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Authors: Leite, Germano Leão Demolin, Veloso, Ronnie Von Dos Santos, Zanuncio, José Cola, Fernandes, Geraldo Wilson, Almeida, Chrystian Iezid Maia, et al.

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SEASONAL ABUNDANCE OF GALLING INSECTS (HYMENOPTERA) ON *CARYOCAR BRASILIENSE* (MALPIGHIALES: CARYOCARACEAE) TREES IN THE CERRADO

Germano Leão Demolin Leite[1*], Ronnie Von Dos Santos Veloso[2], José Cola Zanuncio[2], Geraldo Wilson Fernandes[3], Chrystian Iezid Maia Almeida[1], José Milton Milagres Pereira[2], José Eduardo Serrão[4] and Marcus Alvarenga Soares[5]

[1]Insetário G.W.G. de Moraes, Instituto de Ciências Agrárias, Universidade Federal de Minas Gerais, CP: 135. Montes Claros, MG, Brasil
Endereço eletrônico: gldleite@ig.com.br

[2]Departamento de Entomologia, Universidade Federal de Viçosa, 36571-000, Viçosa, Minas Gerais State, Brazil

[3]Departamento de Biologia Geral, Universidade Federal de Minas Gerais, Belo Horizonte, Minas Gerais State, Brazil

[4]Departamento de Biologia Geral, Universidade Federal de Viçosa, 36571-000, Viçosa, Minas Gerais State, Brazil

[5]Programa de Pós-Graduação em Produção Vegetal, Universidade Federal dos Vales do Jequitinhonha e Mucuri, 39100-000, Diamantina, Minas Gerais State, Brazil

*Corresponding author; E-mail: gldleite@ig.com.br.

Abstract

Caryocar brasiliense Camb. (Malpighiales: Caryocaraceae) trees have a wide distribution in the Cerrado, a tropical Brazilian savanna, with high diversity and endemism. This plant is protected by federal laws and is untouched in deforested areas of the Cerrado. This situation increases the damage to leaves from galling insects (Hymenoptera). We studied populations of galling insects and their natural enemies on *C. brasiliense* trees for 3 successive yr during each season in the Cerrado. A globoid gall-inducing *Eurytoma* sp. (Hymenoptera: Eurytomidae) and its parasitoid *Sycophila* sp. (Hymenoptera: Eurytomidae) adults and predator *Zelus armillatus* (Lepeletier and Serville) (Hemiptera: Reduviidae) on the leaves were most abundant in the winter. The numbers of vein galls correlated negatively with the numbers of discoid and spherical galls, and the numbers of spherical galls correlated negatively with the numbers of discoid galls on *C. brasiliense* leaflets. Increased percentages of defoliation were correlated with reductions in the percentages of leaflets with total galls and leaflet area with total galls. Increased numbers of *Sycophila* sp. and decreased numbers of *Ablerus magistretti* Blanchard (Hymenoptera: Aphelinidae) were correlated with reduction in the numbers of *Eurytoma* sp. Numbers of *Quadrastichus* sp. (Hymenoptera: Eulophidae) and *A. magistretti* correlated negatively with the numbers of *Sycophila* sp. Increased numbers of *Z. armillatus* were correlated with reduction in the numbers of *Eurytoma* sp. and its galls and parasitoids. We concluded that this differential temporal distribution of galling insects and their natural enemies was influenced by plant phenology and time of colonization on *C. brasiliense* leaves.

Key Words: *Eurytoma* sp., *Bruchophagus* sp., natural enemies, seasons, pequi

Resumen

Los árboles de *Caryocar brasiliense* Camb. (Malpighiales: Caryocaraceae) tienen una amplia distribución en lo Cerrado, una sabana tropical de Brasil, con una alta diversidad y endemismo. Esta planta está protegida por las leyes federales y se deja en las áreas deforestadas de lo Cerrado. Esta situación aumenta el daño a las hojas de los insectos que causan agallas (Hymenoptera). Se estudiaron las poblaciones de insectos que causan agallas y sus enemigos naturales de los árboles de *C. brasiliense* durante 3 años sucesivos durante cada temporada en el Cerrado. Agallas globosas inducido por *Eurytoma* sp. y su parasitoide *Sycophila* sp. (Hymenoptera: Eurytomidae) - adultos - y depredador *Zelus armillatus* (Lepeletier and Serville) (Hemiptera: Reduviidae) en las hojas fueron más abundantes en el invierno. El número

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de agallas vena correlacionó negativamente con el número de agallas discoidales y esféricas, así como el número de agallas esféricas correlacionaron negativamente con el número de agallas discoidales en hojas del *C. brasiliense*. El aumento de porcentajes de defoliación se correlacionó con la reducción en los porcentajes de hojas con agallas totales y el área de la hoja con agallas totales. Aumento del número de *Sycophila* sp. y disminución del número de *Ablerus Magistretti* Blanchard (Hymenoptera: Aphelinidae) se correlacionó con la reducción en el número de Eurytoma sp. Números de *Quadrastichus* sp. (Hymenoptera: Eulophidae) y *A. Magistretti* se correlacionó negativamente con el número de *Sycophila* sp.. Aumento del número de *Z. armillatus* se correlacionó con la reducción en el número de *Eurytoma* sp. y sus agallas y parasitoides. Se argumenta que esta distribución diferencial temporal de insectos que causan agallas y sus enemigos naturales se vio influenciado por la fenología de la planta y el tiempo de la colonización en las hojas de *C. brasiliense*.

Palabras Clave: *Eurytoma* sp., *Bruchophagus* sp., enemigos naturales, temporada, pequi

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The Cerrado occupies about 23% of the Brazilian territory (Da Silva & Bates 2002) and is characterized by high diversity of plants and insects and present a high degree of endemism (Bridgewater et al. 2004). Due to increasing threats to is biodiversity the Cerrado has been elected as a biodiversity hotspot (Myers et al. 2000). The Cerrado primary use is for grain and cattle production (Aguiar & Camargo 2004), as well as reforestation with exotic species, primarily *Eucalyptus* (Zanuncio et al. 2002). Through several governmental mechanisms and incentives the Cerrado has been devastated in the last five decades leaving only 20% of the land intact (Klink & Machado 2005). Naturally, the Cerrado is formed by a complex mosaic of phytophysiognomies that range from open Cerrado formations (*campo limpo*) up to tall and woody forests of 10-15 meters high, called *Cerradão* (Oliveira & Marquis 2002). In southeastern Brazil large patches of this rich Cerrado is seen immersed in a matrix of agriculture (primarily soybean and sugar cane), cattle farms and cities (urbanization). This is the case in Montes Claros in northern Minas Gerais state.

Caryocar brasiliense Camb. (Malpighiales: Caryocaraceae) is a flag species of the Cerrado, presents wide distribution (Brandão & Gavilanes 1992; Bridgewater et al. 2004; Leite et al. 2006a) and can reach up to 10 m high while the canopy may reach 6 m wide (Leite et al. 2006a, 2011a, 2012a). The leaves of *C. brasiliense* are alternate, trifoliate and have high trichome density; the flowers are hermaphrodite but mostly cross pollinated. Fruit production is annual, and *C. brasiliense* blooms between Jul and Sep (dry period) with fructification from Oct and Jan (rainy season) (Leite et al. 2006a). The fruit is a drupe with 1-4 seeds, weighing 158.49 ± 8.14 g (fresh weigh) and with a volume of 314.90 ± 20.93 cm^3 (Leite et al. 2006a). Its fruits have an internal mesocarp rich in oil, vitamins, and proteins, and contain many compounds of medicinal importance. Not surprisingly, it is widely used by humans for food, production of cosmetics, lubricants, and in the pharmaceutical industry (Segall et al. 2005; Ferreira & Junqueira 2007; Garcia et al. 2007; Khouri et al. 2007).

This species represents the main source of income of many communities (Leite et al. 2006a). *Caryocar brasiliense* are protected by federal laws and hence are left in deforested areas of the Cerrado**.** Isolated individuals of this plant in the agro-landscape suffer from increased leaf, flower, and fruit damage from insect herbivorous (i.e. Coleoptera, Lepidoptera, and Hemiptera), which affects their natural enemies (i.e. predators) (Leite et al. 2012b, c, d, e). Among these insects, there are four types of galling insects (Hymenoptera) found on the *C. brasiliense* leaves (Leite et al. 2009, 2011c, d, e). These galls, principally galling *Eurytoma* (Eurytomidae), can cause premature leaf abscission when they are found at a high density on *C. brasiliense* seedling and adult plants (Oliveira 1997, Leite et al. 2006b, 2009). But these studies with galling insects on *C. brasiliense* were made with isolated species (no interactions among of them) and not showed the seasonality of these species of galling insects.

In order to better manage and protect the remaining *C. brasiliense* in the wild and on plantations, it is necessary to understand the ecology of the insects that interact with this economically valuable tree. Our objective was to research the seasonality of galling insects (Hymenoptera) and their natural enemies on this tree, in strict sense Cerrado (a species-rich dense scrub of shrubs and trees, 8-10 m high and a dense understory) at Montes Claros in the state of Minas Gerais, Brazil.

Material and Methods

Study sites

The study was done in the municipality of Montes Claros (S 16° 44' 55.6" W 43° 55' 7.3", at 943 m elevation), in the state of Minas Gerais,

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Brazil, during 3 consecutive yr (Jun 2008 through Jun 2011). The region has dry winters and rainy summers, and is classified as climate Aw, i.e., tropical savanna according to Köppen (Vianello & Alves 2000). The area was a strict sense Cerrado having a dystrophic yellow red oxisol with sandy texture, and a density of 13 *C. brasiliense* trees/ha (Leite et al. 2006a, 2011b).

The strict sense Cerrado (a species-rich thicket of shrubs and trees, 8-10 m high with a dense understory) is more typical of the Cerrado than grassland open forms (Ribeiro & Walter 1998; Durigan et al. 2002). Adult trees *C. brasiliense* in the area were 4.07 ± 0.18 m (average ± standard error) in height and crown width of 2.87 ± 0.13 m (Leite et al. 2006a).

Study Design

The design was completely randomized with 27 replicates (1 tree/replicate) in cerrado vegetation. Each month we walked ~600 m in a straight line, and every 50 m we collected data on the *C. brasiliense* tree (producing fruits) in Cerrado vegetation, totalizing 27 trees per month. Despite the 27 trees, we collected data according to this design in 3 consecutive yr to capture the overwhelming majority of species of insects (i.e., rare species), since in a given yr some of them might not occur.

The distribution of galling insects and their galls, predators and parasitoids as well as percentages of defoliation and leaves with galls, numbers of sap sucking hemipterans and leafminers (Lepidoptera) were recorded in 4 fully expanded leaves on each of the 27 *C. brasiliense* trees. This sampling was conducted in the morning (7-11 AM) by direct visual observation every month. Insects were collected with tweezers, brushes, or aspirators and preserved in vials with 70% alcohol for identification by taxonomists. These leaves were collected and transported to laboratory. The dimension of galls was measured using digital caliper. Leaves were scanned and the leaf area was calculated using a computer program, and then we calculated the area of each kind of gall occupied in each leaf. After, these leaves were put inside of a white plastic pot (temperature 25 °C), and we evaluated in each 2 days the emergence of galling insects, parasitoids, hyperparasitoids and inquilines during 30 days in each collected data. The emerged insects were collected and preserved as described above for identification by taxonomists.

TABLE 1. NUMBERS OF GALLING INSECTS (HYMENOPTERA), OTHER INSECTS, NATURAL ENEMIES, AND INQUILINES PER TREE OF *CARYOCAR BRASILIENSE* AT MONTES CLAROS, MINAS GERAIS STATE, BRAZIL, DURING AUTUMN 2008 TO AUTUMN 2011.

Galling insects	Spring	Summer	Autumn	Winter
Eurytoma sp.**	0.29 ± 0.16 B	1.23 ± 0.35 B	1.23 ± 0.60 B	3.49 ± 1.26 A
Bruchophagus sp.[n.s.]	0.000 ± 0.000	0.004 ± 0.003	0.000 ± 0.000	0.000 ± 0.000
Eulophidae[n.s.]	0.006 ± 0.006	0.000 ± 0.000	0.000 ± 0.000	0.001 ± 0.001
Hymenoptera[n.s.]	0.000 ± 0.000	0.082 ± 0.080	0.069 ± 0.069	0.000 ± 0.000
Other herbivore insects				
Hemiptera[n.s.]	0.35 ± 0.12	0.27 ± 0.09	0.30 ± 0.07	0.18 ± 0.05
% of defoliation[n.s.]	4.44 ± 0.66	5.46 ± 0.63	6.06 ± 0.71	3.79 ± 0.63
Leafminers (Lepidoptera)*	0.04 ± 0.01 B	0.07 ± 0.01 AB	0.13 ± 0.03 AB	0.15 ±0.04 A
Natural enemies/inquilines				
Sycophila sp.**	0.02 ± 0.01 B	0.13 ± 0.03 B	0.14 ± 0.05 B	0.60 ± 0.23 A
Ablerus magistretti[n.s.]	0.000 ± 0.000	0.000 ± 0.000	0.003 ± 0.002	0.198 ± 0.198
Total ants*	0.07 ± 0.01 A	0.02 ± 0.01 B	0.06 ± 0.01 AB	0.09 ± 0.02 A
Spiders[n.s.]	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.02 ± 0.02
Holopothrips sp.[n.s.]	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01
*Zelus armillatus***	0.02 ± 0.01 B	0.01 ± 0.01 B	0.02 ± 0.01 B	0.07 ± 0.02 A
Epipolops sp.[n.s.]	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01
Trybonia spp.[n.s.]	0.01 ± 0.01	0.03 ± 0.01	0.08 ± 0.05	0.02 ± 0.01
Quadrastichus sp.[n.s.]	0.002 ± 0.002	0.003 ± 0.002	0.002 ± 0.001	0.212 ± 0.195
Alycaulini[n.s.]	0.000 ± 0.000	0.000 ± 0.000	0.001 ± 0.001	0.000 ± 0.000

Means within a row followed by the same letter (average ± SE) are not different by the test of Tukey (* = $P < 0.01$ and ** = $P < 0.05$). n.s. = not significant by ANOVA ($P > 0.05$).

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TABLE 2. GALLING INSECTS AND THEIR DAMAGE PER TREE OF *CARYOCAR BRASILIENSE* AT MONTES CLAROS, MINAS GERAIS STATE, BRAZIL, DURING AUTUMN 2008 TO AUTUMN 2011.

Insects and theirs damages	Spring	Summer	Autumn	Winter
% of leaflet with total galls n.s.	35.07 ± 4.06	40.26 ± 3.97	36.82 ± 3.95	39.36 ± 4.51
% of leaflet area with total galls n.s.	7.29 ± 3.64	5.08 ± 1.25	7.48 ± 1.96	8.86 ± 2.54
% of leaflet area with discoid galls n.s.	0.01 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.02 ± 0.01
% of leaflet area with vein galls n.s.	0.007 ± 0.003	0.010 ± 0.009	0.001 ± 0.001	0.005 ± 0.003
% of leaflet area with spherical galls n.s.	0.003 ± 0.001	0.000 ± 0.000	0.000 ± 0.000	0.001 ± 0.001
% of leaflet area with globoid galls n.s.	0.09 ± 0.01	0.09 ± 0.01	0.12 ± 0.04	0.15 ± 0.03
% of leaflet area with conglomerate of globoid galls **	7.18 ± 4.05 AB	4.98 ± 1.24 B	7.35 ± 1.94 A	8.68 ± 2.51 A
% of leaflet area with total globoid galls **	7.27 ± 4.05 AB	5.07 ± 1.25 B	7.47 ± 1.96 A	8.83 ± 2.54 A
% of discoid galls/total galls n.s.	5.43 ± 2.15	9.78 ± 2.71	9.18 ± 3.87	12.18 ± 4.36
% of vein galls/total galls n.s.	2.84 ± 1.46	2.44 ± 2.04	0.56 ± 0.45	1.26 ± 0.69
% of spherical galls/total galls n.s.	1.97 ± 1.00	0.52 ± 0.51	0.00 ± 0.00	4.21 ± 3.00
% of globoid galls/total galls n.s.	49.70 ± 3.87	50.86 ± 3.13	52.65 ± 3.18	48.34 ± 3.99
% of conglomerate of globoid galls/total galls n.s.	40.06 ± 3.59	36.40 ± 2.91	37.61 ± 2.77	34.01 ± 3.00
% of total globoid galls/total galls n.s.	89.76 ± 4.44	87.26 ± 3.75	90.26 ± 3.97	82.35 ± 6.04
Number of discoid galls/leaflet n.s.	0.50 ± 0.27	0.31 ± 0.08	0.30 ± 0.18	0.60 ± 0.24
Number of vein galls/leaflet n.s.	0.08 ± 0.04	0.10 ± 0.09	0.02 ± 0.01	0.06 ± 0.03
Number of spherical galls/leaflet n.s.	0.19 ± 0.11	0.02 ± 0.02	0.00 ± 0.00	0.10 ± 0.04
Number of globoid galls/leaflet n.s.	3.93 ± 0.66	3.83 ± 0.65	5.83 ± 2.11	4.12 ± 0.82
Number of conglomerate of globoid galls/leaflet n.s.	2.25 ± 0.37	2.59 ± 0.41	2.68 ± 0.48	2.95 ± 0.56
Number of total globoid galls/leaflet n.s.	6.18 ± 0.97	6.42 ± 1.01	8.51 ± 2.40	7.07 ± 1.35
Area (mm^2) of discoid galls n.s.	2.43 ± 0.37	4.54 ± 0.57	3.62 ± 0.54	3.88 ± 0.71
Area (mm^2) of vein galls n.s.	10.75 ± 3.60	11.42 ± 1.45	8.00 ± 4.00	11.50 ± 2.08
Area (mm^2) of spherical galls n.s.	3.25 ± 1.03	0.79 ± 0.79	0.00 ± 0.00	1.16 ± 0.23
Area (mm^2) of globoid galls **	2.62 ± 0.21 B	2.70 ± 0.24 B	3.02 ± 0.24 AB	4.66 ± 1.02 A
Area (cm^2) of conglomerate of globoid galls n.s.	0.23 ± 0.07	0.18 ± 0.02	0.26 ± 0.04	0.24 ± 0.03
Area (cm^2) of total globoid galls n.s.	0.23 ± 0.07	0.18 ± 0.02	0.27 ± 0.04	0.25 ± 0.03
Length (mm) of conglomerate of globoid galls n.s.	22.07 ± 2.52	22.00 ± 1.97	23.06 ± 2.14	24.05 ± 2.17
Width (mm) of conglomerate of globoid galls**	6.61 ± 0.78 AB	5.61 ± 0.36 B	7.25 ± 0.53 A	7.02 ± 0.60 A

Means within a row followed by the same letter (average ± SE) are not different by the test of Tukey (* = $P < 0.01$ and ** = $P < 0.05$). n.s. = not significant by ANOVA ($P > 0.05$).

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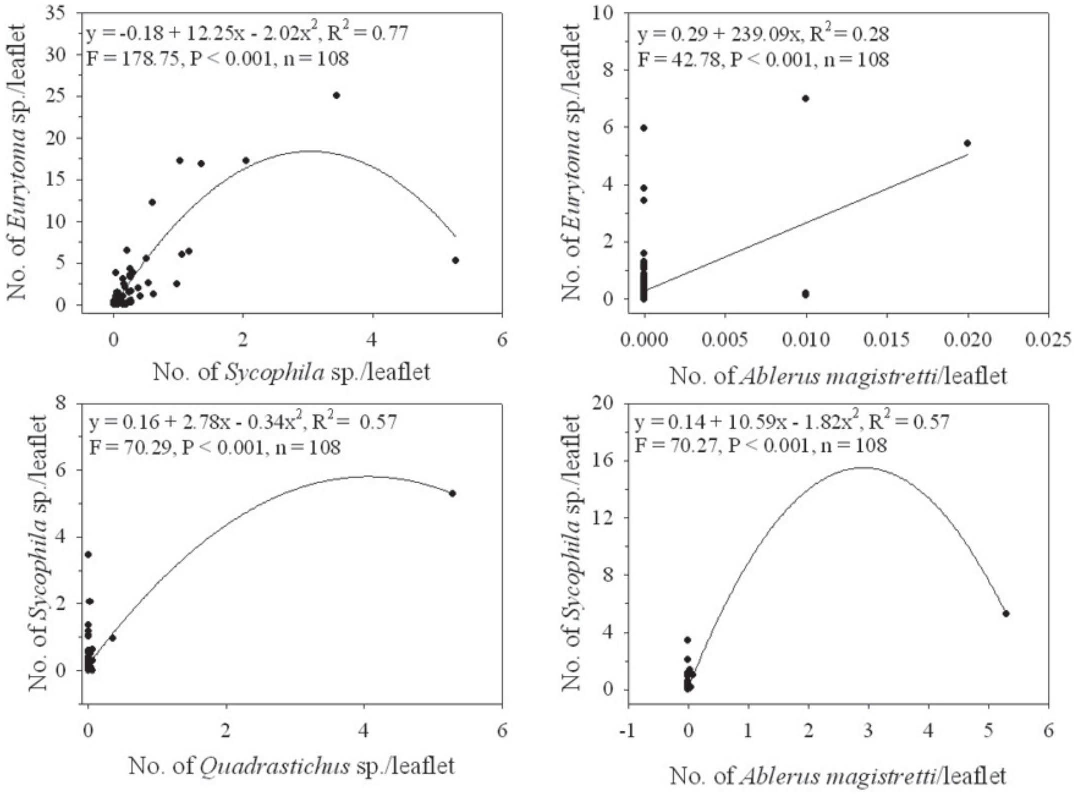

Fig. 1. Relationships between numbers of *Sycophila* sp and *Eurytoma* sp./leaflet; numbers of *Ablerus magistretti* and *Eurytoma* sp. and *Sycophila* sp./leaflet; and numbers of *Quadrastichus* sp. and *Sycophila* sp./leaflet on *Caryocar brasiliense* trees in Montes Claros, Minas Gerais State, Brazil.

Statistical Analyses

Averages were realized reducing the data per tree in each season. Correlations of number of galling insects and their galls with natural enemies, and other groups of herbivores were subjected to analysis of variance (ANOVA) ($P < 0.05$) and simple regression analysis ($P < 0.05$). The effect of the seasons of the yr on the number of galling insects and their galls, natural enemies, and other groups of herbivores (transformed by $\sqrt{x} + 0.5$ or arcsine for percentage data) was tested with ANOVA ($P < 0.05$) with subsequent Tukey's test ($P < 0.05$).

Results

Globoid gall-inducing *Eurytoma* sp. (Hymenoptera: Eurytomidae) adults were most abundant (df = 78, $F = 5.28$, $P < 0.003$) in winter on *C. brasiliense* leaves. However, we did not observe significant differences ($P > 0.05$) among seasons in relation to other galling insect adults as follow: discoid gall-inducing Hymenoptera (not identified), spherical gall-inducing Eulophidae (Hymenoptera), and vein gall-inducing *Bruchophagus* sp. (Hymenoptera: Eurytomidae) (Table 1). Percentages of leaflet areas with conglomerates (df = 78, $F = 3.44$, $P < 0.021$) and total of globoid galls (df = 78, $F = 3.76$, $P < 0.014$) were lowest in the summer. However, we did not observe significant differences ($P > 0.05$) among seasons in relation the percentages of leaflet with total galls; and percentages of leaflet areas with total galls, with discoid galls, with vein galls, with spherical galls, and with globoid galls. For percentages of discoid galls/total galls; vein galls/total galls; spherical galls/total galls; and globoid, conglomerate, and total globoid/total galls were similar ($P > 0.05$) among the seasons of the year. The similar results were observed ($P > 0.05$) in relation the numbers of all kinds of galls per leaflet. The greatest area (mm^2) of globoid galls (df = 78, $F = 2.99$, $P < 0.036$) and lowest width (mm) of conglomerate of globoid galls (df = 78, $F = 3.28$, P

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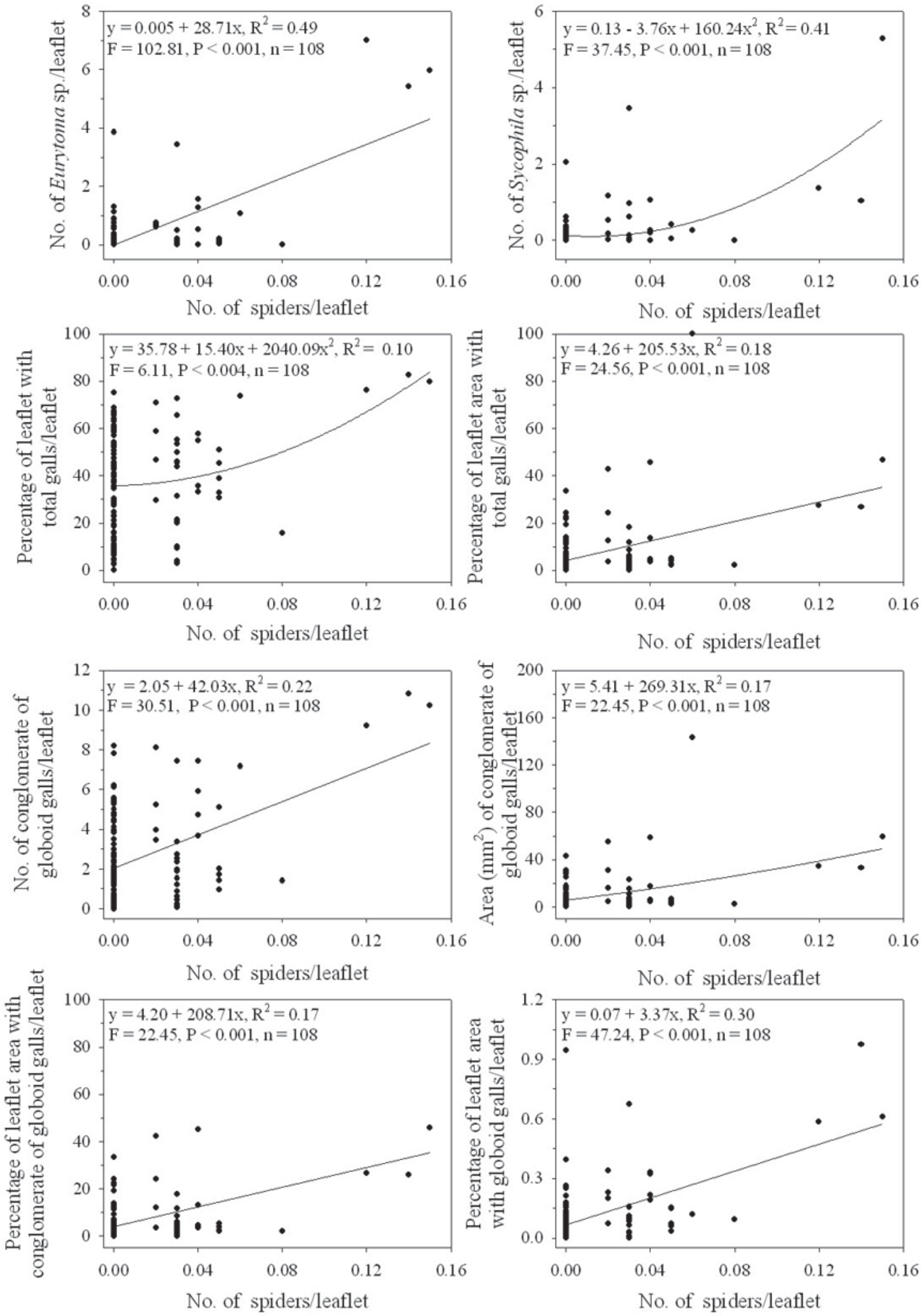

Fig. 2. Relationships between numbers of spiders and *Eurytoma* sp., *Sycophila* sp., and conglomerate of globoid galls/leaflet; numbers of spiders and percentages of leaflet with total galls, leaflet area with total galls, leaflet area with conglomerate of globoid galls, and leaflet area with globoid galls/leaflet; and number of spiders and area (mm^2) of conglomerate of globoid galls/leaflet on *Caryocar brasiliense* trees in Montes Claros, Minas Gerais State, Brazil.

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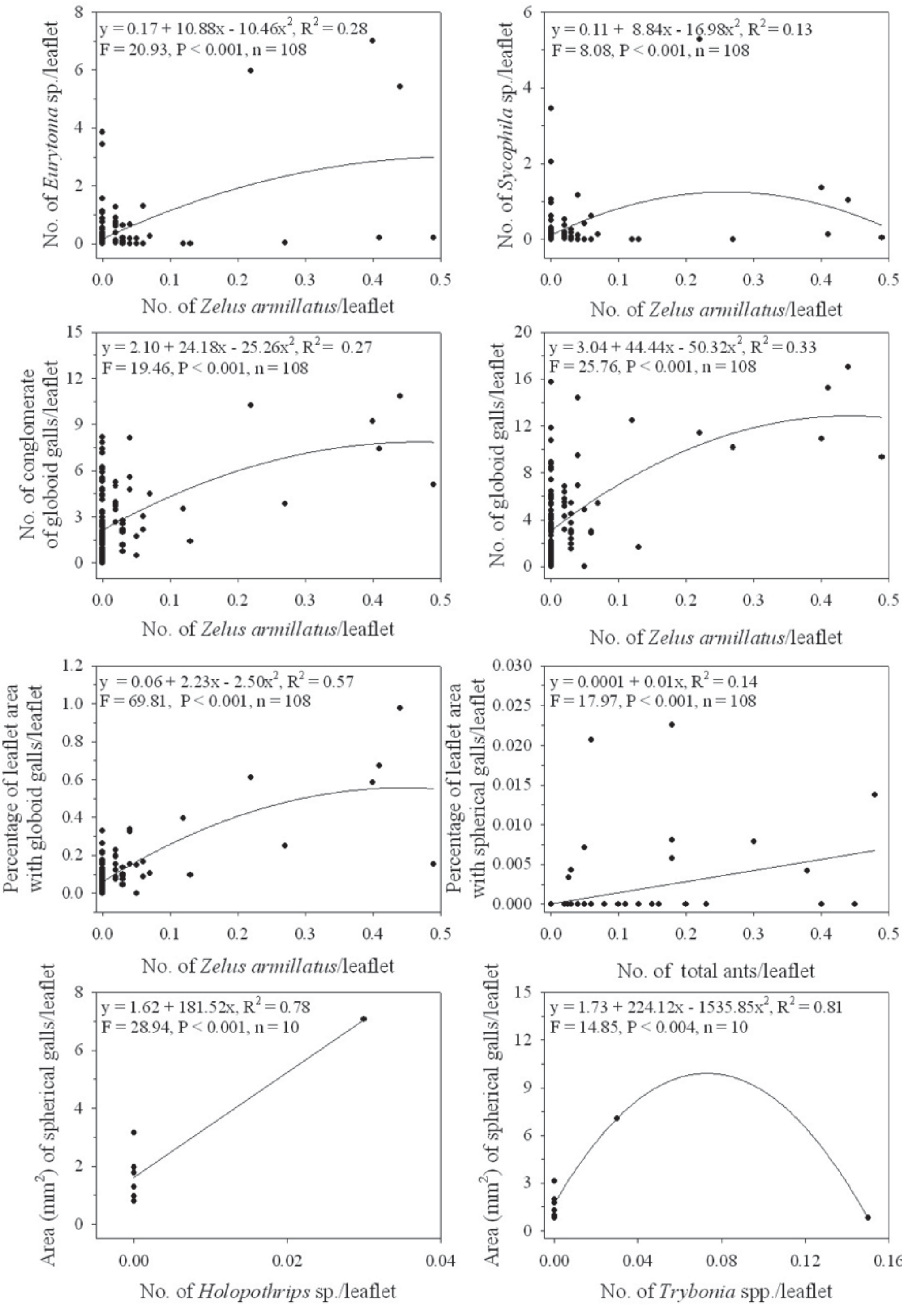

Fig. 3. Relationships between numbers of *Zelus armillatus* and *Eurytoma* sp., *Sycophila* sp., conglomerate of globoid galls, and globoid galls/leaflet; number of *Z. armillatus* and percentage of leaflet area with globoid galls/leaflet; number of total ants and percentage of leaflet area with spherical galls/leaflet; and numbers of *Holopothrips* sp. and *Trybonia* sp. and area (mm^2) of spherical galls/leaflet on *Caryocar brasiliense* trees in Montes Claros, Minas Gerais State, Brazil.

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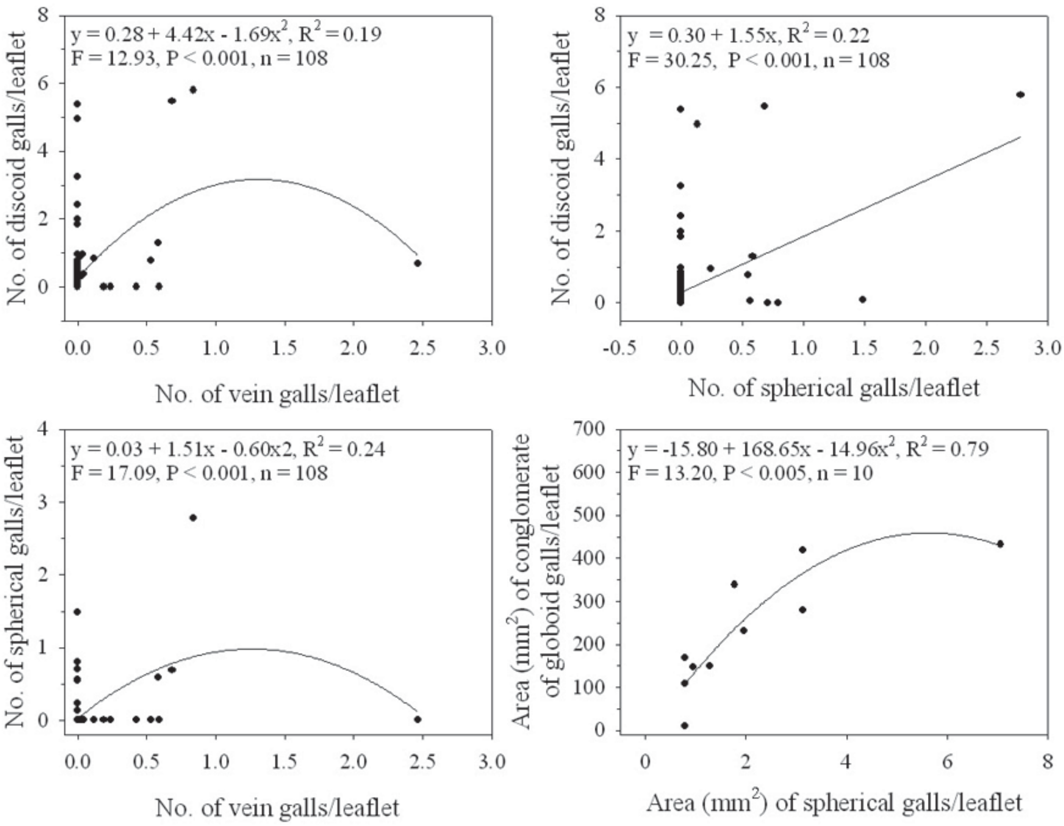

Fig. 4. Relationships between numbers of vein galls and discoid and spherical galls/leaflet; numbers of spherical galls and discoid galls/leaflet; and areas (mm^2) of spherical and conglomerate of globoid galls on *Caryocar brasiliense* trees in Montes Claros, Minas Gerais State, Brazil.

< 0.026) were noted on *C. brasiliense* leaflets in the winter and summer, respectively. However, we did not find significant differences ($P > 0.05$) among seasons of the yr in relation the areas (mm^2) of discoid, vein, spherical, conglomerate and total globoid galls, as well as length (mm) of conglomerate of globoid galls (Table 2). With respect to other herbivore insects, the numbers of individuals sap sucking (Hemiptera) and defoliators – defoliation percent – (Coleoptera and Lepidoptera) were similar ($P > 0.05$) among the seasons of the yr, but lepidopteran leaf miners had lowest (df = 78, $F = 5.85$, $P < 0.002$) numbers in spring (Table 1).

For *Eurytoma* parasitoids, *Sycophila* sp. (Hymenoptera: Eurytomidae) adults were also most abundant (df = 78, $F = 6.49$, $P < 0.001$) in the winter, but differences were not found ($P > 0.05$) for *Ablerus magistretti* Blanchard (Hymenoptera: Aphelinidae). *Quadrastichus* sp. (Hymenoptera: Eulophidae) adults – hyperparasitoids of *Sycophila* sp – and individual adults belonging to the tribe Alycauline (Diptera) – inquiline of *Eurytoma* galls – showed similar numbers ($P > 0.05$) of adults across of the seasons of the yr. For predators, the lowest numbers of total ants, *Crematogaster* sp. and *Pseudomyrmex termitarius* Smith (Hymenoptera: Formicidae), were observed (df = 78, $F = 4.38$, $P < 0.007$) in *C. brasiliense* leaflets in the summer; and *Zelus armillatus* (Lepeletier and Serville) (Hemiptera: Reduviidae) on leaves were most abundant (df = 78, $F = 3.74$, $P < 0.015$) in the winter (Table 1). With respect to other arthropod predators, the numbers of individuals of spiders *Cheiracanthium inclusum* Hentz (Miturgidae) (most frequent); *Peucetia rubrolineata* (Keyserling) (Oxyopidae); *Anelosimus* sp., *Achaearanea hirta* (Taczanowski) (Theridiidae); *Gastromicans albopilosa* Simon, *Chira bicirculigera* Soares and Camargo, *Rudra humilis* Mello-Leitão, *Thiodina melanogaster* Mello-Leitão and *Lyssomanes pauper* Galiano (Salticidae); *Dictyna* sp. and sp.1 (Dic-

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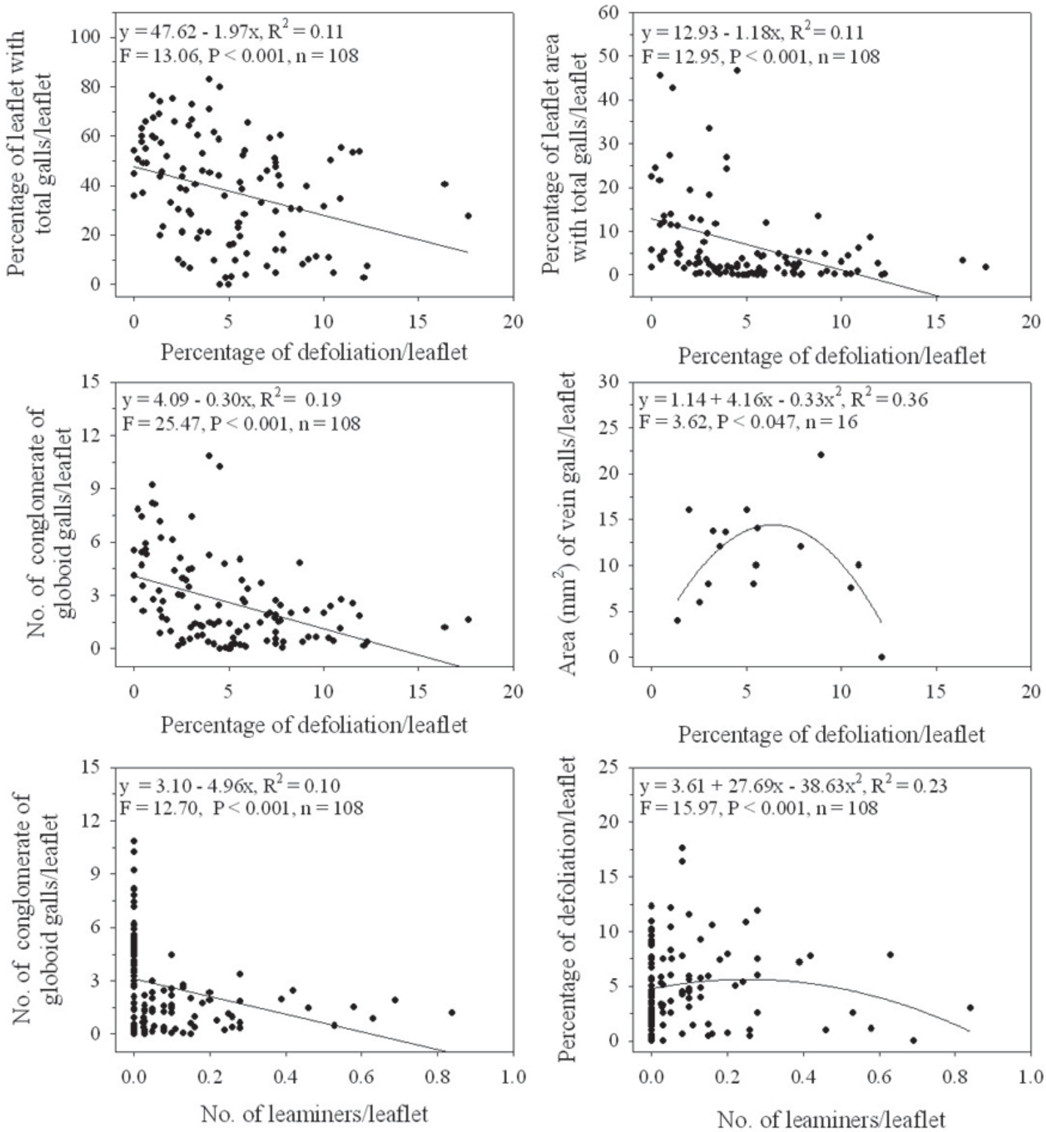

Fig. 5. Relationships between percentages of defoliation and leaflet with total galls and leaflet area with total galls; percentage of defoliation and number of conglomerate of globoid galls and area (mm^2) of vein galls/leaflet; and numbers of lepidopteran leaf miners and numbers of conglomerate of globoid galls and percentage of defoliation on *Caryocar brasiliense* trees in Montes Claros, Minas Gerais State, Brazil.

tynidae); *Tmarus* sp. and sp.1 (Thomisidae); *Argiope argentata* (Fabr.), *Gasteracantha cancriformes*, *Argiope* sp., *Parawixia* sp. and sp.1 (Araneidae); and Anyphaenidae; *Holopothrips* sp., *Trybonia intermedius* Bagnall and *Trybonia mendesi* Moulton (Thysanoptera: Phlaeothripidae); and *Epipolops* sp. (Hemiptera: Geocoridae) on *C. brasiliense* leaflets were similar ($P >$ 0.05) among the seasons of the yr.

Increased numbers of *Sycophila* sp. and decreased numbers of *A. magistretti* were correlated with reduction in the numbers of *Eurytoma* sp. on *C. brasiliense* leaflets. Numbers of *Quadrastichus* sp. and *A. magistretti* correlated negatively with the numbers of *Sycophila* sp. (Fig. 1). Numbers of spiders on *C. brasiliense* leaflets correlated positively with the numbers of *Eurytoma* sp., *Sycophila* sp., and conglomerate of globoid galls; percents of leaflet with total galls, leaflet area with total galls, leaflet areas with conglomerate and globoid galls; and area (mm^2) of conglomerate of globoid galls (Fig.

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2). On the other hand, increased numbers of *Z. armillatus* on *C. brasiliense* leaflets were correlated with reduction in the numbers of *Eurytoma* sp., *Sycophila* sp., conglomerate of globoid galls, and globoid galls per leaflet; and percentage of leaflet area with globoid galls. Numbers of total ants and *Holopothrips* sp. correlated positively with percentage of leaflet area with spherical galls and area (mm^2) of spherical galls, respectively; and *Tyrbonia* spp. correlated negatively with area (mm^2) of this last kind of gall (Fig. 3).

The numbers of vein galls correlated negatively with the numbers of discoid and spherical galls per leaflet as well as the number of spherical galls correlated negatively with the numbers of discoid galls on *C. brasiliense* leaflets. Increased area (mm^2) of spherical galls was correlated with reduction in the area (mm^2) of conglomerate of globoid galls (Fig. 4). Numbers of lepidopteran leaf miners correlated negatively with the numbers of conglomerate of globoid galls per leaflet and percent of defoliation. Increased percentages of defoliation were correlated with reduction in the percents of leaflet with total galls and leaflet area with total galls; numbers of conglomerate of globoid galls per leaflet; and area (mm^2) of vein galls per leaflet (Fig. 5).

Discussion

The higher numbers of *Eurytoma* sp. adults and percentages of leaflet areas with theirs galls as well as lepidopteran leaf miners in the winter were probably due to longer time of exposure of the *C. brasiliense* leaves to the colonization by these herbivorous insects. Greater numbers of globoid, discoid, and vein galls were found in the interior than on the border of the tree crown (Leite et al. 2009, 2011c, d) and these authors suggested that the most distal leaves - interior of the tree crown - (leaves 1 and 2) were too young to be found by the gallers, while leaves 3 and 4 (interior of the tree crown) were exposed to galling insects for a longer period (Leite et al. 2009). Another possibility is a reduction in the number of *C. brasiliense* leaves available due to their gradual loss during the dry period and by the end of the dry season (Leite et al. 2006a), which results in a concentration of herbivore insects per leaf in this plant, such as observed for coleopteran, lepidopteran and hemipteran insects in this plant (Leite et al 2012c,d). The greatest numbers of *Sycophila* sp. and *Z. armillatus*, parasitoids and predators of *Eurytoma* sp., respectively, in the winter probably indicate that their populations depend on their prey and follows those of the galling insects (Oberg et al. 2008; Venturino et al. 2008; Leite et al. 2012d, e).

Caryocar brasiliense loses its leaves in Aug/Sep with new ones in the end of Sep, which is a period without rainfall, strong wind and high sunlight (Leite et al. 2006a). We observed higher numbers of *Eurytoma* sp. and its parasitoid *Sycophila* sp., and discoid galls in Aug; and greater numbers of lepidopteran leaf miners, predators *Z. armillatus* and *Epipolops* sp., and percentage of leaflet with total galls in Sep, a period when *C. brasiliense* trees have old leaves (Leite et al. 2006a). However, lower numbers of herbivorous hemipterans were observed in Sep. On the other hand, in Oct when *C. brasiliense* trees have new leaves (Leite et al. 2006a), higher abundance of sap sucking and vein and spherical galls were observed in this plant, but lower numbers of *Eurytoma* sp. and their galls, *Sycophila* sp., *Trybonia* sp., discoid galls, lepidopteran leaf miners, and percentages of leaflet with total galls, leaflet area with total galls, and defoliation.

We observed a negative correlation between the predator *Z. armillatus* and the parasitoid *Sycophila* sp. with *Eurytoma* sp. These natural enemies can be important in the control of *Eurytoma* sp. on *C. brasiliense* trees (Leite et al. 2007, 2009, 2012e). Positive relationships were found between indole butyric acid (phytohormone) concentrations and successfully induced globoid galls, and also between the number of adults of the galling *Eurytoma* sp. and its major parasitoid, *Sycophila* sp. and the higher concentrations of this hormone on the *C. brasiliense* plants (Leite et al. 2007). These data indicate that the galling insects may select plant modules or plants with higher hormone concentrations and that indole butyric acid may play a role in gall induction (Leite et al. 2007). Further studies are also needed to address hormonal roles in gall formation and their indirect effect on the community of associated parasitoids (Leite et al. 2007). Leite et al. (2012e) asserted that highest number of the predator *Z. armillatus* in *C. brasiliense* trees on the university campus might be due to these trees having more leaves galled by *Eurytoma* sp. than in pastureland and in the Cerrado. *Zelus armillatus* was seen preying upon *Eurytoma* galls, which can colonize up to 70% of the leaf area with galls (Leite et al. 2006b, 2007, 2009). The galls can support higher diversity of natural enemies, and they can cause much mortality—top down impact of natural enemies—(Price et al. 2004; McGeoch and Price 2005; Price 2005).

The decrease in *Eurytoma* galls abundance as numbers another galling insect increased may have resulted from competition among these insects. Almost always galling insects prefer the leaves of *C. brasiliense* that are most exposed to the wind and sunshine and that are on the interior of the branch; and galling insects pre-

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fer the border and median of the leaves (Leite et al. 2009, 2011c, d, e). However, with larger populations of *Eurytoma* sp., other galling insects attack other parts of *C. brasiliense* leaves, and thereby avoid competition. *Eurytoma* sp. seems to be the fastest to colonize plants—being the first to arrive at the plant—and to have greater biotic potential. As for other galls, they only choose areas that are not populated by *Eurytoma* sp. (Leite et al. 2009, 2011c,d,e). *Caryocar brasiliense* trees that were more frequently attacked by *Eurytoma* sp. were rarely colonized by other galling insects. In addition, we observed one *C. brasiliense* tree that was strongly attacked by spherical galls in which *Eurytoma* sp. was not detected, and we observed this tree for 4 yr (unpublished data). Perhaps there is a chemical or visual marker that indicates that a species of galling insect dominates a particular ecological niche (i.e., part of a leaf, branch or even a tree). Another possibility is that there are genetic differences among *C. brasiliense* plants that are responsible for this process or differences in the chemical or morphological composition in different parts of a leaf or in leaves at different positions on a branch, differences in exposure to the sun/wind, or differences in the relationship with other arthropods (i.e., natural enemies).

The decrease in gall abundance as numbers of lepidopteran and coleopteran defoliators and lepidopteran leaf-miners increased may have resulted from competition between the two groups. Also our data suggest competition between lepidopteran leaf miners and defoliators on *C. brasiliense* trees. *Eurytoma* sp. and *A. gossypii* were very abundant on the leaves both of seedlings and adult of *C. brasiliense* trees on the university campus area (Leite et al. 2006b, 2007). The low numbers of coleopteran and lepidopteran defoliators on the university campus may have been caused by competition for food and space with galling insects and aphids in this area (Leite et al. 2012e). Spiders, ants, and *Holopothirps* sp. can reduce defoliation and lepidopteran leaf miners (Leite et al. 2012b, c, d, e), and these factors may favor the colonization of the leaves of this plant by galling insects (free space).

Our data also suggest competition between the *Eurytoma* sp. parasitoids, *A. magistretti* and *Sycophila* sp. for their host, and the negative effect of the possible hyperparasitoid, *Quadrastichus* sp., on its host *Sycophila* sp. However, more research is needed to elucidate this hypothesis. Competition between galls and other phytophagous insects (defoliators, aphids, leafhoppers, miners and mites) and natural enemies shows the importance of this last group on host-plants in the tropics (Morris et al. 2004). The study of food webs is complex due to interactions among host plants, phytophagous insects, predators, parasitoids, and soil and climate conditions (Gratton & Denno 2003). Few studies have examined food webs in complex ecosystems (Gratton & Denno 2003; Morris et al. 2004) such as the Cerrado (Marquis et al. 2001).

The galling insect genus with higher potential to become a pest in commercial *C. brasiliense* plantations is *Eurytoma* because it is the most abundant and causes premature leaf abscission when it is found at a high density on *C. brasiliense* seedling and adult plants (Oliveira 1997; Leite et al. 2006b, 2009). The galling insects were affected by the phenology of the host plant, and by their predators and parasitoids and competition among species of galling insects seems to occur.

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