

Insect herbivores associated with an evergreen tree *Gonorrhachis marginata* Taub. (Leguminosae: Caesalpinoideae) in a tropical dry forest

Silva, JO.^{a*} and Neves, FS.^b

^aLaboratório de Interações Tri-tróficas, Departamento de Ecologia, Instituto de Ciências Biológicas, Universidade de Brasília – UnB, Campus Darcy Ribeiro, Asa Norte, s/n, CEP 70910-900, Brasília, DF, Brazil

^bLaboratório de Ecologia de Insetos, Departamento de Biologia Geral, Universidade Federal de Minas Gerais – UFMG, Campus Universitário, Pampulha, Av. Antônio Carlos, 6627, CEP 30161-970, Belo Horizonte, MG, Brazil

*e-mail: jhonathanos@gmail.com

Received: December 20, 2012 – Accepted: May 16, 2013 – Distributed: August 31, 2014
(With 3 figures)

Abstract

Gonorrhachis marginata Taub. (Leguminosae: Caesalpinoideae) is a tree species found in Brazilian tropical dry forests that retain their leaves during the dry season. That being, we addressed the following question: i) How do insect diversity (sap-sucking and chewing), leaf herbivory and defensive traits (tannin and leaf sclerophyll) vary on the evergreen tree species *G. marginata* between seasons? The abundance of sap-sucking insects was higher in the dry season than in the rainy season. However, we did not verify any difference in the species richness and abundance of chewing insects between seasons. Leaf herbivory was higher in the rainy season, whereas leaf sclerophyll was higher in the dry season. However, herbivory was not related to sclerophyll. Insect herbivores likely decrease their folivory activity during the dry season due to life history patterns or changes in behaviour, possibly entering diapause or inactivity during this period. Therefore, *G. marginata* acts as a likely keystone species, serving as a moist refuge for the insect fauna during the dry season in tropical dry forest, and the presence of this evergreen species is crucial to conservation strategies of this threatened ecosystem.

Keywords: deciduous forest, folivory, insect guilds, specific leaf mass.

Insetos herbívoros associados a uma árvore sempre verde *Gonorrhachis marginata* Taub. (Leguminosae: Caesalpinoideae) em uma floresta tropical seca

Resumo

Gonorrhachis marginata Taub. (Leguminosae: Caesalpinoideae) é uma árvore encontrada em florestas tropicais secas do Brasil que mantém as suas folhas durante a estação seca. Baseado neste fato, nós levantamos a seguinte questão: i) como a diversidade de insetos herbívoros (sugadores e mastigadores), herbivoria foliar e características defensivas (taninos e esclerofilia foliar) variam em *G. marginata* entre as estações seca e chuvosa. A abundância de insetos sugadores foi maior na estação seca, entretanto, a riqueza e abundância de insetos mastigadores não diferiram entre as estações. A herbivoria foliar foi maior na estação chuvosa, enquanto a esclerofilia foliar foi maior na estação seca. Não foi observado efeito significativo da esclerofilia sobre os níveis de herbivoria foliar. Insetos herbívoros reduzem a sua atividade de consumo foliar durante a estação seca, fato este devido à sua história natural e/ou mudança comportamental, provavelmente, entrando em diapausa durante este período. Nossos resultados demonstram que *G. marginata* atua como refúgio para fauna de insetos durante a estação seca, e que a presença desta espécie merece relevante destaque em estratégias de conservação deste ameaçado ecossistema.

Palavras-chave: floresta decidual, folivoria, guilda de insetos, massa foliar específica.

1. Introduction

Seasonally dry tropical forests (SDTFs) are among the most threatened ecosystems in the world (Miles et al., 2006; Portillo-Quintero and Sánchez-Azofeifa, 2010). This vegetation is typically dominated by deciduous trees, with

more than 50% of leaf fall during the dry season (Sánchez-Azofeifa et al., 2005). The average annual temperature is approximately 25 °C, total annual precipitation ranges between 700 and 2000 mm, and there are three or more

dry months (precipitation < 100 mm) every year (Sánchez-Azofeifa et al., 2005). Because of plant deciduousness, herbivory is highly concentrated in the rainy season (Janzen and Waterman, 1984; Filip et al., 1995; Oliveira et al., 2012; Silva et al., 2012). During the dry season there is a strong movement of insects into moist refuges, associated with a general reduction of insect diversity during this period (Janzen, 1973; Janzen, 2004), since most insect herbivores go into diapause or migrate to find food or shelter (Dirzo and Domínguez, 1995). Thus, the diversity of insects in green patches (e.g. adjacent riparian forest or evergreen trees inside the SDTFs) appears to increase during the dry season (Janzen, 1973; Janzen, 2004). Despite this obvious evidence, to our knowledge no detailed study investigated the role of evergreen tree species in maintaining insect diversity in SDTFs during the severe dry season.

In general, plants from SDTFs usually exhibit high photosynthetic and growth rates because of intense exposure to sunlight. Both light and water availability vary seasonally and may cause variation in a number of leaf traits, specifically those that relate to water relations and leaf economics (Gotsch et al., 2010). Moreover, the leaves of evergreen species generally have a longer lifespan than deciduous trees, and the presence of carbon-based defensive compounds is common (Janzen and Waterman, 1984; Coley and Barone, 1996; Gotsch et al., 2010; Pringle et al., 2011). Carbon-based leaf defenses such as leaf sclerophyll and tannin also can vary between seasons, and are higher in evergreen trees in the dry season (Janzen and Waterman, 1984; Dirzo and Boege, 2008; Gotsch et al., 2010). These leaf traits make leaves more tough, thick and unpalatable to avoid loss of water and nutrients, and herbivory during the severe dry season (Pringle et al., 2011). Despite a reduction in the leaf nutritional quality to herbivores from rainy to dry season, evergreen trees provide moisture conditions and shade microsites for insect herbivores during the progression of the six month dry. Then, evergreen trees might be important in maintaining the diversity of insect herbivores between seasons.

Though called evergreen trees, none of these species are truly evergreen. All retain their leaves for approximately 11.5 months of the year, when they shed all their leaves at the end of the dry season or beginning of the rainy season, and immediately replace them within a few days (Janzen and Waterman, 1984). The same is observed in *Goniorrhachis marginata* Taub. (Leguminosae-Caesalpinoideae), commonly known in Brazil as "Itapicuru" (Figure 1), a tree species that reaches up to 30 m in height (Oliveira-Filho, 2006). This species occurs in phytophysiognomies marked by a severe dry season in Minas Gerais, Bahia and Pernambuco Brazilian states (Oliveira-Filho, 2006). At the SDTF of the present study, individuals shed their leaves in September, before the onset of the rainy season, whereas the flushing of young leaves is observed by the end of the same month (Pezzini et al., 2008). Furthermore, *G. marginata* is the only evergreen species recorded at local flora, and provides an ideal scenario to test for insect timing and herbivory attack related to resource availability and seasonality in SDTF.



Figure 1. Evergreen tree species *Goniorrhachis marginata* during the dry season in a seasonally dry tropical forest at the Área de Proteção Ambiental do Rio Pandeiros, northern Minas Gerais, Brazil.

Based on previous studies involving seasonality of insect herbivores between deciduous and evergreen sites, Janzen (1973) found a much greater change in the number of species, number of individuals, and individuals/species of the bugs (sap-sucking) than the beetles (chewing) between seasons, associated to insect movement from drier to wetter sites in the dry season. In this way, we addressed the following question: i) How do insect diversity (sap-sucking and chewing), leaf herbivory and defensive leaf traits (tannin and leaf sclerophyll) vary on the evergreen tree species *G. marginata* between seasons?

2. Methods

2.1. Study area

This study was conducted at the Área de Proteção Ambiental do Rio Pandeiros (APA-RP), located in Januária ($35^{\circ} 36' 02.7''$ S, $44^{\circ} 40' 07.5''$ W), at the middle portion of the São Francisco river basin, northern Minas Gerais state, Brazil (Azevedo et al., 2009). This conservation unit is situated in the transition between the Caatinga (dry forest and scrubland vegetation) and Cerrado (Brazilian savanna) biomes, with an area of approximately 210,000 ha.

The climate in this region is considered tropical rainy (Aw) according to Köppen's classification, and characterized by dry winters (May-October) with an average annual temperature of 23.6°C and average annual rainfall of 1,057.4 mm (Sales et al., 2009). SDTFs comprise important transitional areas at APA-RP, growing in rich-soil patches with canopies up to 35 m in height (Sales et al., 2009). The level and duration of deciduousness vary among tree species, but some as *G. marginata* retain their leaves during the dry season (Pezzini et al., 2008).

2.2. Experimental design

We arbitrarily sampled 12 different individuals of *G. marginata* in each season (n=24), ranging from 20 to 30 m (24.6 ± 2.98 m) in height. Sampling was performed during the dry season (August-2006) and subsequent rainy season (March-2007). The canopy of each tree was reached through the single rope climbing technique (see Neves et al.,

2010, 2013). Free-feeding insects were collected with an entomological umbrella by beating on the branches of each sampled tree. We did ten beats per branch in three branches per tree, totalling 30 beats per tree. All collected insects were grouped by tree and identified at level of morphospecies richness within family considering two feeding guilds (sap-sucking and chewing). We recorded the morphospecies richness (number of morphospecies) and abundance (number of individuals) of each guild per tree. The sap-sucking guild was composed of adults and juveniles of Auchenorrhyncha, Sternorrhyncha and herbivores from the Heteroptera. The chewing guild was composed of adult and juvenile Coleoptera, Orthoptera, Phasmida and juveniles of Lepidoptera (see Moran and Southwood, 1982).

2.3. Leaf herbivory and defensive characteristics

We arbitrarily collected 30 fully expanded leaves in each individual tree sampled (720 leaves in total). During the dry season (August-2006), the leaves were mature, and in the rainy season (March-2007) the leaves were young. In order to quantify leaf damage, each leaf was photographed in the field against a white board with one centimeter marks as scale reference. Then, leaves were stored and taken to the laboratory where chemical analyses were performed. Total and removed leaf areas were calculated from the leaf photographs using the software ImageJ (Rasband, 2006), and the average percentage of leaf damage was calculated per plant. Later, each leaf was dried at 50 °C for 96 hours, and then weighted. We used a common measure of sclerophyllly denominated specific leaf mass (SLM), obtained through the ratio between leaf dry weight and area (Turner, 1994). This method is simple and its use widespread (Silva et al., 2009; Neves et al., 2010; Oliveira et al., 2012). Then, the same 30 leaves were divided into three replicates consisting of ten leaves each. Samples were ground to a fine powder, weighed and used for tannin quantification through the method of radial diffusion (see Hagerman, 1987), with tannic acid used as standard.

2.4. Data analyses

We constructed generalized linear models (GLMs) to test whether plant quality (i.e. leaf sclerophyllly and tannin concentration) varied between seasons, and to check for the effect of leaf sclerophyllly, tannin concentration and season on leaf herbivory, and on species richness and abundance of chewing and sap-sucking insect herbivores. For the latter models, response variables were leaf herbivory and insect herbivore species richness and abundance, whereas explanatory variables were leaf sclerophyllly, tannin concentration and season. Complete models were fitted and then simplified by removing non-significant variables and verifying the effect of removal on deviance (Crawley, 2002). All models were submitted to residual analysis, so as to evaluate adequacy of error distribution. All analyses were conducted using the procedure ‘glm’ in the software R.2.10 (R Development Core Team, 2010).

3. Results

We sampled 405 free-feeding insect herbivores on *Goniorrhachis marginata* distributed into 44 morphospecies (Appendix 1). The dry season sample was composed of 376 individuals belonging to 20 morphospecies, whereas in the rainy season sample we found 29 individuals belonging to 26 morphospecies. In the dry season sample, 28 individuals (7%) were chewing herbivores, whereas 348 individuals (93%) were sap-sucking (Table 1). Among the chewing insects, the family Bruchidae had the highest richness with 9 morphospecies (22 individuals) (Appendix 1). For sap-sucking herbivores, Tingidae and Psyllidae were the commonest families, with 290 (two morphospecies) and 54 individuals (one morphospecies), respectively. In the rainy season insect herbivores were more evenness distributed, with 55% of the sampled insects belonging to the chewing guild (16 individuals), and 45% to the sap-sucking guild (13 individuals) (Table 1). The family Chrysomelidae had the highest richness among the chewing guild, with seven morphospecies and seven individuals, whereas the family Cicadellidae was the most representative among the sap-sucking insects, with three morphospecies and three individuals (Table 1). In general, the insect morphospecies associated with *G. marginata* differed between seasons, with only a single morphospecies of Chrysomelidae (*Syneta* sp.1) and Cicadellidae (*Agalia* sp.1) sampled in both seasons (see Table 1; Appendix 1).

The average abundance and species richness of chewing insects per tree did not differ between the dry and rainy seasons (Figure 2ab; Table 2). On the other hand, the average abundance of sap-sucking insects per tree varied significantly between seasons, with a 26-fold increase in the dry season (Figure 2c; Table 2). In the dry season sample, a single Tingidae morphospecies (*Tingis* sp.1) had 278 individuals and this result was responsible for the discrepancy observed in average insect abundance and standard error in this season (Table 1; Appendix 1). However, the species richness of this guild did not differ between the dry and rainy seasons (Figure 2d; Table 2).

The percentage of leaf herbivory was lower in the dry season than in the rainy season (Figure 3a; Table 2). On the other hand, SLM was higher in the dry season ($F_{1,22} = 461.18$, $p < 0.001$; Figure 3b). However, leaf herbivory was not related to SLM, and this leaf trait positively affected the abundance and species richness of chewing and sap-sucking insects (Table 2). Finally, tannin concentration did not differ significantly between seasons ($F_{1,22} = 0.0027$, $p = 0.9593$), and no relationship was found between tannin concentration and either insect guild or leaf herbivory (Table 2).

4. Discussion

Leaf-chewing herbivore abundance and richness did not differ between seasons, whereas the abundance of sap-sucking insects was higher in the dry season. In general, insect abundance was strongly determined by a single Tingidae morphospecies – *Tingis* sp.1 (see Table 1), which

Table 1. Family richness and abundance of free-feeding insect herbivore guilds associated with *Goniorrhachis marginata* in dry and rainy seasons in a seasonally dry tropical forest at the Área de Proteção Ambiental do Rio Pandeiros, northern Minas Gerais, Brazil (n=24).

Guild	Order /Family	Dry season		Rainy season	
		Richness	Abundance	Richness	Abundance
Chewing	Coleoptera				
	Bruchidae	9	22	0	0
	Cerambycidae	0	0	1	1
	Chrysomelidae	2	2	6	6
	<i>Syneta</i> sp.1	1	1	1	1
	Curculionidae	1	1	5	6
	Tenebrionidae	1	2	1	1
	Orthoptera				
	Tettigoniidae nymph	0	0	1	1
Sap-sucking	Hemiptera				
	Unidentified nymph	1	1	1	3
Heteroptera					
	Pentatomidae nymph	0	0	1	1
	Rophalidae	0	0	1	1
	Tingidae	1	12	1	1
	<i>Tingis</i> sp.1	1	278	0	0
Auchenorrhyncha					
	Unidentified nymph	0	0	1	1
	Cicadellidae	0	0	2	2
	<i>Agalia</i> sp.1	1	2	1	1
	Membracidae	1	1	1	1
	Tropiduchidae	0	0	1	1
Sternorrhyncha					
	Psyllidae	1	54	1	1
Total		20	376	26	29

occurred only in the dry season. White (1969) observed higher attack rates of the sap-sucker *Cardiaspina desintexta* (Taylor) on *Eucalyptus fasciculosa* (F. Muell) in periods of pronounced water stress. The same pattern was also found in a SDTF in Costa Rica during the dry season, with a dramatic increase in bug numbers as opposed to beetles (Janzen, 1973). In a recent stress induced experiment, Walter et al. (2012) found greater herbivore performance in drought-exposed plants due to increased nitrogen and carbohydrates content. Thus, the increase in the number of sap-sucking insects during the dry season may be caused by the following aspects of the plant-insect interaction: i) it is unlikely that phloem fluids contain large concentrations of defensive secondary compounds; and ii) it may be related to a higher concentration of soluble nitrogen that increases herbivore performance.

Only a single morphospecies from each guild Chrysomelidae (*Syneta* sp.1) and Cicadellidae (*Agalia* sp.1) occurred in both seasons. The little overlap in community composition of chewing and sap-sucking insects between seasons was also observed in other SDTFs (Janzen, 1973; Janzen, 2004). In this study, the insect community associated with *G. marginata* probably exhibits strong seasonality, with different herbivore assemblies in each

season. It is likely that insects found in dry season are permanent residents or seasonal visitors. Nevertheless, interpretation of these results needs caution, because some insects may be occasional visitors, and moisture provided by evergreen trees during the dry season is a much needed habitat for an insect.

Although the species richness and abundance of chewing insects remained unchanged between seasons, leaf herbivory was higher on young leaves found in the rainy season. Younger leaves tend to have higher nutritional quality, resulting in herbivory rates that are 5-25% higher compared to mature leaves (Coley and Barone, 1996). Additionally, plant chemistry is different between young and mature leaves, and carbon-based compounds concentration increase with leaf age (Coley and Barone, 1996; Boeger, 2005; Oliveira et al., 2012; Silva et al., 2012). A major line of defense against beetles with chewing mouthparts (e.g. leaf sclerophyll) was verified on mature leaves in the dry season. The occurrence of insect herbivores, mainly tingids in dry season, may be influenced by other factors, confounding the observed relationship between insects and sclerophyll. Probably, a high proportion of the insect community (e.g. leaf-chewing) passes the dry season as adults in reproductive diapause (Janzen, 2004;

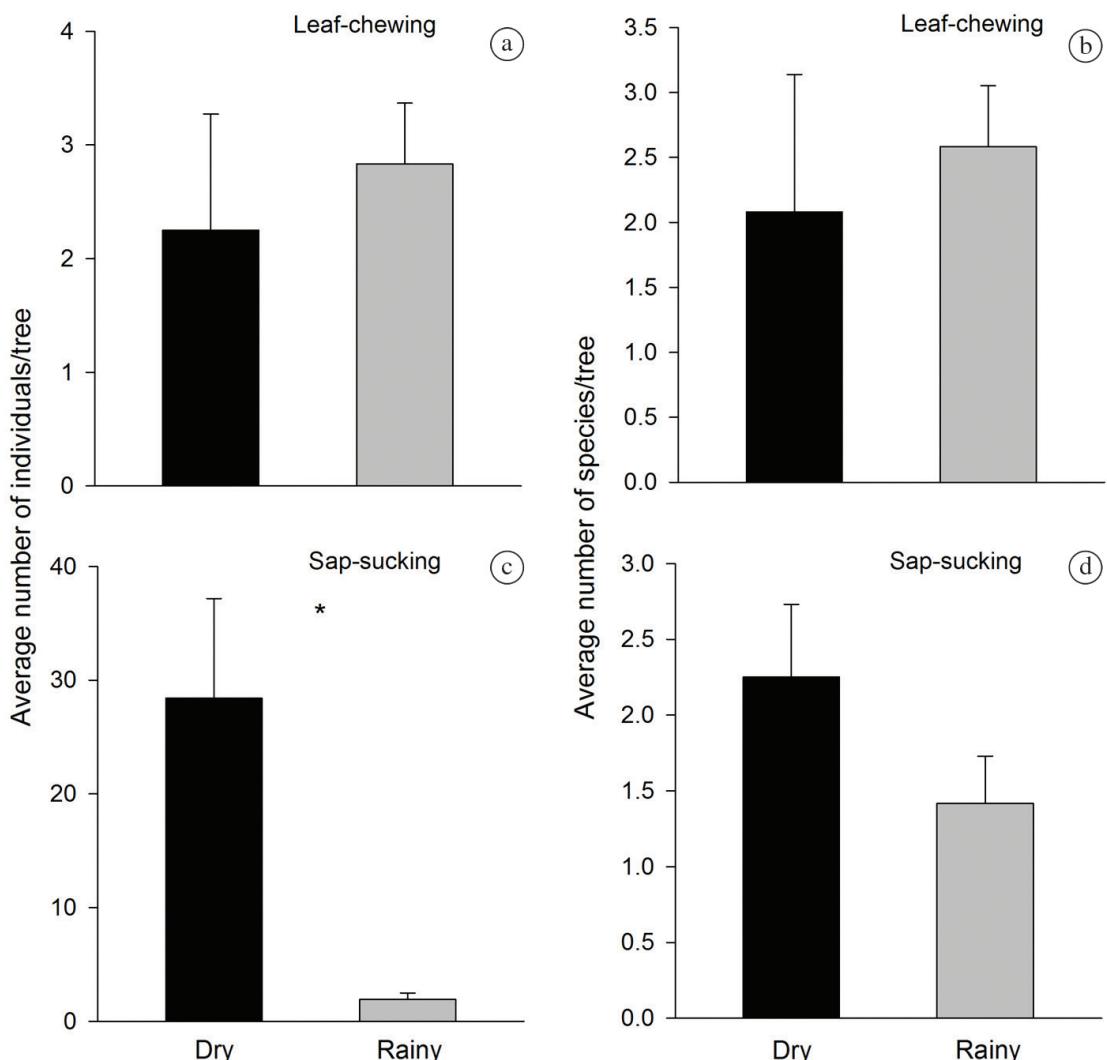


Figure 2. Average (a) abundance and (b) species richness of leaf-chewing insects; (c) abundance and (d) species richness of sap-sucking insects on *Goniorrhachis marginata* in dry and rainy seasons in a seasonally dry tropical forest, Brazil ($n=24$). Error bars indicate one standard error. In the figure, “*” indicates $p < 0.05$.

Dirzo and Domínguez, 1995), and because of their life history may reduce leaf consumption during the dry season. On the other hand, a high leaf sclerophyll in the dry season may protect plants against water and nutrient losses, and help to avoid photodamage (Turner, 1994; Dirzo and Boege, 2008; Silva et al., 2009; Gotsch et al., 2010; Oliveira et al., 2012). We did not find a relation between tannin concentration and any variable tested. In general, insect herbivore diversity is influenced by diffuse factors such as climatic variables (e.g. temperature, air humidity, insulation), and complex multitrophic interactions (e.g. interspecific competition, predation, mutualism), whereas leaf consumption rates are controlled by plant quality (Coley and Barone, 1996; Boege, 2005; Stiling and Moon, 2005). In this way, insect herbivores also likely use evergreen trees as a habitat during the dry season, in they which

provide refuge against harsh microclimatic environmental conditions and natural enemies.

This is the first study to investigate insect herbivore seasonality, leaf herbivory and defensive traits on an evergreen tree in a Brazilian SDTF. The diversity of insect herbivores associated with *G. marginata* remained unchanged in the dry season (i.e. despite higher sap-sucking abundance), but the trees experienced lower herbivore pressure during this period. Plant defensive traits assessed in this study were not related to leaf herbivory, and insects probably use this species during the dry season to avoid harsh environmental conditions. Our results indicate that *G. marginata* acts as a likely keystone species, serving as moist refuge for the insect fauna during the dry season in SDTF, and also highlights the importance of the presence of this evergreen species to tropical conservation strategies in this threatened ecosystem.

Table 2. Deviance analyses of the complete generalized linear models (GLMs) to evaluate the effects of season, specific leaf mass and tannin concentration on response variables (leaf area loss, abundance and species richness of chewing and sap-sucking herbivores) on *Goniorrhachis marginata* in a seasonally dry tropical forest (n=24). None of the tested interactions were significant, therefore they are not shown.

Response Variable	Source	d.f.	Deviance	Residual d.f.	Residual deviance	P (>Chi)
Abundance of chewers	Null Model			23	83.94	
	Season	1	0.80	22	80.14	0.499
	Specific leaf mass	1	31.83	21	51.30	<0.001*
	Tannin concentration	1	0.40	20	50.90	0.635
Richness of chewers	Null Model			23	75.18	
	Season	1	0.65	22	74.53	0.526
	Specific leaf mass	1	27.75	21	46.78	<0.001*
	Tannin concentration	1	0.70	20	46.08	0.510
Abundance of sap-suckers	Null Model			23	1491.45	
	Season	1	333.06	22	1158.39	0.03*
	Specific leaf mass	1	251.04	21	907.35	0.04*
	Tannin concentration	1	181.19	20	726.16	0.072
Richness of sap-suckers	Null Model			23	28.48	
	Season	1	2.30	22	26.18	0.130
	Specific leaf mass	1	1.00	21	25.18	0.317
	Tannin concentration	1	0.30	20	24.88	0.586
% Leaf area loss	Null Model			23	388.77	
	Season	1	227.33	22	161.44	<0.001*
	Specific leaf mass	1	0.02	21	161.42	0.960
	Tannin concentration	1	1.99	20	159.43	0.620

*Independent variable retained in the minimum adequate model (p<0.05).

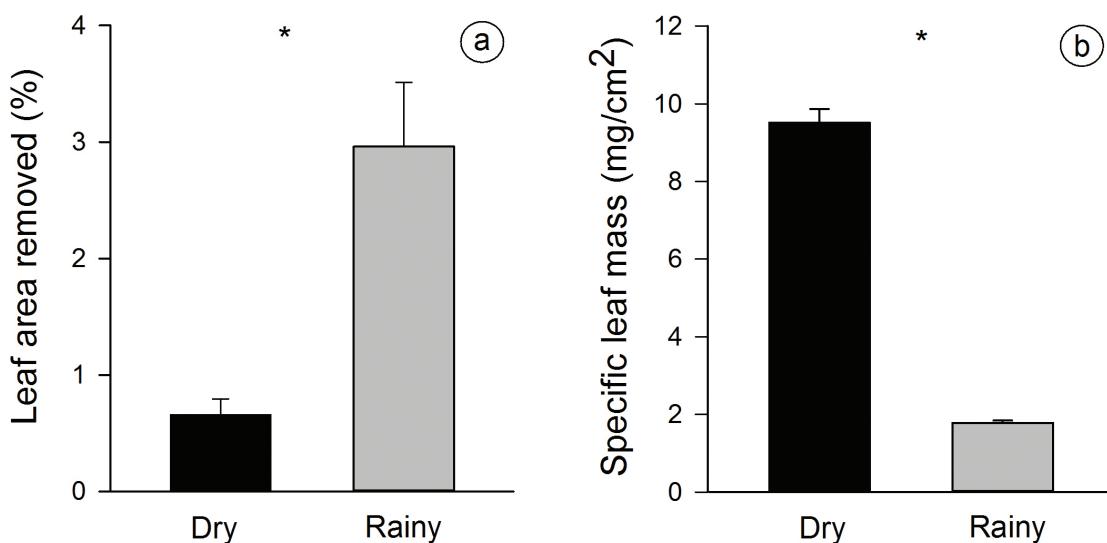


Figure 3. (a) Leaf area removed (%) and (b) specific leaf mass (mg/cm^2) on *Goniorrhachis marginata* in dry and rainy seasons in a seasonally dry tropical forest, Brazil (n=24). Error bars indicate one standard error. In the figure, “*” indicates $p < 0.05$.

Acknowledgements

The authors thank H. Souza-Silva, R.A Andrade and M. G. Camargo for help during field work. We thank all the staff of the Instituto Estadual de Florestas (IEF) for allowing us to stay and work at APA-Rio Pandeiros and for logistical support. We specially thank W.V Neves (IEF) for his invaluable assistance. This work was carried out with the aid of a grant from the Fundação de Amparo à Pesquisa de Minas Gerais (FAPEMIG, CRA 2582/05) and Inter-American Institute for Global Change Research (IAI) CRN II # 021, which is supported by the U.S. National Science Foundation (Grant GEO 0452325). J.O. Silva is grateful for a scholarship from the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), and F.S. Neves from FAPEMIG.

References

- AZEVEDO, IFP., NUNES, YRF., VELOSO, MDM., NEVES, WV. and FERNANDES, GW., 2009. Preservação estratégica para recuperar o São Francisco. *Scientific American Brasil*, vol. 83, p. 74-79.
- BOEGE, K., 2005. Herbivore attack in Casearia nitida influenced by plant ontogenetic variation in foliage quality and plant architecture. *Oecologia*, vol. 143, no. 1, p. 117-125. <http://dx.doi.org/10.1007/s00442-004-1779-9>. PMID:15742219
- COLEY, PD. and BARONE, JA., 1996. Herbivory and plant defenses in tropical forests. *Annual Review of Ecology and Systematics*, vol. 27, no. 1, p. 305-335. <http://dx.doi.org/10.1146/annurev.ecolsys.27.1.305>.
- CRAWLEY, M., 2002. *Statistical computing: an introduction to data analysis using S-Plus*. London: John Wiley & Sons.
- DIRZO, R. and DOMÍNGUEZ, CA., 1995. Plant-herbivore interactions in Mesoamerican tropical dry forest. In BULLOCK, SH., MOONEY, A. and MEDINA, E. (Eds.). *Seasonally Dry Tropical Forests*. Cambridge: University Press. p. 304-325.
- DIRZO, R. and BOEGE, K., 2008. Patterns of herbivory and defense in tropical dry and rain forests. In CARSON, W. and SCHNITZER, SA. (Eds.). *Tropical Forest Community Ecology*. West Sussex: Blackwell Science. p. 63-78.
- FILIP, V., DIRZO, RJ., MAASS, M. and SARUKHÁN, J., 1995. Within and among-year variation in the levels of herbivory on the foliage of trees from a Mexican tropical deciduous forest. *Biotropica*, vol. 27, no. 1, p. 78-86. <http://dx.doi.org/10.2307/2388905>.
- GOTTSCH, SG., POWERS, JS. and LERDAU, MT., 2010. Leaf traits and water relations of 12 evergreen species in Costa Rican wet and dry forests: patterns of intra-specific variation across forests and seasons. *Plant Ecology*, vol. 211, no. 1, p. 133-146. <http://dx.doi.org/10.1007/s11258-010-9779-9>.
- HAGERMAN, AE., 1987. Radial diffusion method for determining tannin in plant extracts. *Journal of Chemical Ecology*, vol. 13, no. 3, p. 437-449. <http://dx.doi.org/10.1007/BF01880091>. PMID:24301886
- JANZEN, DH., 1973. Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. *Ecological Society of America*, vol. 54, p. 687-708.
- JANZEN, DH., 2004. Ecology of dry-forest wildland insects in the Área de Conservación Guanacaste. In GORDON, WF., MATA, A. and VINSON, SB. (Eds.). *Biodiversity conservation in Costa Rica: learning the lessons in a seasonal dry forest*. Los Angeles: University California Press. p. 80-96.
- JANZEN, DH. and WATERMAN, PG., 1984. A seasonal census of phenolics, fibre and alkaloids in foliage of forest trees in Costa Rica: some factors influencing their distribution and relation to host selection by Sphingidae and Saturniidae. *Biological Journal of the Linnean Society: Linnean Society of London*, vol. 21, no. 4, p. 439-454. <http://dx.doi.org/10.1111/j.1095-8312.1984.tb01605.x>.
- MILES, L., NEWTON, A., DEFRIES, R., RAVILIOUS, C., MAY, I., BLYTH, S., KAPOS, V. and GORDON, J., 2006. A global overview of the conservation status of tropical dry forests. *Journal of Biogeography*, vol. 33, no. 3, p. 491-505. <http://dx.doi.org/10.1111/j.1365-2699.2005.01424.x>.
- MORAN, CV. and SOUTHWOOD, TRE., 1982. The guild composition of arthropod communities in trees. *Journal of Animal Ecology*, vol. 51, no. 1, p. 289-306. <http://dx.doi.org/10.2307/4325>.
- NEVES, FS., ARAÚJO, LS., ESPÍRITO-SANTO, MM., FAGUNDES, M., FERNANDES, GW., SANCHEZ-AZOFÉIFA, GA. and QUESADA, M., 2010. Canopy herbivory and insect herbivore diversity in a dry forest-savanna transition in Brazil. *Biotropica*, vol. 42, no. 1, p. 112-118. <http://dx.doi.org/10.1111/j.1744-7429.2009.00541.x>.
- NEVES, FS., SPERBER, CF., CAMPOS, RI., SOARES, JP. and RIBEIRO, SP., 2013. Contrasting effects of sampling scale on insect herbivores distribution in response to canopy structure. *Revista de Biología Tropical*, vol. 61, no. 1, p. 125-137. PMID:23894967.
- OLIVEIRA, KN., ESPÍRITO-SANTO, MM., SILVA, JO. and MELO, GA., 2012. Ontogenetic and temporal variations in herbivory and defense of Handroanthus spongiosus (Bignoniaceae) in a Brazilian tropical dry forest. *Environmental Entomology*, vol. 41, no. 3, p. 541-550. <http://dx.doi.org/10.1603/EN11259>. PMID:22732612
- OLIVEIRA-FILHO, AT., 2006. *Catálogo das árvores nativas de Minas Gerais: mapeamento e inventário da flora nativa e dos reflorestamentos de Minas Gerais*. Lavras: Editora UFLA.
- PEZZINI, FF., BRANDAO, D., RANIERI, BD., ESPÍRITO-SANTO, MM., JACOBI, CM. and FERNANDES, GW., 2008. Polinização, dispersão de sementes e fenologia de espécies arbóreas no Parque Estadual da Mata Seca. *Biota*, vol. 1, p. 37-45.
- PORTILLO-QUINTERO, CA. and SÁNCHEZ-AZOFÉIFA, GA., 2010. Extent and conservation of tropical dry forests in the Americas. *Biological Conservation*, vol. 143, no. 1, p. 144-155. <http://dx.doi.org/10.1016/j.biocon.2009.09.020>.
- PRINGLE, EG., ADAMS, RI., BROADBENT, E., BUSBY, PE., DONATTI, CI., KURTEN, EL., RENTON, K. and DIRZO, R., 2011. Distinct leaf-trait syndromes of evergreen and deciduous trees in a seasonally dry tropical forest. *Biotropica*, vol. 43, no. 3, p. 299-308. <http://dx.doi.org/10.1111/j.1744-7429.2010.00697.x>.
- R DEVELOPMENT CORE TEAM, 2010. *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. Available from: <<http://www.R-project.org>>.
- RASBAND, W., 2006. *ImageJ: image process and analysis in Java*. Bethesda: National Institutes of Health. Available from: <<http://rsb.info.nih.gov/ij>>.
- SALES, HR., SOUZA, SCA., LUZ, GR., MORAIS-COSTA, F., AMARAL, VB., SANTOS, RM., VELOSO, MDM. and NUNES, YRF., 2009. Flora arbórea de uma floresta estacional decidual na APA Estadual do Rio Pandeiros, Januária/MG. *Biota*, vol. 2, p. 31-41.

- SÁNCHEZ-AZOFÉIFA, GA., QUESADA, M., RODRÍGUEZ, JP., NASSAR, JM., STONER, KE., CASTILLO, A., GARVIN, T., ZENT, EL., CALVO-ALVARADO, JC. and KALACSKA, MER., 2005. Research priorities for Neotropical dry forests. *Biotropica*, vol. 37, no. 3, p. 477-485. <http://dx.doi.org/10.1111/j.1744-7429.2005.00066.x>.
- SILVA, JO., JESUS, FM., FAGUNDES, M. and FERNANDES, GW., 2009. Esclerofilia, taninos e insetos herbívoros associados a uma espécie de leguminosa (Fabaceae: Caesalpinioideae) em área de transição Cerrado-Caatinga no Brasil. *Ecologia Austral*, vol. 19, p. 197-206.
- SILVA, JO., ESPÍRITO-SANTO, MM. and MELO, GA., 2012. Herbivory on *Handroanthus ochraceus* (Bignoniaceae) along a successional gradient in a tropical dry forest. *Arthropod-Plant Interactions*, vol. 6, no. 1, p. 45-57. <http://dx.doi.org/10.1007/s11829-011-9160-5>.
- STILING, P. and MOON, DC., 2005. Quality or quantity: the direct and indirect effects of host plants on herbivores and their natural enemies. *Oecologia*, vol. 142, no. 3, p. 413-420. <http://dx.doi.org/10.1007/s00442-004-1739-4>. PMid:15517407
- TURNER, IM., 1994. Sclerophyll: primarily protective? *Functional Ecology*, vol. 8, no. 6, p. 669-675. <http://dx.doi.org/10.2307/2390225>.
- WALTER, J., HEIN, R., AUGÉ, H., BEIERKUHNLEIN, C., LÖFFLER, S., REIFENRATH, K., SCHÄDLER, M., WEBER, M. and JENTSCH, A., 2012. How do extreme drought and plant community composition affect host plant metabolites and herbivore performance? *Arthropod-Plant Interactions*, vol. 6, no. 1, p. 15-25. <http://dx.doi.org/10.1007/s11829-011-9157-0>.
- WHITE, TCR., 1969. An index to measure weather induced stress of trees associated with out-breaks of psyllids in Australia. *Ecology*, vol. 50, no. 5, p. 905-909. <http://dx.doi.org/10.2307/1933707>.

Appendix

Appendix 1. Morphospecies abundance of free-feeding herbivorous insects found on the evergreen tree species *Goniorrhachis marginata* in dry and rainy seasons in a Brazilian tropical dry forest.

Guild	Taxonomic group	Dry season	Rainy season
Leaf-chewing			
	Coleoptera		
	Bruchidae sp.1	11	0
	Bruchidae sp.2	2	0
	Bruchidae sp.3	2	0
	Bruchidae sp.4	2	0
	Bruchidae sp.5	1	0
	Bruchidae sp.6	1	0
	Bruchidae sp.7	1	0
	Bruchidae sp.8	1	0
	Bruchidae sp.9	1	0
	Cerambycidae sp.1	0	1
	Chrysomelidae sp.1	1	0
	Chrysomelidae sp.2	1	0
	Chrysomelidae sp.3	0	1
	Chrysomelidae sp.4	0	1
	Chrysomelidae sp.5	0	1
	Chrysomelidae sp.6	0	1
	Chrysomelidae sp.7	0	1
	Chrysomelidae sp.8	0	1
	<i>Syneta</i> sp.1	1	1
	Curculionidae sp.1	1	0
	Curculionidae sp.2	0	2
	Curculionidae sp.3	0	1
	Curculionidae sp.4	0	1
	Curculionidae sp.5	0	1
	Curculionidae sp.6	0	1
	Tenebrionidae sp.1	2	0
	Tenebrionidae sp.2	0	1
	Orthoptera		
	Tettigoniidae nymph	0	1
Sap-sucking	Hemiptera		
	unidentified nymphs sp.1	0	3
	unidentified nymphs sp.2	1	0
Heteroptera	Pentatomidae sp.1	0	1
	Rophalidae sp.1	0	1
	Tingidae sp.1	0	1
	Tingidae sp.2	12	0
	<i>Tingis</i> sp.1	278	0
Auchenorrhyncha	Unidentified nymph	0	1
	Cicadellidae sp.1	0	1
	Cicadellidae sp.2	0	1
	<i>Agalia</i> sp.1	2	1
	Membracidae sp.1	1	0
	Membracidae sp.2	0	1
	Tropiduchidae sp.1	0	1
Sternorrhyncha	Psyllidae sp.1	54	0
	Psyllidae sp.2	0	1
Total		376	29