

Within tree distribution of a discoid gall on *Caryocar brasiliense* (Caryocaraceae)

Distribución de una agalla discoide en el dosel de *Caryocar brasiliense* (Caryocaraceae)

GERMANO LEÃO DEMOLIN LEITE¹, ALINE FONSECA DO NASCIMENTO², FABIENE MARIA DE JESUS¹, SÉRGIO MONTEZE ALVES¹, and GERALDO WILSON FERNANDES²

Resumen: Se evaluó la distribución de agallas discoide en el dosel de *Caryocar brasiliense* en dos áreas de pastos y cerrado. El mayor número de agallas discoide se observó en el cerrado. Más agallas discoide se encuentran en la cara noreste, mientras que menor número se observaron en el follaje hacia el sur en la sabana. Sin embargo, en un potrero, el menor número de agallas discoide se observó en la cara este. Más agallas discoide se encuentran en las hojas de interior de la copa (hojas uno y dos) que en el borde (hojas tres y cuatro), especialmente en la posición de la hoja tres en el cerrado. Hojas de posición tres y cuatro reportan 83,6% de todas las agallas en la muestra. Este insecto cambia su comportamiento en potreros, atacando más en la segunda hoja y en este caso, las hojas de posición tres y cuatro llevaban el 32,8% de todas las agallas en la muestra. En sabana y pastizales se encontraron más agallas discoide en la línea media en comparación con la porción distal y proximal al eje longitudinal de las láminas en una. La agalla discoide prefiere colonizar la parte central de la hoja o cerca de la vena principal de las hojas en toda la región en una pradera. En el cerrado, este insecto sigue la misma tendencia, pero quizás debido a una mayor población, se extendió sobre la hoja.

Palabras clave: Sabana. Insectos agalla. Pequi. Hymenoptera. Competencia.

Abstract. We recorded the discoid gall spatial distribution within *Caryocar brasiliense* trees in two areas of pasture and one of savanna. A higher number of discoid gall/leaflet was observed in savanna than in the pastures. More discoid galls were found on the eastern slope trees followed by the northern slope trees while fewer galls were found on the foliage in the southern slope trees in savanna. However, in the pasture one, the lower discoid galls were observed on the eastern slope. More discoid galls were found on the leaves in the interior (leaves one and two) of the tree crown than at the border (leaves three and four), principally in the leaf position three in savanna. Leaf positions three and four supported 83.6% of all galls sampled. On the other hand, this insect changed its behavior in pasture one, attacking more the second leaf and, in this case, leaf positions three and four supported 32.8% of all galls sampled. More discoid galls were found on the median region compared to the distal and proximal longitudinal regions on leaflet in savanna and in pasture one. The discoid gall insect preferred colonized the central portion than the border portion or near mid vein on transversal regions on a leaflet in the pasture one. In the savanna, followed the same trend, but perhaps due to greater population, the discoid galls have spread more evenly by the leaf of the tree.

Key words: Cerrado. Insect galls. Pequi. Hymenoptera. Competition.

Introduction

Insect galls are known to distribute differentially within host organs. Many galling larva achieve higher density, size, and even higher fitness at the proximal portion compared to more distal portion of the leaf due to be the more rapid and efficient interception of plant photosynthates at the leaf base (Auslander *et al.* 2003; Leite *et al.* 2009). In a similar way, galls are also more abundant and larger at the basal portion of the stems of its host plant perhaps due to stronger sinks in this region of the plant (De Souza *et al.* 2001). On the other hand, more galls of *Eurytoma* sp. (Hymenoptera: Eurytomidae) were found on the median region of the leaf compared to the distal and proximal areas of *Caryocar brasiliense* Cambess. (Caryocaraceae) leaves maybe due to the lower density of trichomes in this portion (Leite *et al.* 2009). Leaf trichomes are known to have a strong influence on the behavior, selection, and fitness of insect herbivores (Agrawal 2004; Leite *et al.* 2009).

Galling larva achieve higher density at leaf margin compared to more central portion of the leaf, like observed for *Eurytoma* sp. galls in leaves of *C. brasiliense* (Leite *et al.* 2009), although the density of trichomes are higher on the leaf margin than on the other transversal leaf portions (Leite

et al. 2009), extra floral nectaries were also mostly frequent on the leaf margins (Rezende 1998). The role of extra floral nectaries on the host plant interaction with galling insects is not well known (Lach and Hoffmann 2011). Otherwise, Leite *et al.* (2009) postulated that they might influence the *Eurytoma* sp. female preference as they may have an indirect positive role in protecting the galling insects against natural enemies by attracting ants. Ants were reported to be associated with extra floral nectaries of *Caryocar* (Oliveira 1997) and in the studied plants they were commonly seen associated with the leaf extra floral nectaries.

The position of the leaves in the stems can also affect the colonization of gall insects. More *Eurytoma* sp. galls were found on the leaves of *C. brasiliense* in the interior of the tree crown than at the border, i.e. leaf positions three and four supported 66.7% of all galls sampled (Leite *et al.* 2009). Several mechanisms may influence the trend found. First, differential mortality caused by parasitoids, predators, and even differential plant resistance could diminish the galling success on the more proximal region of the stems (Leite *et al.* 2009). Even if females prefer leaves at the border, stronger selective pressures would impair their success at such habitat (Leite *et al.* 2009). An alternative hypothesis is that the most distal leaves (leaves one and two) were too young to be found by

¹ Insetário G.W.G. de Moraes, ICA/UFMG, CP: 135. Montes Claros, MG, Brasil. Endereço eletrônico: gldleite@ig.com.br. Autor para correspondência. D.Sc., M.Sc., D.Sc., and M.Sc., respectively. ² Ecologia Evolutiva & Biodiversidade/DBG/UFMG, Belo Horizonte, MG, Brasil. PhD.

the galling insects while leaves three and four were exposed to galling for a longer period (Leite *et al.* 2009). The last hypotheses can explain this trend is the microclimatic differences between the interior of the tree crown and the border.

Insect galls may also distribute differentially between habitats as well as within the host crown. Plants in sunny habitats are known to support higher density of galls compared to plants in shaded habitats (Fernandes and Price 1992; Auslander *et al.* 2003; Leite *et al.* 2009) due to sun exposure may influence the quality of the host plant tissue as well as the gall tissue or even the plant ability to find and elicit induced responses to the invading organism (Fernandes *et al.* 2000, 2005). Furthermore, natural enemies could also be strong selective forces against galling on more favorable, shaded habitats (Fernandes and Price 1992). Therefore, differential selection could lead to female preference and larval fitness for foliage in sunny habitats. More *Eurytoma* sp. galls were found on the eastern slope tree compared to the other slopes tree while fewer galls were found on the foliage in the northern slope of *C. brasiliense* tree maybe due to the dispersion by winds (Leite *et al.* 2009). These authors postulated that the foliage on the eastern slope of the host trees are the most exposed to higher winds and strong sunlight in the South Hemisphere.

Caryocar brasiliense Camb. (Caryocaraceae) is one of the most common and important plant species in the dry and harsh semi arid vegetation of Brazil, called cerrado (Leite *et al.* 2006). It is host to a large number of invertebrate and vertebrate herbivores (Oliveira 1997; Leite *et al.* 2011) as the gall insects (Oliveira 1997; Leite *et al.* 2009), showing four species of leaf galls in the cerrado of northern Minas Gerais State, Brazil.

In an effort to initiate ecological studies in this system, we obtained the first data on spatial distribution of a discoid galling insect (Hymenoptera) (Fig. 1) at the tree level aimed at sampling because this plant has been domesticated for future commercial plantations. This gall is discoid with 3.70

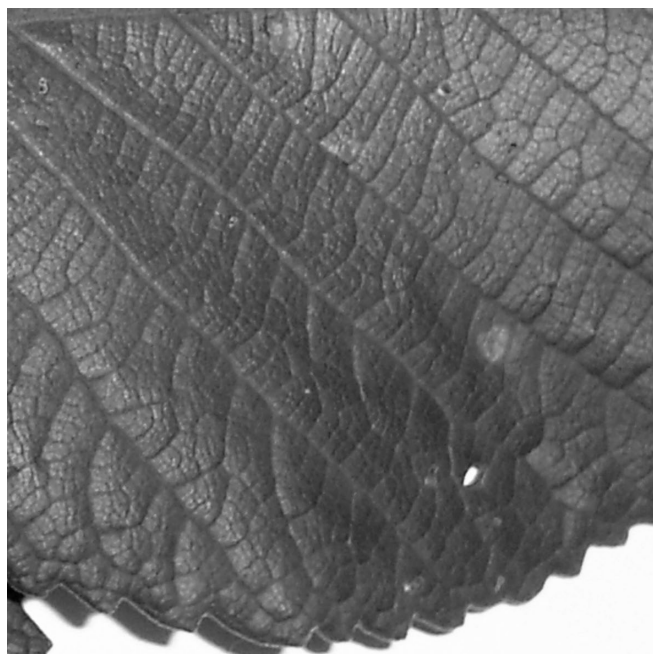


Figure 1. Discoid galls on *Caryocar brasiliense* leaflet.

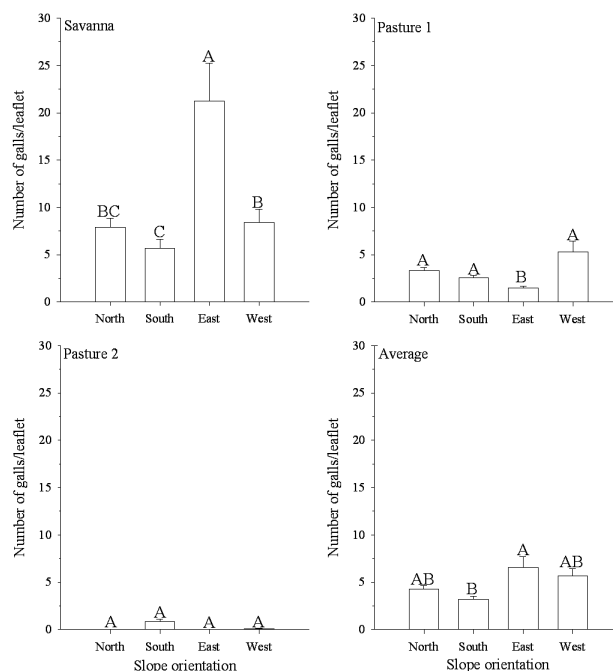


Figure 2. Number of discoid galls induced according to stem orientation on *Caryocar brasiliense* leaves. Averages followed by the same letters did not differ statistically at $P < 0.05$ (Tukey test). The bars represent the standard error.

mm² of diameter and 0.57 mm of height, without hairs, its color is light green, and located between the leaf veins (Fig. 1). As *C. brasiliense* has three leaflet compound leaves we firstly asked whether gall abundance would differ among the leaflets on a single leaf. Second, we studied the effect of foliage slope orientation on gall abundance. A third analysis addressed the distribution of the galls on the leaves along the host stem (within tree). Fourthly, because the grouping of galls on a given leaf portion may indicate site preference, we analyze the within leaf (longitudinal) distribution of galls, and addressed the transversal zonation of discoid galls within leaves. Finally we studied the differences among areas of pasture and savanna.

Material and Methods

This work was developed in one savanna and two pastures (prior savanna) of the Municipality of Montes Claros, Minas Gerais State, Brazil in April, June, August and October 2006, where the average temperatures were 22.5, 19.0, 22.3 and 23.5°C; air relative humidity 80.0, 68.0, 54.0 and 78.0%, month round accumulated precipitation of 211.5, 0.3, 3.8 and 279.0mm; winds prevailed from the northeast at an average speed of 1.60, 1.70, 2.10 and 2.0m/s; insolation 7.21, 8.3, 9.4 and 4.7h, respectively, obtained from the main climate station of Montes Claros of the “Estação Nacional de Meteorologia” (see Leite *et al.* 2006). The north of Minas Gerais State has a climate Aw: tropical of savanna, according to the classification of Köppen, with dry winter and rainy summer (Vianello & Alves 2000). The areas studied were: savannah vegetation *stricto sensu*, pasture 1 (in activity) and pasture 2 (abandoned pasture = savanna in recovery). These areas show different characteristics of soil and floristic diversity. The geographical coordinates, altitude, soil type, physiochemical characteris-

tics of the soil, floristic density, height and width of the crown as well as diameter at breast height of *C. brasiliense* were published in Leite *et al.* (2011).

As the discoid gall density on *C. brasiliense* leaves is highly variable among trees - (data not published), we chose 10 trees per area that had the discoid gall infestation. To evaluate the distribution of discoid galls within the tree crown we recorded the number of galls on the compound leaves of *C. brasiliense* of four randomly selected stems positioned on north, south, east, and west slope trees of ten adult trees per area. To evaluate the distribution of discoid galls among the leaflets we recorded: i) gall abundance according to foliage orientation (slope); ii) the differential abundance of galls on the right, central and left leaflets (Leite *et al.* 2009); iii) gall abundance on the distal, median, and proximal region of a leaflet (see Leite *et al.* 2009); iv) gall abundance on the leaflet border, central area, and adjacent to the mid leaf vein of the leaflet (Leite *et al.* 2009), and v) difference among areas. 1.269 leaflets of 423 leaves in savanna, 3.030 leaflets of 1010 leaves in pasture 1 and 2.613 leaflets of 432 leaves in pasture 2 were censused for discoid galls.

All data were transformed to $\sqrt{x} + 0.5$ and were analyzed by analysis of variance and followed by the Tukey test at the significance level $P < 0.05$.

Results and Discussion

The higher number of discoid galls was observed in savanna (10.86 ± 1.17 A - Tukey test), followed by pasture one (3.17 ± 0.31 B) and pasture two (0.23 ± 0.08 C) ($F=76.955$; $df=1563$; $P < 0.001$). The pasture one (in activity) has less floristic diversity (< trees, groves, shrubs and herbs) and more soil covering by grass than pasture two - savanna in recovery - and

savanna, without differences between last two areas (Leite *et al.* 2011). Savanna has less *C. brasiliense* per hectare than the pastures and these trees are higher in pasture one than other areas (Leite *et al.* 2011). In addition, the soils in the pasture one and savanna are more acid, pasture one is richer in aluminum and sum of bases and less sandy than the other areas (Leite *et al.* 2011). Perhaps these variables can explain the difference in density of the discoid gall among savanna and pastures studied (Fernandes and Price 1988, 1992; Gonçalves-Alvim and Fernandes 2001; Fernandes *et al.* 2005). With the increase in the floristic diversity increases the diversity of leaf galls species (total four species) on *C. brasiliense* as well as increased the density of other galls while decreases that of *Eurytoma* sp. (Hymenoptera: Eurytomidae), the most abundant species (unpublished data). Moreover, in the pasture one had more galls of *Eurytoma* sp. (~ 3 /leaflet) than the savanna (~ 0.8 /leaflet) (unpublished data) and pasture two ~ 0.3 /leaflet, (Leite *et al.* 2009). Maybe this fact is due to a competition between discoid gall and *Eurytoma* sp. explaining why we observed more discoid gall in savanna than in the pastures.

We did not find significant differences in the distribution of discoid galls in pasture two ($P > 0.05$) according to slope orientation of the tree crown, leaf position in the branches, longitudinal and transversal regions on a leaflet on *C. brasiliense* (Figs. 2-6) probably due to the low density of this gall in this area. On the other hand, more discoid galls were found on the eastern slope tree followed the northern slope tree while fewer galls were found on the foliage in the southern slope tree in savanna ($F=8.477$; $df=408$; $P < 0.001$), and in the pasture one, the lower discoid galls were observed on the eastern slope tree ($F=8.076$; $df=1004$; $P < 0.001$) (Fig. 2). Leite *et al.* (2009) observed more *Eurytoma* sp. galls on

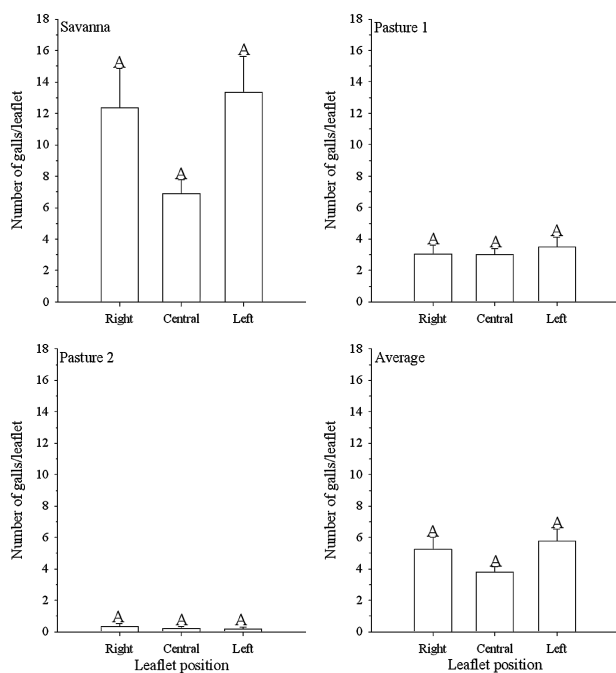


Figure 3. Number of discoid galls induced according to position leaflet on *Caryocar brasiliense* leaves. Averages followed by the same letters did not differ statistically at $P < 0.05$ (Tukey test). The bars represent the standard error.

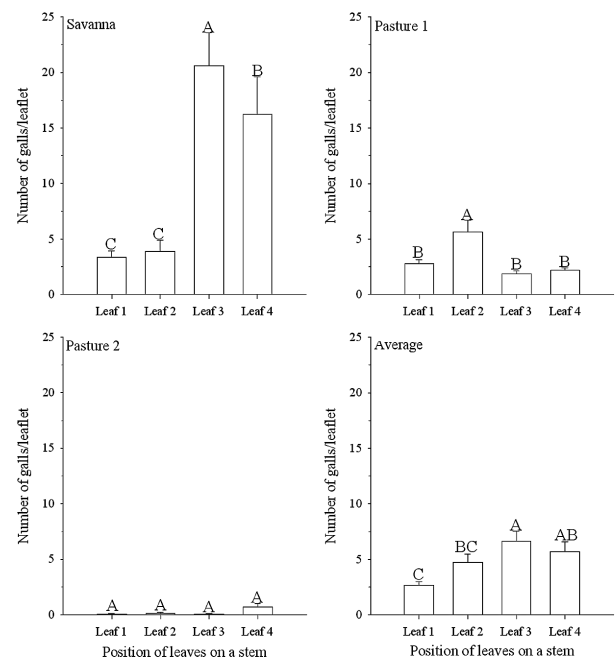


Figure 4. Number of discoid galls induced according to position leaves on *Caryocar brasiliense* stem. Averages followed by the same letters did not differ statistically at $P < 0.05$ (Tukey test). The bars represent the standard error.

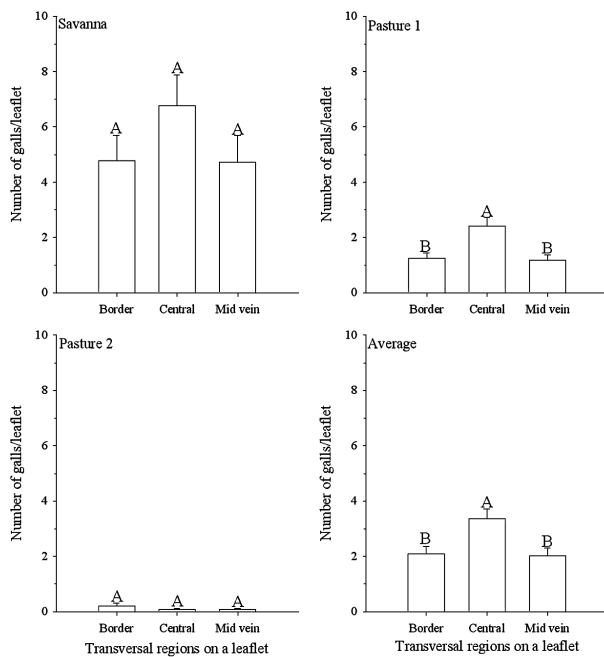


Figure 5. Number of discoid galls induced according to transversal regions on *Caryocar brasiliense* leaflet. Averages followed by the same letters did not differ statistically at $P < 0.05$ (Tukey test). The bars represent the standard error.

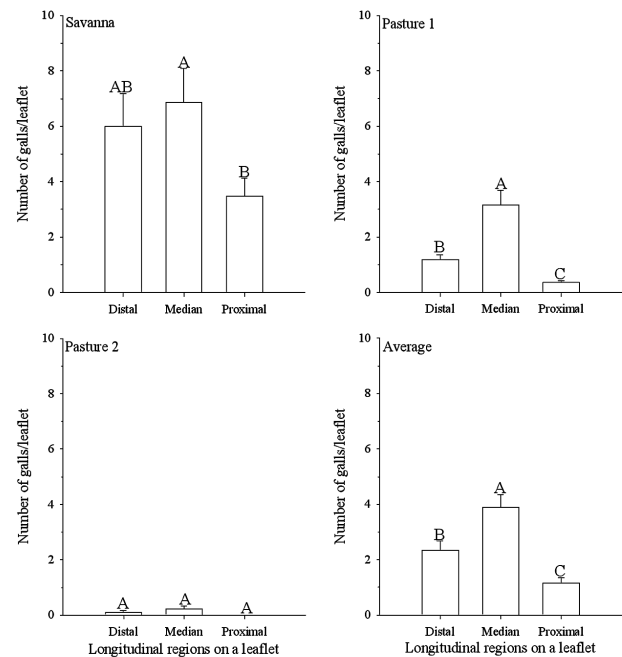


Figure 6. Number of discoid galls induced according to longitudinal regions on *Caryocar brasiliense* leaflet. Averages followed by the same letters did not differ statistically at $P < 0.05$ (Tukey test). The bars represent the standard error.

the eastern slope tree compared to the other slopes tree while fewer galls were found on the foliage in the northern slope of *C. brasiliense* tree maybe due to the dispersion by winds. Leite *et al.* (2009) postulated that the foliage on the eastern slope of the host trees are the most exposed to higher winds and strong sunlight, since prevalent winds in the region are northeaster/eastern (Leite *et al.* 2006), corroborating previous findings in which galling insects are most abundant on sunlight-exposed foliage (Fernandes and Price 1988). Why did the discoid gall show different behaviors in the savanna and pasture one? Perhaps the answer is to avoid competition with the major galling insect on *C. brasiliense* leaves, the *Eurytoma* sp.

The average number of discoid galls did not differ statistically among the three leaflets of *C. brasiliense* in the three areas studied ($P > 0.05$) (Fig. 3). The same result was obtained by Leite *et al.* (2009) with *Eurytoma* sp.. More discoid galls were found ($F=45.508$; $df=408$; $P < 0.001$) on the leaves in the interior of the tree crown than at the border, principally in the leaf position three in savanna. Leaf positions three and four supported 83.6% of all galls sampled (Fig. 4). On the other hand, this insect changed its behavior in the pasture one, attacking more ($F=7.679$; $df=1004$; $P < 0.001$) the second leaf and, in this case, leaf positions three and four supported 32.8% of all galls sampled (Fig. 4), maybe avoiding or reducing the competition with *Eurytoma* sp., since this last gall insect were found on the leaves of *C. brasiliense* in the interior (leaf three and leaf four) of the tree crown than at the border (Leite *et al.* 2009), being in higher population in pasture one than in savanna (unpublished data). Several mechanisms may influence the trend found in the case of *Eurytoma* sp.. First, differential mortality caused by parasitoids, predators, and even differential plant resistance could diminish the galling success on the more proximal region of the stems (Leite *et al.*

2009). Even if females prefer leaves at the border, stronger selective pressures would impair their success at such habitat (Leite *et al.* 2009). An alternative hypothesis is that the most distal leaves (leaves one and two) were too young to be found by the galling insects while leaves three and four were exposed to galling for a longer period (Leite *et al.* 2009). The last hypotheses can explain this trend is the microclimatic differences between the interior of the tree crown and the border.

More discoid galls were found on the median region compared to the distal and proximal longitudinal regions on leaflet in savanna ($F=5.155$; $df=414$; $P < 0.001$) and in pasture one ($F=58.831$; $df=1006$; $P < 0.001$) (Fig. 5). Similar results were observed for galls of *Eurytoma* sp. maybe due to the lower density of trichomes in this portion (Leite *et al.* 2009). Leaf trichomes are known to have a strong influence on the behavior, selection, and fitness of insect herbivores (Agrawal 2004). Many galling larva achieve higher density, size, and even higher fitness at the proximal portion compared to more distal portion of the leaf or stems because in these areas are more rapid and efficient interception of plant photosynthates, being stronger sinks (De Souza *et al.* 2001; Auslander *et al.* 2003).

The discoid gall insect preferred colonized ($F=31.855$; $df=1005$; $P < 0.001$) the central portion than the border portion or near mid vein on transversal regions on a leaflet in the pasture one (Fig. 6). In the savanna, followed the same trend ($F=3.498$; $df=409$; $P=0.03$), but perhaps due to greater population, the discoid galls have spread more evenly by the leaf of the tree (Fig. 6). Leite *et al.* (2009) postulated that extra floral nectaries, mostly frequent on the leaf margins (Rezende 1998), might influence the *Eurytoma* sp. female preference as they may have an indirect positive role in protecting the galling insects against natural enemies by attracting ants. Ants

were reported to be associated with the leaf extra flora nectaries of *C. brasiliense* (Oliveira 1997) and in the studied plants they were commonly seen associated with the leaf extra floral nectaries (Lach and Hoffmann 2011). The preference of the discoid gall insect attacks the central portion of leaflet than the border portion, where has extra floral nectaries and ants (less natural enemies) maybe due to the higher number of *Eurytoma* sp. galls, principally in pasture one (unpublished data), in the border portion of leaflets (Leite *et al.* 2009), avoiding or reducing the competition with *Eurytoma* sp.

Conclusions

Some mechanisms may influence the fitness of discoid gall in *C. brasiliense* trees. Discoid galls are most abundant in the foliages most exposed to higher winds and strong sunlight (stressed micro area). This galling insect prefers to attack the leaves in the interior of the tree crown than at the border maybe due to natural enemies, differential plant resistance, time of colonization, and microclimatic differences between these parts of the tree crown. Trichomes and competition with others galling insects can effect the colonization of discoid gall because it occurs more on the median region of leaflet where less density of trichomes and *Eurytoma* sp. has.

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