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ARTICLE

Differential distribution of *Jatrophobia brasiliensis* (Diptera, Cecidomyiidae) on *Manihot caerulenses* (Euphorbiaceae) in edge and interior environments in a cerrado in Brazil

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Abstract. In the present study we tested whether the distribution of insect galls induced by *Jatrophobia brasiliensis* (Rübsaamen, 1907) (Diptera, Cecidomyiidae) on *Manihot caerulenses* (Euphorbiaceae) differs between edge and interior environments in a Neotropical savanna in Brazil. We tested the hypothesis that the abundance of galls is higher in the vegetation edge, which is exposed to constant dust from an unpaved road, than in the interior of the savanna, where the penetration of dust is smaller. The study was in the Parque Estadual da Serra do Cabral where 28 plants were sampled, being selected 14 plants inside the vegetation and 14 plants on the road edge. We sampled a total of 269 galls of *Jatrophobia brasiliensis,* being 203 galls on edge plants and 66 galls on interior plants. Corroborating our expectation, we registered a higher number of insect galls on the edge plants than interior plants. We suggest that dust is the main stressor in border environments of Neotropical savannas, unlike forest vegetation, where microclimatic changes can be more important. Our findings suggest that the environmental changes caused by dust deposition in the edge affect the distribution of insect galls in Neotropical savannas.

Keywords. Anthropization; Bioindicators; Galling insects; Gall-midges; Habitat modification.

INTRODUCTION

Several studies have reported that gall-inducing insects have their distribution affected by environmental and climatic characteristics of habitats (Price *et al.,* 1998; Gonçalves-Alvim & Fernandes, 2001; Cuevas-Reyes *et al.,* 2011; Jesus *et al.,* 2012; Kelch *et al.,* 2016; Julião *et al.,* 2017). For example, the classic hypothesis of the hygrothermal stress of the environment predicts a higher occurrence of gall-inducing insects in stressed habitats and with greater environmental severity (Fernandes & Price, 1988). Testing this hypothesis, many studies have found greater abundance and species richness of gall-inducing insects in xeric vegetation when compared to mesic vegetations (Price *et al.,* 1998; Wright & Samways, 1998; Gonçalves-Alvim & Fernandes, 2001; Cuevas-Reyes *et al.,* 2004; Julião *et al.,* 2014). Going in the same direction there is some evidence that the anthropogenic stress caused by the opening of the vegetation, also called the edge effect, can affect the distribution of gall-inducing insects (Araújo *et al.,* 2011; Araújo & Espírito-Santo Filho, 2012; Toma *et al.,* 2014; Altamirano *et al.,* 2016; Kelch *et al.,* 2016).

A metanalytical analysis has shown that habitat fragmentation and the edge effect have negative effects on the abundance and species richness of

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distinct guilds of herbivorous insects (Rossetti *et al.,* 2017). On the other hand, for gall-inducing insects some empirical studies have shown that these insects can benefit from the environmental stress of edge environments (Araújo & Espírito-Santo Filho, 2012; Maldonado-López *et al.,* 2015; Altamirano *et al.,* 2016). The main explanation for this is that in border environments, plants undergo physiological changes that modify the allocation of resources and induce the production of defense compounds (Araújo *et al.,* 2011). Gall-inducing insects can benefit from these physiological changes as they have the ability to sequester nutrients and defense compounds in gall tissue and use them for nutrition and protection against natural enemies, respectively (Cuevas-Reyes *et al.,* 2014; Hall *et al.,* 2017). The edge effect acting on gall-inducing insects is more frequent in fragments of forest vegetation (review in Toma *et al.,* 2014), being scarce the evidence about existence of an edge effect influencing the distribution of gall-inducing insects in fragmented open vegetation, such as Neotropical savannas.

In forest environments the plant edge stress can be induced by microclimatic changes such as diminution of water availability and increment in the temperature (Murcia, 1995). This occurs because the border of a forest fragment is exposed to an open matrix that interferes with the environmental dynamics of the outer layers of the forest (Wirth *et al.,* 2008). These factors tend not to be important in open vegetation because the absence of a closed canopy makes the vegetation as a whole exposed to conditions of high insolation (Mendonça *et al.,* 2015). On the other hand, a factor that can be quite important at the edges of open vegetation is dust (Farmer, 1993), which tends to penetrate far more open vegetation than in forests (Supe & Gawande, 2013). Dust is an important stressor for plants of savannas (Ndibalema *et al.,* 2008) because may affect evapotranspiration, photosynthesis, and the penetration of gaseous pollutants (Farmer, 1993). In this sense, plants exposed to constant sources of dust, such as unpaved roads, tend to have their physiological dynamics altered, which can also affect their interactions as insects that use their resources (Reis *et al.,* 2013; Waser *et al.,* 2017).

In the present study, we tested whether the distribution of gall-inducing insects differs between edge and interior environments in a Neotropical savanna area in Brazil. For this we sampled insect galls induced by *Jatrophobia brasiliensis* (Rübsaamen, 1907) (Diptera, Cecidomyiidae) on host plants of *Manihot caerulenses* (Euphorbiaceae). In this way, we tested the hypothesis that the abundance of galls on the plants located at the edge of the vegetation, which is exposed to constant dust from an unpaved road, is greater than in the interior of the savanna, where the penetration of dust is smaller.

MATERIAL AND METHODS

Study area

The study was conducted in an area of Neotropical savanna (*i.e.,* cerrado *sensu stricto*) in the Parque Estadual Serra do Cabral, localized between the municipalities of Buenópolis and Joaquim Felício, northern of Minas Gerais, Brazil (Fig. 1). The climate of the region (*Aw* of Köppen) has dry winters and wet summers, with mean annual precipitation is 1,000 mm, and mean annual temperature is 23.2°C (Alvares *et al.,* 2013). The park presents an area of 250,000 ha, with an altitudinal ranging from 600 m to 1,385 m. Most of park area is composed by savanna and grassland vegetation, but other phytophysiognomies also occurs in the area, such as dry forest (semidecidual forest) and flooded vegetation (vereda) (Fig. 1). The studied Neotropical savanna (17°43′13.08″S, 44°11′25.80″W, 1,045 m) is characterized by dense tree-shrub strata with plants with crooked, woody, and sloping stems (Ribeiro & Walter, 2008), composed mainly by grasses (Poaceae) and tree species from Fabaceae, Vochysiaceae and Bombacaceae families.

Field sampling

Sampling was performed in the July of 2019 on 28 individuals of *Manihot caerulenses* distributed in the study area (Fig. 1A). Were selected randomly 14 plants inside the vegetation (located between 100 m and 120 m from the road) (Fig. 1B) and 14 plants on the edge (located in the first 5 m on the edge of the road) (Fig. 1C). Plants located inside the vegetation had clean leaves (Fig. 1D), while on the roadside the plants were dirty and had a large dust cover (Fig. 1E). In each of the selected plants, three branches were randomly sampled, which were sent to the laboratory, where were counted the number of leaves and the number of galls. Galls induced by gall-midge *Jatrophobia brasiliensis* on *Manihot caerulenses* (Fig. 1F) are characterized by cylindrical shape, color ranging between green and brown, and size of approximately 3 mm in width and 8 mm in length (Durães & Araújo, 2020).

Statistical analyses

We used the number of galls as a measure of abundance of *Jatrophobia brasiliensis* per plant in the edge and interior environments. A generalized linear model was constructed using the type of environment (edge vs. interior), number of leaves on the branch and interaction between these two variables as explanatory variables for the abundance of galls. The number of leaves per branch was used in order to control the effect of the number of resources that is an important factor for the distribution of insect galls (review in Cornelissen *et al.,* 2008). For distribution of errors, we checked for overdispersion in the data and used the family Poisson. Chi-square tests and *p*-values were calculated using the *Anova* function in the package *car* in the R software version 4.3.1 (R Development Core Team, 2023).

RESULTS

A total of 269 galls of *Jatrophobia brasiliensis* were collected from the 28 plants of *Manihot caerulenses,* being

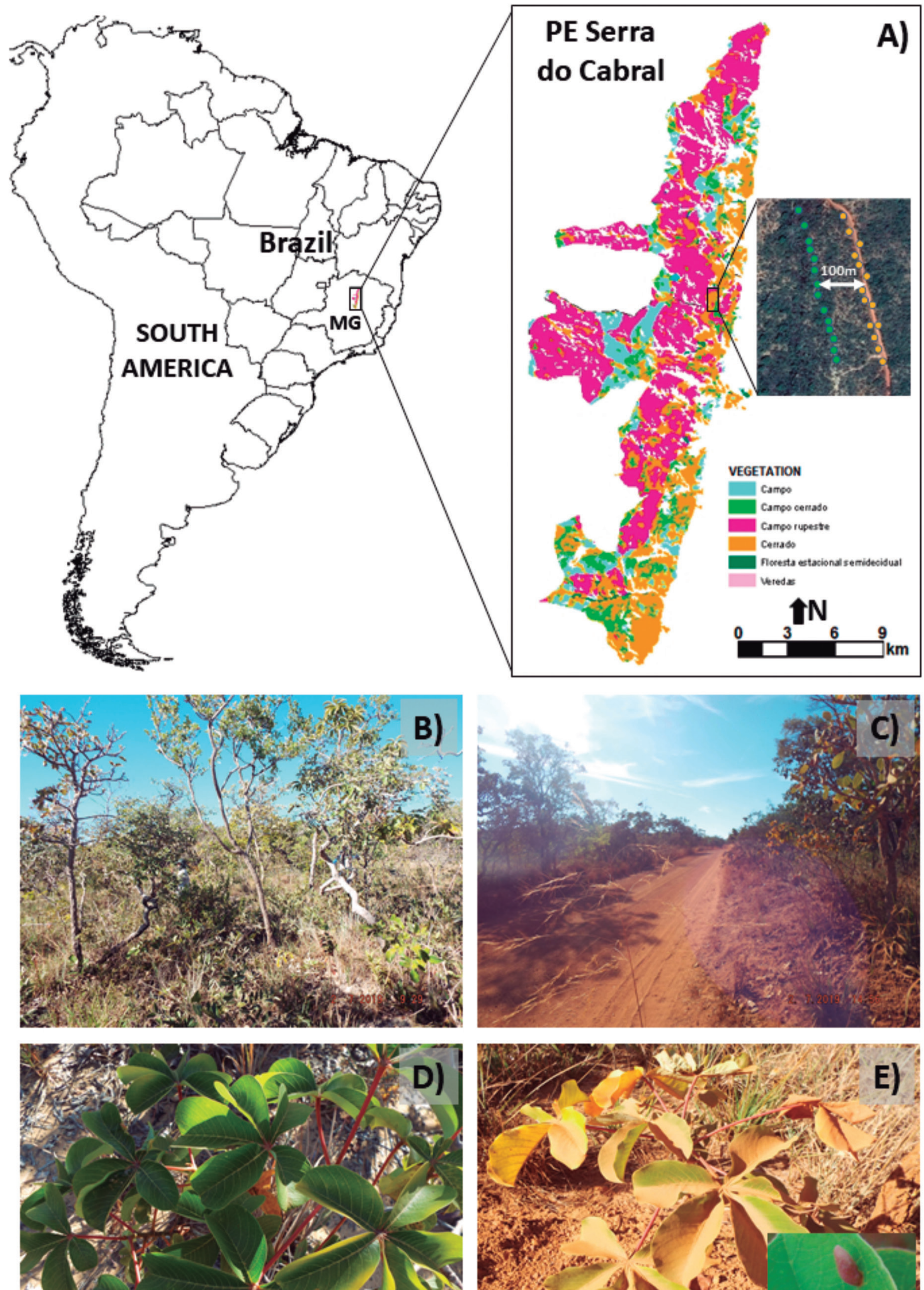

Figure 1. Location of study area and details of sample design. (A) Area of the Parque Estadual da Serra do Cabral and representation of the distribution of the 18 plants (nine in the interior and nine on the edge of the road) sampled in an area of Neotropical savanna in the park. (B) Details of the interior of the Neotropical savanna. (C) Details of the edge of the Neotropical savanna. (D) Plants located inside the vegetation had clean leaves. (E) Plants located on the roadside had leaves dirty and covered of dust. (F) Details of the galls induced by *Jatrophobia brasiliensis* on the leaves of *Manihot caerulenses.*

Table 1. Results of the generalized linear model of effects of type of environment (edge vs. interior) and number of leaves on the branch on the abundance of galls induced by *Jatrophobia brasiliensis* on *Manihot caerulenses.*

Explanatory variables	Df	Resid. Dev	Chisq	P
Environment (edge vs. interior)	26	73.155	482.76	< 0.001
Number of leaves	25	133.885	348.88	< 0.001
Environment*Number of leaves	24	28.337	320.54	< 0.001

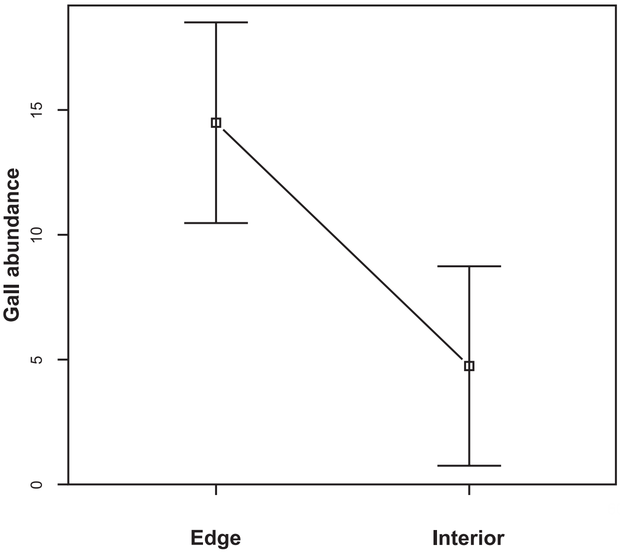

Figure 2. Comparison of the abundance of galls induced by *Jatrophobia brasiliensis* on *Manihot caerulenses* in edge and interior plants.

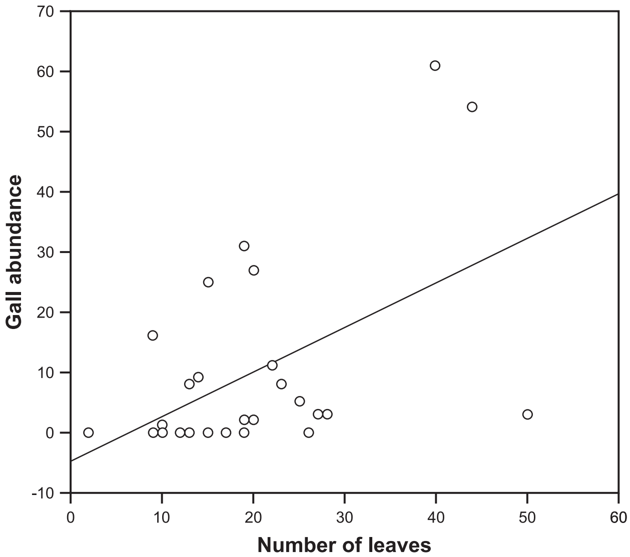

Figure 3. Effect of the number of leaves on the branches of *Manihot caerulenses* on the abundance of galls induced by *Jatrophobia brasiliensis.*

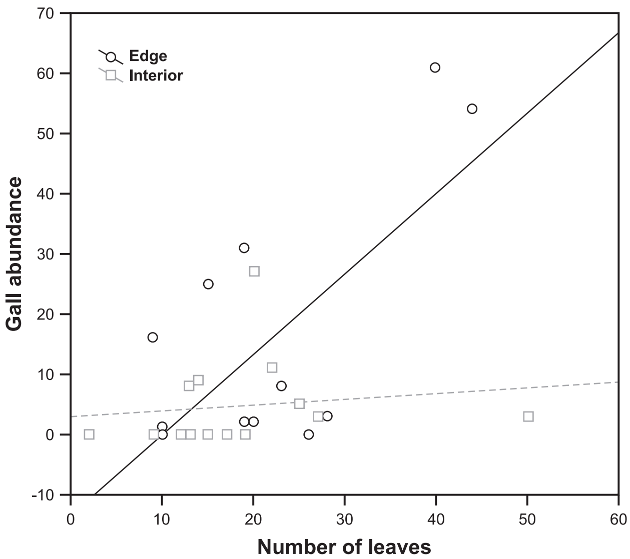

Figure 4. Comparison of the effects of the number of leaves on the branches of *Manihot caerulenses* on the abundance of galls induced by *Jatrophobia brasiliensis* in plants located in edge (black circles) and interior plants (gray squares).

203 galls on edge plants and 66 galls on interior plants. Abundance of galls ranged from 0 to 61 (9.6 ± 16.1), and was significantly affected by type of environment, number of leaves and interaction between these two variables (Table 1). We found three times more galls in the edge plants than in the interior plants ($p < 0.001$; Fig. 2). The abundance of galls was also positively influenced by number of leaves on the branch ($p < 0.001$; Fig. 3), but this relationship was only observed for plants in the edge environment ($p < 0.001$; Fig. 4).

DISCUSSION

Corroborating our expectation, we found that distribution of galls induced by *Jatrophobia brasiliensis* on plants of *Manihot caerulenses* differed between the edge and interior of the studied savanna. We found that the abundance of gall-inducing insects was three times greater in the plants on the edge than in the interior of the vegetation. After controlling the effects of resource availability on the plants (*i.e.,* number of leaves on the branch), we found that on the edge plants with more resources had more galls, but no effect was observed for the plants in the interior of vegetation. This shows that inside the vegetation even the plants with a lot of resources had a low abundance of galls, contrary to expectative. Our results corroborate previous studies that found differences in the distribution of gall-inducing insects between edge and interior vegetation environments (Araújo *et al.,* 2011; Araújo & Espírito-Santo Filho, 2012).

Plant stress can be an important predictor for distribution and performance of species of gall-inducing insects (Galway *et al.,* 2004). The environmental stress can modify the chemistry of plants and induces the production of distinct secondary metabolites, such as nitrogen-containing compounds (cyanogenic glycosides, alkaloids, and glucosinolates), phenolic compounds (flavonoids and phenylpropanoids), and terpenes (isoprenoids) (Ashraf *et al.,* 2018). As indicated earlier, gall-inducing insects are adapted to sequester secondary metabolites and concentrate these compounds in the gall tissues for their consumption and protection (Hall *et al.,* 2017). Classical evidence to support this has been noted for *Asphondylia* (Cecidomyiidae) by Waring & Price (1990) and *Lipara lucens* (Chloropidae) by De Bruyn (1995), which found that gall-inducing insects were more abundant and had better performance on stressed than on non-stressed plants.

We hypothesize that the main stressor in the edge environments of the studied savanna is dust from the unpaved road. The dust particles cover green surfaces of plants which decrease its photosynthetic capacity (Supe & Gawande, 2013) and can also impair gas exchange due to clogging of stomata (Farmer, 1993). Based on previous studies, there is also evidence that dusted leaves allowed the greater penetration of road salt, which increases water stress (Farmer, 1993). Under constant pressure of dust, plants may have their growth slowed and their physiological balance changed. According to Farmer (1993) dust may also potentiate the effects of secondary stresses, such as drought, pathogens and herbivores.

Galls induced by *Jatrophobia brasiliensis* on *Manihot caerulenses* has been previously recorded in other areas of Brazil, such as Luiz Antônio, SP (Saito & Urso-Guimarães, 2012) and Jequitaí, MG (Durães & Araújo, 2020). The host plant occurs in the Brazilian states of Bahia, Maranhão, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Piaui and São Paulo (Martins *et al.,* 2024). Because the host plant has wide distribution in the Brazilian territory, possibly the distribution of the gall-midge is much greater. In a recent study, Durães & Araújo (2020) registered a higher frequency of *Jatrophobia brasiliensis* in plants of *Manihot caerulenses* located on xeric areas (rocky savanna) than mesic ones (typical savannah). The authors also found that the size of the galls of *Jatrophobia brasiliensis* was higher in plants in the xeric area than in mesic area. These results support the findings of the present study, indicating a greater fitness of the gall-midge in plants in the more stressed environment.

Some evidence indicates that road dust can repel some types of herbivores as predicted by dust aversion hypothesis (Ndibalema *et al.,* 2008). This hypothesis assumes that herbivores that eat the outer tissues of plants, such as chewers, tend to avoid dusty plants (Ndibalema *et al.,* 2008). However, as gall-inducing insects are endophagous herbivores, dust deposited on the leaf surface is not a factor that interferes with feeding. A possible problem of dust for biology of the gall-midge is related to the difficulty of oviposition. Although the biology of *Jatrophobia brasiliensis* is little known, this problem can be minimized with the females ovipositing on the bottom surface of the leaf (where the dust deposit is low), which seems to be the case with this gall-midge (Bellotti & Schoonhoven, 1978; Brathwaite *et al.,* 1987).

CONCLUSION

In summary, our study corroborates previous evidence that edge environments have characteristics that can increase the occurrence of herbivorous insects, such as altered microclimatic conditions and changes in host plant chemistry (review in Wirth *et al.,* 2008). Here we show evidence for the first time that there is an edge effect on the distribution of insect galls in a Neotropical savanna. Our results indicate that gall-inducing insects respond positively to the edge effect, as previously demonstrated for tropical forests (*e.g.,* Araújo & Espírito-Santo Filho, 2012; Altamirano *et al.,* 2016). On the other hand, we suggest that the mechanisms causing the edge effect in Neotropical savannas are different from those acting in forest environments, with dust being a pivotal factor. Our findings suggest that the environmental changes of the edge, especially caused by dust deposition, affect the distribution and the fitness of gall-inducing insects on their host plants. Future studies can assess more direct responses of dust deposition on the occurrence of gall-inducing insects, by quantifying the amount of dust deposited on the leaves.

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