves, for example, are less likely to be attacked by herbivorous insects (Ribeiro et al., 1994; Paleari and Santos, 1998). Some of these relationships are not always straightforward, however. A study on six Melastomataceae species, including *Miconia ferruginata* DC., in a Cerrado in Lagoa Santa (Minas Gerais, Brazil) found no relationship between insect abundance and tannin concentration in leaves (Ribeiro et al., 1999).

In the markedly seasonal cerrados of central Brazil, insect abundance fluctuates throughout the year. For most orders, peak abundance occurs between October and November (after the first rains). The first half of the dry season (April-June), however, is also favourable for some insects, which become abundant during this period (Pinheiro et al., 2002). This is the case of Lepidoptera caterpillars, which show an abundance peak between May and June (Morais et al., 1999).

Cerrado folivore caterpillars, however, are present in host plants at low frequencies throughout the year (Price et al., 1995), and such frequencies vary according to each host species (Diniz et al., 1999; Morais and Diniz, 2004). The goals of the present paper are to analyse the effects of climatic variation and host-plant characteristics on caterpillar abundance in two species of *Miconia* (Melastomataceae) in a cerrado in central Brazil.

2. Material and Methods

The study was carried at the University of Brasília's Farm (Fazenda Água Limpa, FAL, Brasília, Federal District, Brazil; 15° 57' S and 47° 57' W) in a cerrado sensu stricto area (Goodland, 1971), from May 1998 to September 1999.

The region has a typical cerrado climate, with a marked seasonality and a dry season from May to September (Espinoza et al., 1982), with mean annual temperature and precipitation of 22 °C and 1,431 mm, respectively. Study area characteristics such as soil, climate, and vegetation are described in Felfili et al. (1993, 1994). A precise description of the vegetation at FAL can be found in Ratter (1991).

The Melastomataceae is one of the most representative families in cerrado sensu lato, with 74 genera. *Miconia* is a large genus, represented by 25 species in the Federal District (Cavalcanti and Ramos, 2001). We selected two species from this genus, *Miconia ferruginata* DC. and *M. pohliana* Cogn for the present study. These are shrubs or small trees with star-shaped hair on both leaf sides, frequently found in cerrado sensu stricto near Brasília. They are evergreen sclerophyls that are known to accumulate aluminum (Haridasan, 1982; 1988).

In a 5 km^2 area subdivided into 17 smaller parcels, we carefully searched 200 plants monthly (100 for each species) for Lepidoptera caterpillars. Presence, characteristics, and location of caterpillars were recorded for each plant. Caterpillar specimens were brought to the laboratory and raised without temperature or humidity control in individual plastic jars, with host leaves as food source. Leaves were kept turgid with wet cotton wrapped around the petiole, regularly changed every two days. We recorded date of pupae collection, adult emergence, and presence of parasitoids. Adults were dry mount, identified by Vitor Osmar Becker, and deposited at the Entomology collection of the Department of Zoology at the University of Brasília.

We recorded the estimated percentage of new leaves (foliar phenology) and plant height for each plant examined. We ranked plants in to five classes, according to the percentage of new leaves: 1) 0%; 2) 1 to 25%; 3) 26 to 50%; 4) 51 to 75% e 5) 76 to 100% of new leaves. Tree height was measured with a 2 m collapsible wood ruler.

We determined density and spatial distribution of each species' individuals using a 1 km long transect with 30 randomly chosen 100 m^2 sites. Each site had a randomly chosen perpendicular distance (left or right) from the main transect. We counted all individuals from both species in each site. We used three methods to confidently detect spatial distribution patterns of *M. ferruginata* and *M. pholiana* (Meirelles and Luiz, 1995): Morisita and Poisson indexes and the ratio between observed and expected densities (Brower et al., 1997).

To quantify the hosts' nutritional content, we collected four young and four mature leaves in different locations in the plant from 10 individuals of each species. In the laboratory, we washed each leaf with distilled water, packed them individually in paper bags, and placed them in an oven for 48 hours at 75 °C. The following characters were measured for each sample at the Embrapa-Cerrados laboratory: nitrogen percentage, total protein percentage, and in vitro digestibility. We arcsine transformed each of the above percentages, calculated the average and standard deviation, and compared the results with a *t* test.

We measured foliar pilosity under a dissection scope by counting the number of hair stems in a 1 cm^2 area delimited with a cardboard frame. We measured 10 new and 10 mature leaves from 10 individuals of each species taken from the dry and rainy seasons.

Because the number of plants with caterpillars varies periodically throughout the year, we used a circular distribution (Zar, 1996) do describe and analyse our abundance data. Months were converted to angles with May randomly chosen as month 1 (30°) and April 1999 as 12 (360°). We then calculated the average angle (average month) and the angular dispersion (standard deviation) to identify which months had higher frequencies of plants with caterpillars.

For each month we used maximal and minimal temperatures, average air humidity, and average rainfall for the study period (May 1998 to September 1999) as climatic variables. Data were obtained from IBGE's reserve (RECOR) meteorologic station. We used a multiple regression to evaluate the correlation between caterpillar occurrence in each host species and climatic variables.

3. Results

Only 7.1% of the 3,400 plants checked had caterpillars (Table 1). The species richness was very high (n = 35), but only twelve species representing nine families were identified by their binomial names (Table 2). Caterpillar frequency in *M. pohliana* (10.2%) was more than twice times that found in *M. ferruginata* (4%) ($\chi^2 = 49.24$; $p < 0.0001$; df = 1). The number of caterpillars was also larger in *M. pohliana* (74.2% of the 330 larvae found).

Frequency of hosts with caterpillars varied during the study period in both species (Figure 1). In May (beginning of the dry season) hosts show the largest caterpillar abundance in both species (Table 3), and the distribution of larvae during the dry season is aggregated in both *Miconia* (Rayleigh's test, Z = 22.75).

There was no significant difference in the frequency of plants with caterpillars between May and September of two consecutive years for *M. pohliana* ($\chi^2 = 6.69$; $p < 0.15$; df = 4) and *M. ferruginata* ($\chi^2 = 7.46$; $p < 0.11$; df = 4) (Figure 1).

Miconia pohliana was present at a higher density than *M. ferruginata* ($t = 2.889$; $p < 0.05$), and both species distribution were considered aggregated by all indexes used (Table 4). Species heights did not differ in our

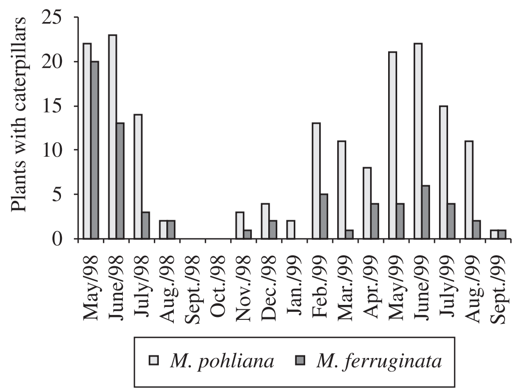

Figure 1. Number of *Miconia ferruginata* and *M. pohliana* plants containing caterpillars in the study area (FAL, Brasília, Brazil) from May 1998 to September 1999. A total of 100 plants of each species were examined in each month.

Table 1. Number of plant individuals checked and number of plants containing immature Lepidoptera from May 1998 to September 1999 in a cerrado at FAL (Brasília, Federal District, Brazil).

Species	Plants checked	Plants with immature		Immature found	
		Caterpillars	Pupae	Caterpillars	Pupae
Miconia pohliana	1,700	173	6	245	6
Miconia ferruginata	1,700	68	6	85	6
Total	-	241	12	330	12
Grand Total	3,400	253		342	

Table 2. Identified species of Lepidoptera collected and reared on *Miconia ferruginata* and *M. pohliana*, from May 1998 to September 1999 in a cerrado at FAL (Brasília, Federal District, Brazil).

Lepidoptera		Hostplants	
Family	Species	*M. pohliana*	*M. ferruginata*
Arctiidae	*Lophocampa citrina* (Sepp., [1852])	x	-
Elachistidae	*Stenoma hoplítica* (Meyrick, 1925)	x	-
	Stenoma ochropa Walsingham, 1913	-	x
Geometridae	*Pleuroprucha asthenaria* (Walker, 1861)	-	x
Hesperiidae	*Sophista latifasciata* (Spitz, 1930)	x	x
Megalopygidae	*Podalia albescens* (Schaus, 1900)	x	x
Noctuiidae	*Epidromia conspersata* Dognin, 1912	-	x
Oecophoridae	*Inga phaeocrossa* (Meyrick, 1912)	-	x
Pyralidae	*Quadraforma obliqualis* (Hampson, 1906)	x	x
Riodinidae	*Anteros lectabilis* Stichel, 1909	-	x
	Parcella amarynthina (Felder and Felder, 1865)	x	-
	Theope ca. *apheles* Bates, 1868	x	-

Table 3. Circular analysis of caterpillar temporal abundance (number of plants with caterpillars) in *Miconia ferruginata* and *M. pohliana*, in a cerrado at FAL (Brasília, Federal District, Brazil).

Species	Month												r	Distribution	Season
	M	J	J	A	S	O	N	D	J	F	M	A			
Miconia ferruginata													0.668	aggregated	Dry
Miconia pohliana													0.530	aggregated	Dry

Caterpillar abundance: largest number of plants with caterpillars (month + standard deviation)
Peak of plants with caterpillars:
Average vector: concentration measure of plants with caterpillars.
Season (dry: May to September; rainy: October to April)

Table 4. Density (in 30 parcels of 100 m^2) and spatial distribution of *Miconia pohliana* and *Miconia ferruginata* in the study area (FAL, Brasília, Brazil).

Species	Individuals	largest N/area	Areas without individuals	Average density	Id	D/D'
M. pohliana	76	8	9	2.53 ± 2.5	1.54	2.11
M. ferruginata	31	6	15	1.03 ± 1.4	1.94	1.49

Id = Morisita index; D/D' = ratio between expected and observed densities

Table 5. Dry and rainy season leaf pilosity (hair density in 1 cm^2; n = 10 leaves) in new and mature leaves (average ± standard deviation) in both *Miconia* species in the study area (FAL, Brasília, Brazil).

	Season	*M. pohliana*	*M. ferruginata*	t	P
New leaves	dry	331.6 ± 123.8	147.4 ± 116.6	4.705	<0.001
	rainy	250.0 ± 125.6	203.2 ± 115.3	0.868	>0.30
Mature leaves	dry	2.3 ± 5.1	3.5 ± 6.2	0.473	>0.70
	rainy	12.6 ± 39.1	1.5 ± 3.6	0.894	>0.40

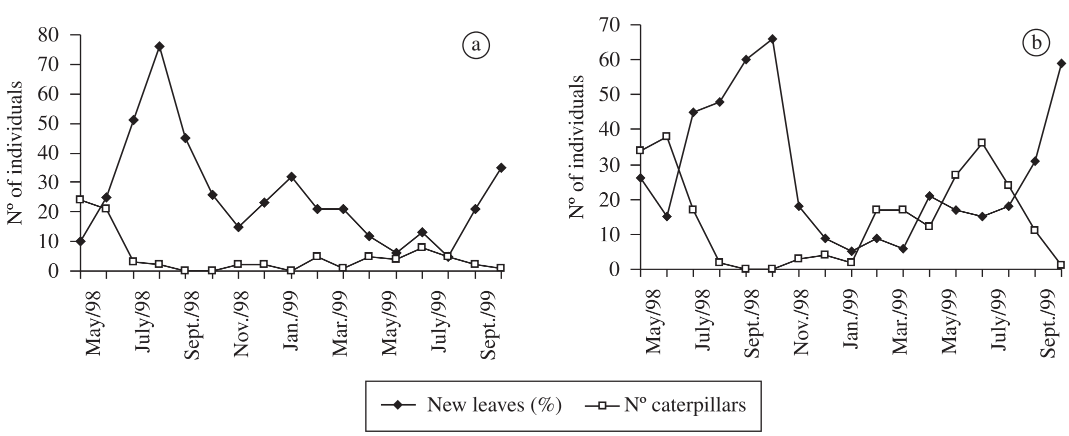

Figure 2. Number of individuals with more than 50% new leaves and number of caterpillars found in each month from May 1998 to September 1999 a) *Miconia ferruginata*; b) *Miconia pohliana*.

study area (*M. pohliana* 1.22 m ± 0.58 e *M. ferruginata* 1.25 m ± 0.58). Caterpillars were more frequent and abundant on *M. pohliana*.

Both species showed similar foliar phenology. They do not loose leaves synchronically, and leaf production peak occurs from July to September in both species. Results indicate that caterpillar abundance is not correlated with the increase in leaf production in either species (Figure 2).

The new leaves of *M. pohliana* had a higher hair density than *M. ferruginata* in the drier season (Table 5). This difference was not observed in new leaves in the rainy season or in mature leaves of either season. Both species showed higher hair density in new leaves com-

Table 6. New and mature leaves nutritional quality (average and standard deviation; data arcsin transformed) in *Miconia pohliana* and *M. ferruginata*.

	Nitrogen		t	P
	Average	**Standard deviation**		
New leaves				
M. pohliana	0.084	0.0038	2.866	>0.02
M. ferruginata	0.089	0.0040		
Mature leaves				
M. pohliana	0.078	0.0037	4.036	>0.001
M. ferruginata	0.084	0.0029		
	Gross protein		**t**	**P**
	Average	**Standard deviation**		
New leaves				
M. pohliana	0.219	0.009	2.586	>0.05
M. ferruginata	0.230	0.010		
Mature leaves				
M. pohliana	0.203	0.010	3.704	>0.01
M. ferruginata	0.218	0.008		
	Digestibility		**t**	**P**
	Average	**Standard deviation**		
New leaves				
M. pohliana	0.447	0.024	15.754	>0.001
M. ferruginata	0.306	0.015		
Mature leaves				
M. pohliana	0.410	0.020	9.049	>0.001
M. ferruginata	0.333	0.018		

pared to mature ones. Even though *M. pohliana* shows a higher hair density in new leaves, its hairs are shorter and become detached from the leaf more easily than in *M. ferruginata*, which shows longer hairs forming an intricate mesh on the leaf's surface.

New and young *M. ferruginata* leaves show a significantly higher nitrogen and absolute protein content, but have significantly lower digestibility (Table 6).

Monthly abundance of caterpillars in *M. ferruginata* showed no significant correlation with the climatic variables considered ($F = 2.244$; $p < 0.125$). For *M. pohliana*, however, climatic variables explain most of the abundance variation ($F = 8.740$; $p < 0.002$).

4. Discussion

We found a low proportion of caterpillars in *Miconia ferruginata* and *M. pohliana*. This result has been found recurrently for different plant species in the cerrado (Price et al., 1995; Diniz and Morais, 1997; Diniz et al., 1999), and seems to be a consistent pattern of folivore insects in this biome (Loyola and Fernandes, 1993; Ribeiro et al., 1999).

The higher caterpillar abundance we found in the beginning of the dry season in *Miconia* species has also been detected in other cerrado species (Morais et al., 1999; Morais and Diniz, 2004). *Miconia ferruginata* and *M. pohliana* are evergreen plants that show new, mature, and old leaves throughout the year. A peak in leaf production occurs, however, at the end of the dry season and beginning of the rainy season. This leaf production pattern also occurs in deciduous plants such as *Erythroxylum* spp. (Erythroxylaceae) and, as in *Miconia*, the time of higher caterpillar abundance is not coincident with the peak of leaf production (Price et al., 1995).

Temporal variation in caterpillar abundance is expected in a highly seasonal environment such as the Cerrado. Still, why is caterpillar abundance so low during the peak of leaf production in the *Miconia* species studied? One possible explanation is that leaf production peak (July to September) is also the period of lowest air humidity in the region. Climatic conditions explain most of the caterpillar abundance fluctuation in *M. pohliana*, and their aggregation in the dry season's first half (May to July), when conditions are less harsh, specially air humidity and minimum temperature. Another possible explanation could be the tendency for higher caterpillar parasitism pressure during the peak of leaf production in cerrados of the Federal District (Morais et al., 1999).

Furthermore, both *Miconia* species new leaves are heavily covered by hair. Paleari and Santos (1998) showed that the experimental removal of hair from *M. albicans* new leaves caused them to be attacked more frequently, indicating that pilosity may be an efficient barrier for herbivore insects. A similar result was found by Ribeiro et al. (1994) with *Tabebuia ochracea* (Bignoniaceae). Still, *M. ferruginata* and *M. pohliana* share 74% of the caterpillar species, and of all caterpillar species found in *M. pohliana* 30% were in new leaves while in *M. ferruginata* 57.6% were using this resource. Hence, new leaves characteristics cannot be used to explain caterpillar low frequency during the period of higher leaf production.

Caterpillars were more abundant in *M. pohliana* than in *M. ferruginata*. Both species have an aggregated distribution pattern and similar heights, but *M. pohliana* was two times more abundant in the study area. This characteristic may explain the higher caterpillar abundance in this species, in accordance with the resource concentration hypothesis (Root, 1973). Plants with higher local densities are more easily located in a shorter period of time by females, representing therefore a more attractive and available resource for Lepidoptera.

Therefore, higher leaf digestibility and higher local abundance, as well as other factors not analysed herein, may explain higher caterpillar abundance in *M. pohliana*. Digestibility is correlated to tissue fiber content and, indirectly, to leaf hardness and sclerophyly. Leaf hardness was the best predictor for variation in herbivore attack in a dry forest in Panama (Coley, 1983), but a similar result was not found for cerrado plants (Marquis et al., 2001).

Variation in precipitation and other climatic characteristics unquestionably influence temporal caterpillar abundance variation in *Miconia* spp. and other cerrado plant species. Some variables not examined in the present work, such as predator and parasite pressure, secondary chemical compounds concentration, and leaf nutritional quality, which varies with the plant's age and phenophase (Medeiros and Haridasan, 1985; Leitão and Silva, 2004), may also contribute to temporal variation in caterpillar abundance in the cerrado.

Caterpillar frequency in *M. pohliana* (10.2%) was more than twice times that found in *M. ferruginata* (4%). Frequency of hosts with caterpillars varied during the study period in both species but caterpillar abundance is not correlated with the leaf production. Nutritional characteristics (nitrogen and gross protein content) are higher for *M. ferruginata* young and mature leaves, but their digestibility is lower than *M. pohliana* leaves. Higher digestibility of *M. pohliana* leaves may be an important factor to explain the higher caterpillar abundance found in this host plant.

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